# Geographic Variation in the Forelimb and Hindlimb Skeletons of African Apes

by

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## ABSTRACT

Geographic Variation in the Forelimb and Hindlimb Skeletons of African Apes

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Advisor: Professor Thomas Plummer

Understanding geographic variation in African ape skeletal morphology is important for the study of both modern and fossil apes. Regarding modern apes, it is important for the study of their taxonomy, biogeography, evolutionary history, and adaptations. Regarding fossil apes, it is important in order to enhance our ability to refer to a modern analog when interpreting variation among specimens. While species-level variation in *Gorilla* and *Pan* is relatively well-studied, variation among subspecies and populations has received little attention, and most of this work has focused on craniodental morphology.

This study documents patterns of geographic variation in the forelimb and hindlimb skeletons of African apes. Linear measurements of ten limb bones were collected from 266 *Gorilla* and 274 *Pan* adults. Univariate and multivariate analyses were conducted on raw measurements from all ten bones and on ratios of hand and foot bone measurements.

Results from analyses of both raw measurements and hand and foot ratios are generally consistent in the patterns of geographic variation they reveal. Variation is present at the species, subspecies, and population levels in both *Gorilla* and *Pan*, but greater differences exist among subspecies and populations in *Gorilla*, and *Pan*

populations do not cluster as reliably into their assigned subspecies. These are the same patterns detected in studies of *Gorilla* and *Pan* craniodental morphology and genetics.

Analyses of hand and foot bone ratios also permit exploration of the potential functional significance of hand and foot bone morphology. These ratios were proposed to reflect relative frequencies of characteristically arboreal and characteristically terrestrial positional behaviors; however, in comparisons of taxa with documented differences in degrees of arboreality and terrestriality, only four of twenty-two ratios vary as predicted.

The results of this study have implications for the interpretation of variation in hominoid fossils. Although hominoid fossil taxonomy is usually based on craniodental morphology, limb bones are likely to reflect the same patterns of variation between geographic groups. Many features of the hand and foot that have been proposed to reflect differences among hominoids in arboreality and terrestriality do not appear to be reliable indicators of functional differences between taxa of African apes.

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# CHAPTER 1

# INTRODUCTION

## Introduction

The study of geographic variation in African ape skeletal morphology is fundamental to understanding the evolutionary history of living hominoids, including humans, and their ancestors. Variation at the population and subspecies levels is particularly significant, because these are the levels at which evolutionary processes occur. Surprisingly, few researchers have studied African ape skeletal variation at these levels, and most of this work has concentrated on craniodental anatomy. Numerous authors have cited the necessity for further subspecies- and population-level study of African ape morphology to shed light on evolutionary and taxonomic questions (Zihlman and Cramer, 1978; Jungers and Susman, 1984; Groves, 1986; Shea et al., 1993; Uchida, 1996; Bromage, 1999; Szalay, 2001).

Previous research on African ape craniodental morphology and genetics has revealed substantial evidence of geographic patterning, as well as intriguing differences between patterns identified in gorillas and chimpanzees. According to studies of the skull (Groves, 1970; Shea and Coolidge, 1988; Groves et al., 1992; Taylor and Groves, 2003) and teeth (Uchida, 1993; Pilbrow, 2003, 2006a, 2006b), variation exists between geographically-defined groups (subspecies and populations) in both gorillas and chimpanzees, but gorillas demonstrate greater population- and subspecies-level distinctions, and chimpanzee populations do not always separate along traditional subspecific lines. Similarly, genetic studies have found a high degree of geographic structuring among gorillas, reflecting distinctions between most recognized subspecies

and relative isolation between populations (Garner and Ryder, 1996), but greater phylogeographic complexity and high long-distance gene flow in chimpanzees (Morin et al., 1994; Gagneux et al., 1999). Genetic and craniodental data have been used to model differences between chimpanzees and gorillas in their microevolutionary histories (Uchida, 1996; Gagneux et al., 1999; Yu et al., 2004; Thalmann et al., 2007).

Research on geographic variation in African ape postcranial morphology has been anatomically and geographically limited. Postcranial differences between mountain gorillas and western lowland gorillas have long been researched (Schultz, 1934; Sarmiento, 1994; Taylor, 1997a,b; Inouye, 2003), but little is known about postcrania of eastern lowland gorillas and Cross River gorillas. Geographic variation in chimpanzee postcrania has only begun to be explored (Jungers and Susman, 1984; Morbeck and Zihlman, 1989; Carlson, 2005; Zihlman et al., 2007), and postcranial variation between bonobo populations has not been studied at all.

Further study of geographic variation in African ape postcranial morphology is important simply to improve our understanding of patterns of skeletal variation within these taxa; however, postcranial skeletal variation also has the potential to reflect between-group differences in habitat and positional behavior. Gorillas, chimpanzees, and bonobos are each known to live under a diversity of local ecological conditions, such as varying canopy height and fruit tree abundance, which are likely to affect degrees of arboreality and terrestriality (Horn, 1980; McGrew et al., 1981; Kano, 1983; Kano and Mulavwa, 1984; Collins and McGrew, 1988; White, 1992; Remis, 1998; Doran and McNeilage, 2001; McNeilage, 2001). In addition, variation in frequencies of arboreal versus terrestrial positional behaviors has been observed between populations within each

of these taxa and, in each case, has been attributed to differences in habitat (Doran and Hunt, 1994; Doran, 1996; Remis, 1998). This variation in habitats and flexibility in positional profiles, in conjunction with the known responsiveness of bone to functional stress (Burr, 1980; Currey, 1984; Lanyon and Rubin, 1985; Martin and Burr, 1989; Bromage, 1992; Trinkaus et al., 1994; Skedros et al., 1997; Martin et al., 1998; Szalay, 2000; Lieberman et al., 2001; Ruff, 2002), prompt the question of whether adaptive differences between geographic groups may be detected in the postcranial skeleton.

Documentation of geographic variation in African ape postcranial morphology, and its potential relationship to adaptive diversity, will offer new baseline data for studies of fossil hominoid skeletal variation and African ape and human evolutionary history. The observed patterns and extents of postcranial variation between geographic groups of living African ape taxa will provide models for interpreting the evolutionary significance of variation in fossil hominoids, especially early human ancestors (e.g., Bromage, 1999). These models of variation may also be used to build hypotheses about adaptive and demographic events responsible for African ape diversity and distribution today, and for the initial divergence of the human lineage from the apes (e.g., Shea and Coolidge, 1988).

This study begins to address questions about patterns of geographic variation in the African ape postcranium by concentrating on the skeletal morphology of the forelimb and hindlimb. The primary questions asked are:

1. Do African apes exhibit geographic variation, particularly at the levels of subspecies and populations, in forelimb and hindlimb skeletal morphology?
2. If so, how do *Gorilla* and *Pan* differ in the patterns and extents of such variation?

Further questions and predictions are detailed in the final section of this chapter, entitled "This study".

**Background: Taxonomy**

Taxonomic names and classifications used in this study follow Groves (2001). Latin names and common names are listed in Table 1.1. However, in the course of reviewing the literature, other taxonomic names may sometimes be used for consistency with the work being discussed, as long as there is no potential for confusion. Geographic ranges of species and subspecies of *Gorilla* and *Pan* are illustrated in Figures 1.1 (*Gorilla*) and 1.2 (*Pan*).

Table 1.1. Taxonomic nomenclature used in this study

| | | | |
|---|---|---|---|
| ***Gorilla*** | gorilla | ***Pan*** | [none] |
| ***G. beringei*** | eastern gorilla | ***P. troglodytes*** | chimpanzee |
| *G. b. beringei* | mountain gorilla | *P. t. troglodytes* | central chimpanzee |
| *G. b. graueri* | eastern lowland gorilla | *P. t. schweinfurthii* | eastern chimpanzee |
| ***G. gorilla*** | western gorilla | *P. t. verus* | western chimpanzee |
| *G. g. gorilla* | western lowland gorilla | *P. t. vellerosus* | Nigerian chimpanzee |
| *G. g. diehli* | Cross River gorilla | ***P. paniscus*** | bonobo |

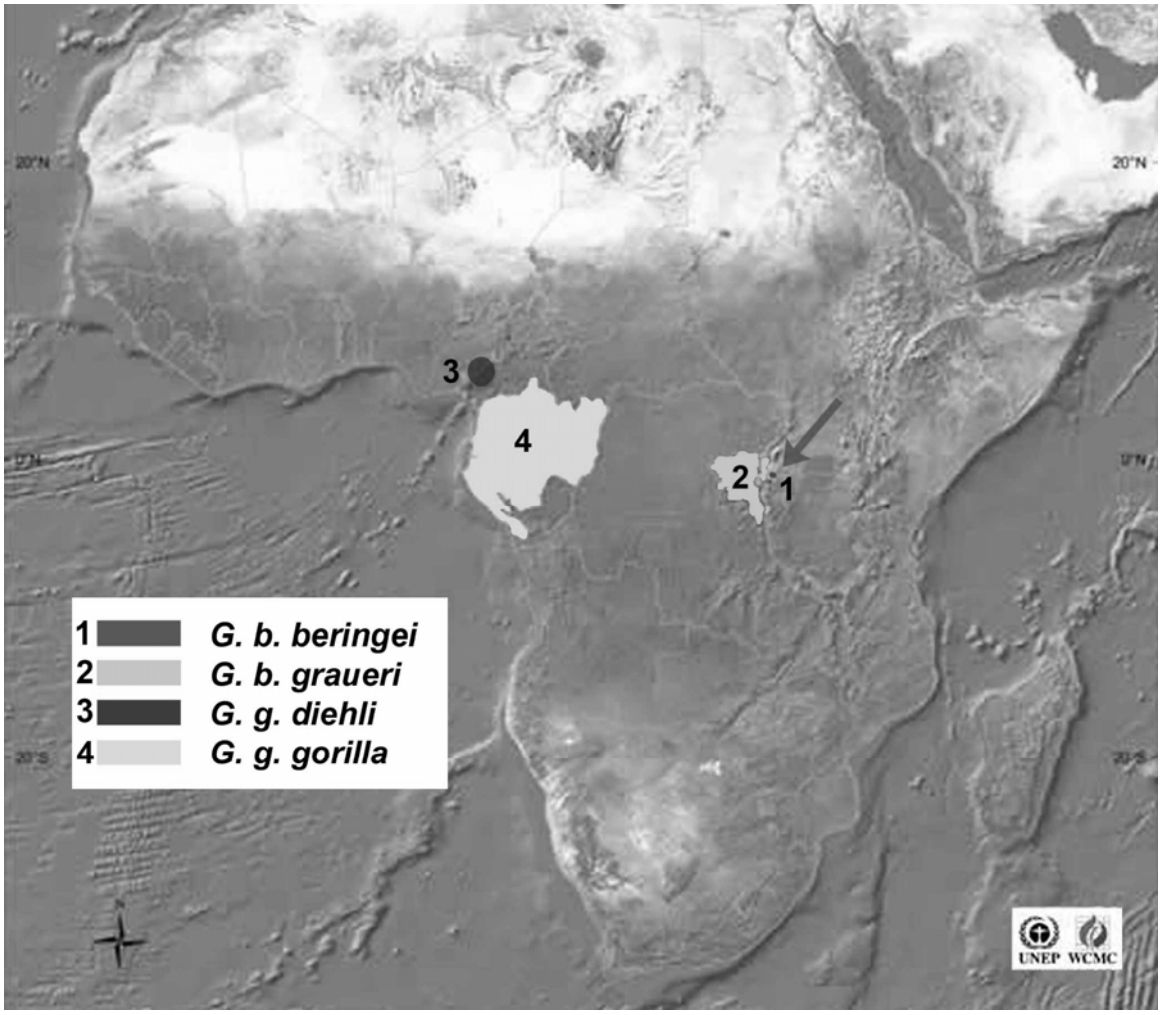


Figure 1.1. Geographic ranges of *Gorilla* species and subspecies. Adapted from Caldecott and Miles (2005).

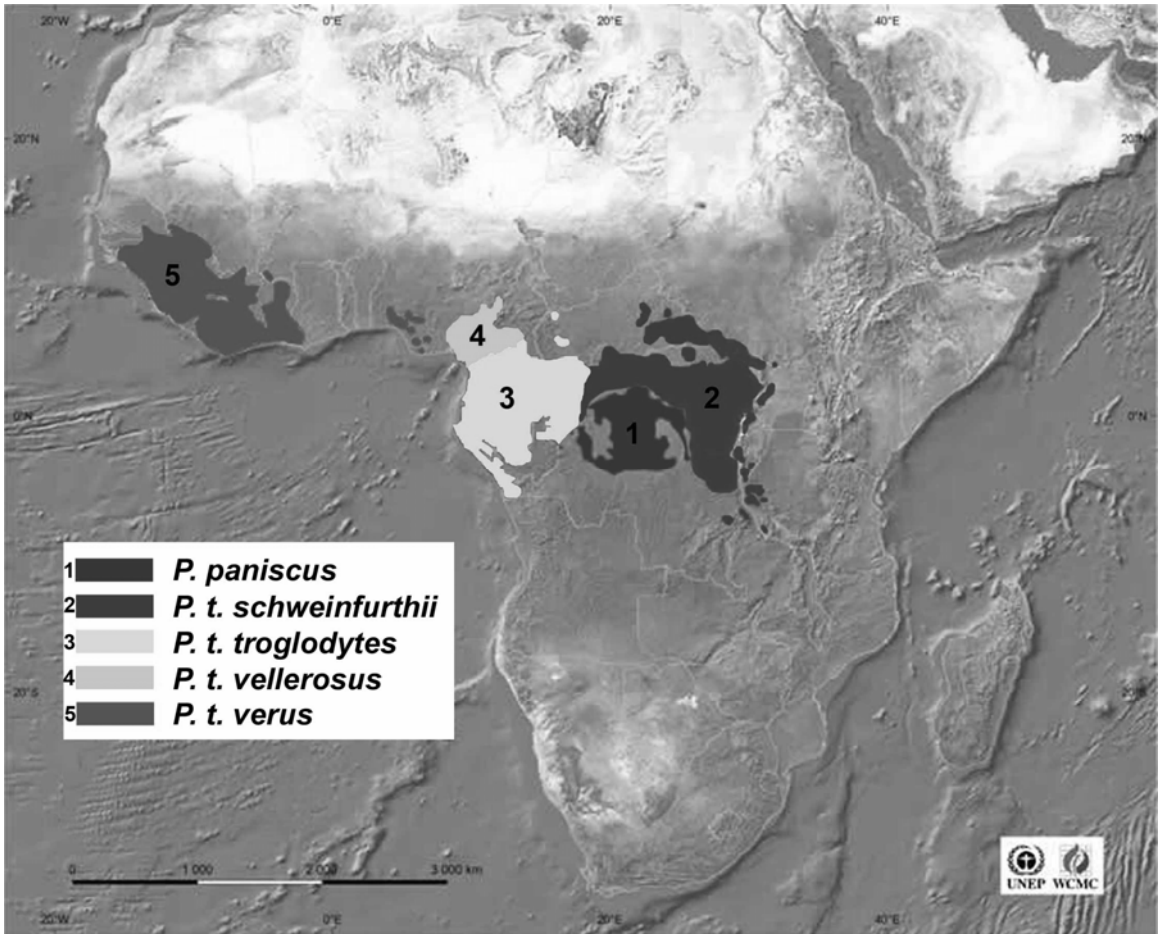


Figure 1.2. Geographic ranges of *Pan* species and subspecies. Adapted from Caldecott and Miles (2005).

## Background: Skeletal morphology and genetics

This section reviews previous work on geographic variation in African ape skeletal morphology and genetics. It is divided into separate subsections for *Gorilla* and *Pan*, and each subsection is further divided into discussions of variation in skeletal morphology and variation in genetics. Postcranial skeletal morphology is discussed in greater detail than craniodental morphology, and ecological interpretations of variation are emphasized. This summary of evidence for geographic patterning of variation in African ape bones, teeth, and genes provides the basis for the predictions tested in this study.

### *Gorilla*

#### *Skeletal morphology*

Early gorilla taxonomy was characterized by abundant named taxa, as reviewed by Groves (2003). Keith (1927) was one of the first researchers to recognize the importance for taxonomy of studying variation in gorillas. He found cranial proportions to vary greatly within one western lowland gorilla population and was unable to find craniodental characteristics which consistently separated eastern and western gorillas. Coolidge (1929) revised the genus *Gorilla*, based primarily on a large series of male skull measurements. He emphasized a high level of individual variation and collapsed numerous named species and subspecies of gorilla into two subspecies: the western *G. gorilla gorilla* (including both the western lowland gorillas and the Cross River gorillas of current classification) and the eastern *G. g. beringei* (including both the mountain gorillas and the eastern lowland gorillas of current classification). His study examined five geographic groups – three western and two eastern groups – but did not find

sufficient differences among the western or eastern groups to merit designation as separate subspecies. Schultz (1934), summing up and expanding upon several of his previous publications, concluded that differences between the "mountain gorilla" (including all eastern gorillas) and the western lowland gorilla, in both external and skeletal features, were great enough to justify separating them into two species, *G. beringei* and *G. gorilla*, although many researchers continued to follow Coolidge (1929) in viewing gorillas as a single species.

The current generation of studies on gorilla morphological diversity was initiated with a study by Groves (1970). Groves sorted a large sample of gorilla skulls into nineteen geographical groupings and collected measurements of the cranium and mandible. Using canonical analysis and squared generalized distances, he separated the genus into three major groups and diagnosed the groups as three subspecies of the single species *G. gorilla*. These three subspecies, *G. g. gorilla*, *G. g. beringei*, and *G. g. graueri*, were the only generally recognized subspecies of gorilla until the recent revival of *G. g. diehli* (see below). The study further identified population clusters within both eastern and western taxa which, according to Groves, may be correlated with variations in habitat. Subsequently, Groves and Stott (1979) attempted to clarify the relationships of three eastern gorilla populations which previously (Groves, 1970) had been found to have ambiguous affinities: Mt. Kahuzi, Mt. Tshiaberimu, and Kayonza Forest (now known as Bwindi). They evaluated external features, cranial metrics and nonmetrics, and several aspects of the postcranial skeleton. The patterns of similarities to and differences from other populations were shown to be complex. The Kayonza (Bwindi) sample was small and its morphological affinities were indeterminate, but most evidence seemed to

indicate a close relationship with the Virungas (*G. g. beringei*) population. The Mt. Kahuzi and Mt. Tshiaberimu samples were assigned to *G. g. graueri*, but they had resemblances to *G. g. beringei*. These resemblances were suggested either to be due to independent adaptations to similar montane climates or to be the remnants of a now-disrupted cline between what are now recognized as subspecies.

More recently, geographic and ecological variation in the gorilla cranium and mandible have been studied by a number of researchers using a variety of approaches. A suite of studies by Taylor (2002, 2003, 2005, 2006) and by Taylor and Groves (2003) have focused on linear measurements of the bony components of the masticatory complex, especially the mandible. Taylor and Groves (2003) examined patterns of mandibular variation and their implications for taxonomy in both *Pan* and *Gorilla*. Their analysis found the greatest separation in gorillas to be between eastern and western groups, seemingly supporting the recently-advocated two-species taxonomy (Groves, 2001), but the authors argued that species-level distinctiveness is not apparent in these results, because the overlap between eastern and western groups is too great. The three traditional gorilla subspecies were distinct, but *G. g. diehli* was not. Several other studies of masticatory morphology by Taylor (2002, 2003, 2005, 2006) have looked at separation of African ape groups on the basis of dietary differences. Most of these studies use an ontogenetic allometric approach, which documents changes in scaling during growth and then distinguishes between shape differences that result from occupying different points on a common growth curve and shape differences that result from altered growth patterns and are, therefore, independent of size. Taylor (2002) first compared mountain gorillas and western lowland gorillas. Given the more folivorous and mechanically resistant diet

of mountain gorillas, she tested the hypothesis that they show greater development of features related to load resistance and force production than western lowland gorillas. Her results did not consistently fit the predictions, but several predicted differences were found between the two taxa which appeared to reflect differing biomechanical demands based on differing degrees of folivory. Taylor (2003) expanded on this earlier work by including eastern lowland gorillas in the analysis of gorilla variation. She found that mountain gorillas differed from both western and eastern lowland gorillas according to some predictions based on the highly folivorous diet of the mountain gorilla, but eastern lowland gorillas, which have been observed to be more folivorous than western lowland gorillas, did not show any of the expected differences from western lowland gorillas. Results of further studies (Taylor, 2005, 2006), which concentrated on specific regions of the mandible, were consistent with the earlier studies. Some predicted differences were found between mountain gorillas and the other two subspecies; however, despite dietary differences, eastern lowland gorilla morphology was very similar to that of western lowland gorillas.

Several other studies (Stumpf et al., 2003; Albrecht et al., 2003; Leigh et al., 2003) have used different methods to study subsets of the cranial data originally collected by Groves (1970) and made publicly available by him. Stumpf et al. (2003) examined whether patterns of geographic variation differed between canonical variates analyses of raw data and of size-adjusted data. Size-adjusted variables were created by dividing each measurement by a generalized cranial size factor, and results from analyses of size-adjusted data were essentially the same as results from analyses of raw data. The greatest separation was between eastern and western groups, and the Virungas population was the

most distinctive of the eastern groups. Albrecht et al. (2003) investigated the patterns and degrees of variation at multiple hierarchical levels within the genus *Gorilla* in order to illustrate the importance of "population thinking" to characterizing variation within a taxon. Supplementing the Groves sample with some additional specimens and applying principal components analysis, they demonstrated differences in variance among the gorilla subspecies and populations and pointed out that these differences, in addition to the differences in means which are usually studied, hold clues to the evolutionary histories of the groups. Leigh et al. (2003) employed Wright's $F_{ST}$, a familiar statistic in genetics, to study the partitioning of subspecific variation in gorillas. In addition to craniometrics from the Groves dataset, they also analyzed data on discrete cranial traits which they collected themselves. They found a high level of total variation in gorillas and a small amount of variation among subspecies relative to total variation. From this perspective, differences between subspecies did not appear to be as great as previous analyses have indicated. Leigh and co-authors also pointed out, as Albrecht et al. (2003) did, that evaluating relative amounts of variance, in addition to group means, offers a new source of data from which clues to evolutionary history may be gleaned.

Guy et al. (2003) approached the question of subspecies-level differentiation in African apes using geometric morphometric analysis of facial landmarks. Their discriminant function analysis classified western lowland gorillas, eastern lowland gorillas, and mountain gorillas to the correct subspecies over 90% of the time. The two eastern subspecies were more similar to one another based on Mahalanobis distances.

Differences between gorilla taxa have also been demonstrated using dental morphology. Studies by Uchida (1993, 1998) of dental metrics, including molar cusp

proportions, in great apes supported the distinctiveness of the three gorilla subspecies recognized at that time: *G. g. gorilla*, *G. g. beringei*, and *G. g. graueri*. Uchida suggested that these dental differences were the result of divergent dietary adaptations and population isolation. These three subspecies of gorilla showed greater differences in molar cusp size and shape than observed between traditional subspecies of other great apes (Uchida, 1993). Pilbrow (2003) analyzed dental metrics and discrete traits and found clear separation of eastern and western gorilla populations. Among the eastern populations, Tshiaberimu and Kahuzi clustered with other eastern lowland groups, as predicted based on the conclusions of Groves and Stott (1979). Pilbrow (2006a) compared frequencies of incisor discrete traits in the three traditional gorilla subspecies. She found them all to be significantly different from one another, based on mean measures of divergence, with greater separation between the eastern and western groups than between the two eastern subspecies. All the same, a very high percentage of the variance in the genus was found in individual subspecies, and a local population of *G. g. gorilla* had almost as high a percentage as the subspecies as a whole. She suggested that incisor discrete traits may be adaptively neutral.

Variation in postcranial morphology between gorilla groups has long been observed and has frequently been associated with variation in ecology. When Schultz (1934) separated the genus *Gorilla* into two species, *G. beringei* and *G. gorilla*, he found many distinguishing features in the postcranial skeleton. Among the most distinctive characteristics of *G. beringei* he cited was a short humerus, both absolutely and relative to other measurements. Other differentiating features of the *G. beringei* postcranial skeleton were a smaller average number of thoracolumbar vertebrae, a sinuous vertebral

border of the scapula, and the lengths of various elements. In an earlier publication, Schultz (1927) related postcranial differences between these two gorilla groups to greater terrestriality in *G. beringei*.

Groves (1970) used postcranial observations to test the distinctiveness of his proposed intermediate eastern subspecies, *G. g. graueri*. Using skeletal indices from Schultz (1934), he found *G. g. graueri* to be in the middle of an east-to-west cline on the basis of brachial and clavicle-humerus length indices and to be at one end of the range of variation for intermembral and femur-humerus length indices. Almost all specimens of *G. g. graueri* had a straight vertebral border of the scapula, as found in the distant *G. g. gorilla* populations and in contrast to the adjacent *G. g. beringei* sample. On the other hand, the index of great toe to foot length revealed a contrast between the Mwenga-Fizi and Tshiaberimu populations of *G. g. graueri*, with the Mwenga-Fizi index more similar to that of *G. g. gorilla* and the Tshiaberimu index more similar to that of specimens from the Virungas and Kahuzi.

The postcranial features examined by Groves and Stott (1979) in their effort to untangle the relationships of the Kahuzi and Tshiaberimu gorillas were the shape of the vertebral border of the scapula and four postcranial skeletal indices (femur-humerus, brachial, clavicle-humerus, and hallux-foot). No postcrania from Kayonza (Bwindi) were examined. Interestingly, the Kahuzi and Tshiaberimu populations, which were assigned to *G. g. graueri* but had similarities to the Virungas population, resembled the Virungas gorillas in different ways. The Tshiaberimu gorillas were similar to the Virungas gorillas in the skull, while the Kahuzi gorillas were similar to the Virungas gorillas in the postcranial skeleton, notably in the expression of a sinuous vertebral border of the

scapula. The authors interpreted the intermediate morphologies of these populations as results of selection for high altitude adaptations, on the one hand, and genetic admixture with lowland populations on the other, although they were puzzled about why their morphologies would become intermediate in contrasting ways.

Groves and Stott (1979) also concluded, based on a larger sample than was available to Schultz (1934), that the humerus of *G. g. beringei* (limited to the type locality of the Virungas) was not as distinctively short as previously thought. This finding was further substantiated by Jungers and Susman (1984), who found no significant differences in several long bone lengths, including the humerus, between samples of western lowland gorillas and mountain gorillas. On the other hand, a sample of mountain gorillas measured by Taylor (1997a) had shorter humeri relative to body size, as measured by combined weights of several large skeletal elements, than a sample of western lowland gorillas.

Two studies by Taylor (1997a,b) sought morphological differences in the postcranial skeletons of mountain gorillas and western lowland gorillas which might relate to known ecological differences, specifically degrees of terrestriality and arboreality. Both studies found the two taxa to be ontogenetically scaled for most measured features, leading the author to conclude that most differences could be explained by allometry and did not represent morphological divergences due to differences in positional behavior. In one of these papers, Taylor (1997b) concentrated on linear measurements of the scapula. Although most predictions based on ecological differences were not well supported, the scapular spine was longer in western lowland gorillas. This result was consistent with the prediction that more frequent arboreal

behavior would be related to a longer scapular spine in order to increase the attachment area for the trapezius and deltoid, which are used in elevation of the humerus. In the other paper, Taylor (1997a) analyzed a set of linear measurements, mostly lengths, from the humerus, femur, scapula and ilium. She identified different patterns of growth between the two taxa, but she concluded that her data set did not show any evidence of divergent morphological adaptations, although she urged further study of other skeletal elements and of articular surfaces.

Inouye (2003) studied differences in the forelimbs of mountain gorillas and western lowland gorillas, using an ontogenetic allometric approach. The two groups were ontogenetically scaled for shoulder dimensions, but mountain gorillas had a significantly higher average degree of humeral medial torsion. Several dimensions of the elbow and one of the wrist were significantly different between groups; however, these differences appeared to reflect less stability in the mountain gorilla elbow and wrist, contrary to expectations based on greater terrestriality in mountain gorillas. Interestingly, the two species of *Pan* were distinguished by some of the same dimensions of the elbow and wrist.

In a study of humeral and femoral cross-sectional properties, specifically ratios of principal moments of area (PMA), Carlson (2005) analyzed variation among three gorilla taxa: mountain gorillas, eastern lowland gorillas, and western lowland gorillas. He found significant differences between groups at many of the six humeral and femoral diaphyseal regions examined. Then, incorporating quantitative data from studies of locomotor behaviors in male and female mountain gorillas and western lowland gorillas, he found negative correlations between most PMA ratios and the percentage of locomotor

behaviors taking place in arboreal settings. In other words, humeral and femoral shafts were more circular in groups which engage in a higher percentage of arboreal locomotion. This finding is consistent with predictions based on the presence of bending loads from many directions during arboreal locomotor activities, in contrast to the more restricted directionality of bending loads experienced during terrestrial locomotion.

Geographic variation in *Gorilla* hand and foot morphology has historically been interpreted in terms of functional adaptation. Further studies that concentrate on such variation are discussed in the section "Variation in hand and foot morphology".

An acceleration of interest in re-examining the taxonomic assignments of African ape populations seems to be underway, and several proposals in the past decade have called attention to differences between gorilla groups. These have included proposals at both the subspecies and species levels.

Sarmiento and colleagues (Sarmiento et al., 1996; Sarmiento and Oates, 2000) have revised the subspecies membership of two gorilla populations. According to Sarmiento et al. (1996), the gorillas from Bwindi are different from the Virungas gorillas and should not be assigned to *G. g. beringei*, for which the Virungas is the type locality. The authors did not make comparisons of the Bwindi gorillas and populations assigned to *G. g. graueri*; therefore, they were unable to conclude whether the Bwindi gorillas belong to that taxon or a new one. In comparison to Virungas gorillas, their study found Bwindi gorillas to have smaller bodies, relatively longer limbs, hands, and feet, shorter trunks, thumbs, big toes, and tooth row lengths, and narrower trunks and orbital breadths. They argued that these anatomical differences reflect the lower altitude, warmer temperature, and greater number of fruit-bearing trees in the Bwindi habitat. In reaction to this

taxonomic proposal, Stanford (2001) cautioned that such anatomical variation could result from developmentally plastic responses to ecological differences and may not indicate an evolutionary divergence. On the basis of dental variation, Pilbrow (2003) found the Bwindi gorillas to be more similar to the Virungas gorillas than to other populations.

In another taxonomic proposal, Sarmiento and Oates (2000) concluded that the gorillas of the Cross River headwaters of Nigeria and Cameroon, long assigned to *G. g. gorilla*, are a separate subspecies, *G. g. diehli*. In addition to this population's geographic isolation, they demonstrated these specimens to have distinctively small craniodental measurements and other distinguishing skull traits. Postcranial comparisons were limited by very small Cross River sample sizes. Variation in habitat and scarcity of behavioral data prevented the authors from correlating morphology and ecology in the Cross River gorillas, although ecomorphological hypotheses were proposed. The Cross River population was the most distinct of the western groups in the original study by Groves (1970), who referred to it as the Nigeria population, but he did not emphasize this result. The distinctiveness of the Cross River population is also supported by the craniometric analysis of Stumpf et al. (2003) and the dental analysis of Pilbrow (2003).

Groves (2001) reconsidered gorilla taxonomy as a whole. He argued for separation of a western species, *G. gorilla*, and an eastern species, *G. beringei*, reviving the taxonomy supported by Schultz (1934). Although earlier studies had shown gorilla variation to be clinal in many respects, influencing him to view gorillas as a single species, he changed his mind based on clearer differences in the mitochondrial D-loop, pelage, and external face. In addition to the three subspecies he had previously

recognized, he also endorsed the distinctiveness of the Cross River gorilla, *G. g. diehli*. Regarding the Bwindi population, he wrote that it "supposedly" (p. 302) belongs to *G. b. beringei*, noting both the morphological arguments of Sarmiento et al. (1996) for separation of the Bwindi and Virungas gorillas and the mitochondrial DNA (mtDNA) evidence of Garner and Ryder (1996) against the split. Groves (2001) used postcranial differences cited in earlier studies to distinguish the *G. b. beringei* and *G. b. graueri* subspecies, but postcranial features are absent from all other diagnoses.

In summary, studies of variation in gorilla skeletal morphology have generally supported the distinctiveness of the four currently-recognized subspecies and demonstrated the existence of differences between populations. Mountain gorillas and western lowland gorillas have been shown, in many studies over the course of many years, to differ in their skulls, teeth, and postcrania. Eastern lowland gorillas and Cross River gorillas have been more poorly studied. A few large multivariate studies of skulls and teeth have indicated that all four subspecies can be distinguished from one another, but little is known about the postcranial morphology of eastern lowland gorillas and Cross River gorillas. The recent proposal that eastern and western gorillas are separate species has been addressed with studies of skulls and teeth but has not been addressed using postcranial data. Open questions remain about the taxonomy and affinities of some eastern populations.

*Genetics*

Most studies of genetic variation within the genus *Gorilla* have been based on mtDNA, and this work is currently undergoing a reassessment in the field following the realization that numerous segments of mtDNA have become inserted into the nuclear

genome over the course of gorilla evolution. These segments, called numts, have evolved separately from the mitochondrial genome since their translocations and are sometimes unintentionally amplified in addition to, or even in preference to, the actual mtDNA (Thalmann et al., 2004). The presence of numts can lead to false results when sequences assumed to be from the mitochondrial genome are compared between individuals or groups. Some researchers (Clifford et al., 2004) have introduced methods to address this problem, but others (Thalmann et al., 2005) argue that these measures are inadequate. Encouragingly, the small number of studies using nuclear DNA and authenticated mtDNA have supported the broad patterns of geographic structuring identified within the genus *Gorilla* in previous mtDNA studies. Work on genetic variation in gorillas is briefly summarized here, with the caveat that the validity of the mtDNA sequences on which some studies are based is in question.

Studies of genetic variation have consistently revealed a clear separation between eastern and western gorillas. Studies of mtDNA sequences which support the east-west split include those by Ruvolo et al. (1994), Garner and Ryder (1996), and Gagneux et al. (1999), all of which found the genetic distance between eastern and western gorillas to be as great or greater than the genetic distance between chimpanzees and bonobos. Ruvolo et al. (1994) suggested that a two-species gorilla taxonomy might be justified. A study of nuclear DNA sequences in eastern and western gorillas by Jensen-Seaman et al. (2003) found them to diverge significantly less than those in chimpanzees and bonobos. They discussed evolutionary scenarios which might explain this discrepancy between results from the mitochondrial and nuclear genomes and did not consider their results to have any bearing on the number of species of gorilla. Thalmann et al. (2005) compared numts

in eastern and western gorillas and calculated a divergence date of 1.3 million years ago, which is comparable to some estimates of the divergence date for chimpanzees and bonobos. Further research by Thalmann et al. (2007) on noncoding autosomal sequences resulted in an estimated divergence between eastern and western gorillas at between 0.9 and 1.6 million years ago. Jensen-Seaman et al. (2003) argued that different biogeographic forces are probably responsible for the splits between eastern and western gorillas and between chimpanzees and bonobos, while Thalmann et al. (2005) argued that both splits are probably due to the same climatic and geologic changes.

Separations between gorilla subspecies have also been apparent in genetic studies, and genetic analyses have been used to identify relationships between eastern gorilla populations. Studies of mtDNA by Garner and Ryder (1996) and Gagneux et al. (1999) found the three traditional subspecies (mountain gorillas, eastern lowland gorillas, and western lowland gorillas) to be distinct, with a closer relationship between the two eastern taxa. The gorillas from Bwindi and the Virungas formed a mountain gorilla clade separate from that of the eastern lowland gorillas in the study by Garner and Ryder (1996), failing to concord with arguments by Sarmiento et al. (1996) that the Bwindi and Virungas gorillas are morphologically and ecologically distinct. The classification of the Mt. Kahuzi gorillas, which were previously found to share morphological features of both eastern lowland and Virungas gorillas (Groves, 1970; Groves and Stott, 1979), was revisited with mtDNA data by Saltonstall et al. (1998). Populations from Mt. Kahuzi and the lowland region of Kahuzi-Biega National Park (DRC), both currently considered to be eastern lowland gorillas, were found to be identical to each other but different from mountain gorillas, supporting the current classification of the Mt. Kahuzi gorillas. In

addition, Jensen-Seaman and Kidd (2001) examined mtDNA sequences from several populations of eastern gorillas and found samples from Bwindi and the Virungas to form a distinct clade, with a second clade made up of samples from Tshiaberimu, the Kahuzi-Biega highlands (Mt. Kahuzi), and the Kahuzi-Biega lowlands.

While the two currently-recognized subspecies of eastern gorilla exhibit clear genetic separation, the western lowland gorilla and the Cross River gorilla may not be so genetically distinct. A preliminary analysis based on mtDNA suggested that the Cross River gorillas formed a clade separate from other western gorillas (Oates et al., 2003), but further mtDNA work by Clifford et al. (2004), which better sampled the geographic distribution of western lowland gorillas, found that the Cross River gorillas formed a clade with other gorillas from areas of Cameroon outside of the Cross River gorilla range. Although there were two western gorilla clades, they did not correspond exactly to the two currently-recognized subspecies. Despite the geographic isolation and craniometric distinctiveness of the Cross River populations, substantial genetic exchange has occurred over time between them and the closest populations to the south.

Evidence from mtDNA of a deep split within western gorillas, greater than the split between eastern and western gorillas, was reported by Garner and Ryder (1996). If, in fact, there were a greater divergence within western gorillas than between eastern and western gorillas, it would be difficult to justify the separation of eastern and western gorillas into separate species. Following the realization that many gorilla mtDNA sequences published in the past were likely to be numts, Jensen-Seaman et al. (2004) re-examined the question of a deep split within western gorillas. They removed a number of apparent numts from the analysis and concluded that western gorillas are monophyletic,

after all, and the deepest split within gorillas is, in fact, between eastern and western gorillas.

A high degree of geographic structuring among populations has been reported in both western gorillas (Garner and Ryder, 1996; Clifford et al., 2004) and eastern gorillas (Saltonstall et al., 1998; Jensen-Seaman and Kidd, 2001). Results from all of these mtDNA studies indicated low genetic variability within populations and limited gene flow between them. Clifford et al. (2004) hypothesized that geographic patterns observed in western gorillas reflect an evolutionary history in which gorilla populations were isolated in Pleistocene refugia during cool and arid times and later expanded from these population centers. Gagneux et al. (1999), whose mtDNA study found gorilla clades to be less "bushy" than those of chimpanzees, suggested this difference between African ape genera may be due to smaller group sizes and greater population isolation over time in gorillas. They proposed that gorillas may be less ecologically flexible, leading to a greater susceptibility to isolation in forest refugia during dry periods. In a study of noncoding autosomal segments, Yu et al. (2004) found greater nucleotide diversity and greater evidence of population subdivision in western gorillas than in chimpanzees (*P. t. troglodytes*) in the same geographic range. Similarly to Gagneux et al. (1999), they attributed this difference in patterns of genetic variation to different responses to Pleistocene forest fragmentation, as chimpanzees are better adapted to more open environments and would have been able to maintain larger home ranges.

### *Pan*

*Skeletal morphology*

The species-level separation of chimpanzees and bonobos is uncontroversial and supported by evidence from cranial, dental, and postcranial skeletal morphology. The bonobo was originally described as a chimpanzee subspecies (Schwarz, 1929, as referenced and translated from German to English by Coolidge [1933]). In his argument for species-level recognition of the bonobo, Coolidge (1933) provided a detailed description of a complete bonobo skeleton and hide, which happened to be unusually small, and also referred to the external field measurements of this specimen and measurements of the other bonobo skulls available at the time. Zihlman and Cramer (1978) expanded the postcranial skeletal dataset and confirmed the postcranial distinctiveness of bonobos and chimpanzees. Analyses of craniometrics (Shea and Coolidge, 1988), mandibular measurements (Taylor and Groves, 2003), skull discrete traits (Braga, 1995), and dental morphology (Pilbrow, 2006b) have continued to find clear separation of these two taxa. Although the species-level status of bonobos is not under debate, researchers tend to include bonobos in studies of geographic variation within chimpanzees to provide a frame of reference for observed differences between groups.

Three of the subspecies of chimpanzee recognized today were defined by Schwarz (1934). He collapsed a profusion of species names into one species, *P. satyrus*, and described subspecies-level variation in three geographic subunits, now designated *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*. He considered the bonobo to be a fourth subspecies, but he did not describe it and referred the reader to publications by other authors. His diagnoses relied primarily on features of the skin and pelage but also included qualitative descriptions of several skull characteristics. Schwarz (1934) built on

the work of Allen (1925), among others, who was notable for his early recognition of intraspecific variation in chimpanzees. At a time when single specimens frequently formed the basis for naming new chimpanzee species, Allen (1925) described great individual variation in the skin and skull among chimpanzees from two localities in the Upper Congo region (which would be considered *P. t. schweinfurthii* today). He also compared his observations with published observations of another population of *P. t. schweinfurthii* and found similar variation in both samples.

Further detailed studies of geographic diversity in chimpanzee morphology did not appear until Groves (1986) began to reexamine this subject in his revision of great ape systematics. He compiled an updated list of differences between the "putative taxa of chimpanzee" (*P. t. troglodytes*, *P. t. schweinfurthii*, *P. t. verus*, and *P. paniscus*), composed of morphological and behavioral data. Observations of the skeleton included a few postcranial bone lengths and length indices, the number of sacral vertebrae, a few skull metrics, and a few craniodental nonmetric traits. No single postcranial feature on the list was available for all three listed subspecies. Pointing out the paucity of some kinds of data, he stepped back from acknowledging the named subspecies and called for population-level studies of chimpanzee variation. In a later population-level study of skull metrics, Groves et al. (1992) reported that the samples were poorly distinguished from one another and did not separate along traditional subspecific lines. Further studies of skull metrics found significant discrimination between the three traditional subspecies (Shea and Coolidge, 1988; Shea et al., 1993) but with much less differentiation than measured between other great ape subspecies (Shea and Coolidge, 1988). Investigation of skull discrete traits by Braga (1995) demonstrated a significant difference, in mean

measure of divergence, between *P. t. verus* and *P. t. troglodytes* but not between other subspecies pairs. Geometric morphometric analyses of cranial landmarks (Guy et al., 2003; Lockwood et al., 2004) have found *P. t. verus* to diverge from the more similar morphology seen in *P. t. troglodytes* and *P. t. schweinfurthii*. Patterns of mandibular variation in both *Pan* and *Gorilla* were examined by Taylor and Groves (2003). The three traditional subspecies of chimpanzee were differentiated from one another, although with more overlap than the subspecies of gorilla, and *P. t. verus* differed the most from the other two subspecies.

In a more recent contribution to chimpanzee taxonomy, Groves (2001) identified and diagnosed four chimpanzee subspecies: *P. t. troglodytes*, *P. t. schweinfurthii*, *P. t. verus*, and *P. t. vellerosus*. *P. t. vellerosus* had been recently revived on the basis of genetic evidence (see Genetics subsection below) by Gonder et al. (1997). Groves argued that, although the proposed subspecies are not well-distinguished phenotypically, they are genetically distinct and can be broadly characterized morphologically. He provided original data on three cranial nonmetric traits to support the separation of *P. t. verus* and *P. t. vellerosus*, but these data did not distinguish *P. t. vellerosus* from the other two subspecies. The postcranial skeleton entered into the diagnoses only to distinguish *P. t. troglodytes*, with long limbs relative to skull size, from the relatively shorter-limbed *P. t. verus* and *P. t. schweinfurthii*. After further analysis of cranial measurements, Groves (2005) has concluded that two subspecies of eastern chimpanzee should be recognized, *P. t. schweinfurthii* in the northwestern part of their range and *P. t. marungensis* in the southeastern part.

Work by Uchida (1993) and Pilbrow (2001, 2003, 2006a, 2006b) on chimpanzee dental morphology found geographic variation at both the subspecies and population levels. The most distinct chimpanzee subspecies in these dental studies was *P. t. verus* (Uchida, 1993; Pilbrow, 2003, 2006b). Pilbrow's (2003, 2006b) research also supported the distinctiveness of *P. t. vellerosus*, bounded by the Niger River to the northwest and the Sanaga River to the southeast, and this group was more similar to *P. t. troglodytes* than to the other subspecies. Based on frequencies of incisor discrete traits, Pilbrow (2006a) found that *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* were all significantly different from one another, and significant differences were found between adjacent populations, as well. All the same, Pilbrow (2003) observed that, when the chimpanzee and gorilla patterns of dental metric variation are compared, much more of the species-level variation is expressed at the population level in chimpanzees. Eastern and western gorillas were considered as a single species in this analysis, but the comparison between chimpanzee and gorilla patterns of variation is worthwhile even if gorillas are made up of two species, because the range of gorillas is essentially contained within the range of chimpanzees, permitting the difference in patterns to be compared across the same geography.

Two studies focusing on the relationship of bonobos to other African apes have also contributed data on postcranial differences between subspecies of *P. troglodytes*. Jungers and Susman (1984) conducted a study of allometry and scaling in African apes, using postcranial measurements including bone lengths and articular dimensions. A few differences were found between *P. t. schweinfurthii* and *P. t. troglodytes* in linear measurements and ontogenetic allometries – male *P. t. schweinfurthii* had a narrower

scapula and smaller radial head diameter than male *P. t. troglodytes*, female *P. t. schweinfurthii* had a narrower distal humerus than female *P. t. troglodytes*, and subtle differences in the growth patterns of the hindlimb and forelimb were revealed – but there was little discussion of intraspecific differences in chimpanzees except as they related to differences between chimpanzees and bonobos. Unfortunately, *P. t. verus* was excluded from most analyses because of small sample size. Morbeck and Zihlman (1989) compared Gombe chimpanzees to a sample of other *P. t. schweinfurthii* and samples of *P. t. troglodytes* and *P. t. verus*, in addition to a *Pan paniscus* sample. Gombe chimpanzee body weights and long bone lengths were smaller than those of other chimpanzees, including other *P. t. schweinfurthii*, but limb proportions, cranial capacity, and tooth size fell within the range of other chimpanzees. In comparison to a small sample of captive chimpanzees, joint surface areas from the shoulder and hip joint were smaller in Gombe individuals, and the ratio between surface areas of the femoral head and the acetabulum was significantly smaller in the Gombe sample. These studies demonstrated the existence of postcranial differences between geographically-defined groups of chimpanzees and the need for further work to explore the patterns, extents, and correlates of this variation.

Surprisingly, further work on postcranial differences between chimpanzee groups has been slow in coming. Not until recent work by Carlson (2005) was geographic variation in chimpanzee postcranial morphology, and its potential functional correlates, explicitly addressed again. In a study of cross-sectional properties which included both *Pan* and *Gorilla* taxa, Carlson (2005) investigated ratios of principal moments of area (PMA) in humeral and femoral diaphyses at three positions on each element. Within

*Pan*, significant differences were found between *P. paniscus* and subspecies of *P. troglodytes* in both sexes, but comparisons between the subspecies found only one significant difference. Females of *P. t. verus* were significantly different from the other subspecies at one of the six diaphyseal regions examined. The bone shafts were predicted to be more circular, as reflected by lower PMA ratios, in groups in which higher frequencies of arboreal locomotion relative to terrestrial locomotion have been observed, but only two of the six humeral and femoral diaphyseal regions examined showed the predicted relationship, and neither of these relationships was statistically significant. These results contrast with those for gorillas, which showed predicted correlations between PMA ratios and locomotor behavior at five of the six diaphyseal positions examined.

Zihlman (2007) further explored geographic variation within *P. troglodytes* in a comparison of skeletons collected from Gombe (*P. t. schweinfurthii*) and Taï Forest (*P. t. verus*) by long-term field projects. These two samples each represent a real population of actually or potentially interacting and interbreeding individuals. This makes the comparison between them particularly interesting from the standpoint of examining the immediate result, in terms of variation, of evolutionary processes acting on the population. Long bones of the *P. t. verus* specimens from Taï were significantly longer than those of the *P. t. schweinfurthii* specimens from Gombe, but length indices of the same bones were not significantly different.

Ecological interpretations of differences in morphology have played a much larger part in the discussion of gorilla variation than they have in work on variation among chimpanzees. Perhaps this is because of the inviting contrast provided by the

habitat and ecology of the mountain gorillas, especially those from the Virungas, and the habitat and ecology of the western lowland gorillas. While chimpanzees live in a wide variety of habitats, no chimpanzee subspecies is characterized by a distinctive habitat in the way that the mountain gorilla is. This difference between gorillas and chimpanzees was noted by Shea and Coolidge (1988) and brought to bear on the question of why chimpanzee subspecies appear to be less clearly differentiated than gorilla subspecies. They suggested that one possible explanation for the difference in patterns of variation is that chimpanzees are adapted to broader ecological niches than gorillas, resulting in a lower correlation between subspecies and habitat.

In summary, morphological studies show that there are differences between geographic subunits of chimpanzees, although chimpanzee groups generally do not separate as well as gorilla groups. A number of studies have indicated that the most distinct subspecies is *P. t. verus*. The distinctiveness of *P. t. vellerosus*, and its similarities to and differences from other subspecies, have only begun to be explored. Few studies have explored postcranial variation in chimpanzees.

*Genetics*

Genetic studies of variation within *Pan* have examined all four compartments of the genome: mitochondrial, autosomal, X-chromosome, and Y-chromosome. Nuclear insertions of mtDNA (numts) have been identified in chimpanzees, but they do not appear to pose as much of a problem to mtDNA research as gorilla numts do (Thalmann et al., 2004).

The two species of *Pan* consistently show a greater degree of genetic divergence than do any of the subspecies of *Pan* (Morin et al., 1994; Ruvolo et al., 1994; Gagneux et

al., 1999; Kaessmann et al., 1999; Stone et al., 2002), based on studies of mitochondrial, X-chromosomal, and Y-chromosomal DNA. All the same, distances between individual chimpanzee sequences are sometimes greater than distances between individual chimpanzee and bonobo sequences (Kaessmann et al., 1999).

Analyses of some DNA sequences separate the chimpanzee subspecies into distinct clades, while analyses of other data do not. A consistent theme is the differentiation of *P. t. verus* relative to *P. t. schweinfurthii* and *P. t. troglodytes*.

Morin et al. (1994) analyzed mtDNA sequences and found the three traditional chimpanzee subspecies to form separate clades. Further, *P. t. schweinfurthii* and *P. t. troglodytes* shared a number of synapomorphies to the exclusion of *P. t. verus*. The great distance between the western clade and the central and eastern clades led the authors to suggest *P. t. verus* should be elevated to species rank if nuclear DNA and eco-behavioral data supported this result. Additional support for the separation of these three subspecies, in addition to *P. t. vellerosus*, was provided by Gagneux et al. (1999) in a mtDNA study. All four taxa were found to be monophyletic, but the authors suggested that the eastern chimpanzees may be best considered as a subset of a deeper central/eastern clade.

Analysis of X-chromosome sequences by Kaessmann et al. (1999) did not show monophyly of the three traditional subspecies. One sequence was shared by *P. t. verus* and *P. t. troglodytes*, and the single *P. t. schweinfurthii* specimen shared a clade with a number of *P. t. verus* individuals and a *P. t. troglodytes* individual. Sequences from *P. t. troglodytes* were more widely distributed among the clades than sequences from *P. t. verus*. Y-chromosome sequences were examined by Stone et al. (2002) and did not separate into clades at the level of the three traditional subspecies; however, each

haplotype was contained within a single subspecies. Deinard and Kidd (2000) studied DNA sequences from autosomes, sex chromosomes, and mitochondria. Combining the data, the three traditional chimpanzee subspecies clustered separately. For most loci, *P. t. schweinfurthii* and *P. t. troglodytes* clustered close to each other, with *P. t. verus* distant from them.

Genetic studies have resulted in the recent identification of a distinctive geographic group of chimpanzees in parts of Nigeria and Cameroon, which has been widely accepted as a separate subspecies. In response to the results of Morin et al. (1994), Jolly et al. (1995) countered that the distinctiveness of the *P. t. verus* sample in their study could be due to extinction or non-sampling of populations between the central and western samples. Gonder et al. (1997) then sampled this region between the *P. t. verus* and *P. t. troglodytes* samples of Morin et al. (1994) in a study of mtDNA from Nigerian chimpanzees. The Nigerian sample formed a distinct cluster most closely related to *P. t. verus*, but it was as different from *P. t. verus* as the central and eastern forms are from one another. These authors concluded that either: 1) the Nigerian sample belonged to *P. t. verus*, in which case the central and eastern subspecies should be collapsed, or 2) the Nigerian sample constituted a new subspecies, in which case the name *P. t. vellerosus* was available. They called for further genetic and morphological data to resolve this issue. The genetic distinctiveness of the Nigerian chimpanzees was further supported by a mtDNA study by Gagneux et al. (1999), which included an expanded sample of *P. t. verus*.

Gagneux et al. (2001), with Gonder as the second author, reported that further work by Gonder on mtDNA samples from Nigeria and Cameroon had found the Niger

River and the Sanaga River to be probable phylogeographic boundaries of the chimpanzee population proposed to belong to *P. t. vellerosus*. Analysis of mtDNA sequences found a small amount of gene flow across the Sanaga River. The near-extinction of chimpanzee populations to the west of the Niger River makes it difficult to determine the amount of gene flow across this potential barrier, but the two available samples from this area clustered with *P. t. verus* populations and not with the *P. t. vellerosus* sample. Further analysis of microsatellite data from multiple loci has added weak support to the suggestion that the Sanaga River has been an important barrier for chimpanzees (Gonder and Disotell, 2006).

In their full publication of the mtDNA data relating to the distinctiveness of chimpanzees from the region of the border between Cameroon and Nigeria, Gonder et al. (2006) concluded that the data best support a two-subspecies taxonomy for *P. troglodytes*. Under their proposed scheme, *P. t. troglodytes* and *P. t. schweinfurthii* would be collapsed into one subspecies, *P. t. troglodytes*, and the western chimpanzees, including all those north and west of the Sanaga River, would constitute the subspecies *P. t. vellerosus*, which nomen has precedence over the nomen *P. t. verus*. Alternatively, if *P. t. schweinfurthii* and *P. t. troglodytes* are retained as separate subspecies, western chimpanzees should be split into *P. t. verus* and *P. t. vellerosus*, although the boundary between the two is not yet clear.

Genetic variation within chimpanzee subspecies has also been investigated. These data can be used to propose demographic models of populations in the past. Morin et al. (1994) showed high long-distance gene flow within each of the three subspecies clades they identified. In *P. t. schweinfurthii*, studies have found low levels of variation

and a lack of geographic substructuring, although there is a relationship between genetic similarity and geographic distance (Morin et al., 1994; Goldberg and Ruvolo, 1997a,b; Gagneux et al., 1999). Studies of *P. t. troglodytes* have found high levels of variation (Kaessmann et al., 1999; Fischer et al., 2004).

Although no bonobo subspecies have been identified, genetics researchers have begun to examine variation and geographic substructuring within this taxon. Bonobo variation has been found to be less than that of chimpanzees as a whole, but comparable to that of chimpanzee subspecies or populations, at most sampled mitochondrial and nuclear loci (Gagneux et al., 1999; Reinartz et al., 2000; Deinard and Kidd, 2000; Eriksson et al., 2004). A study of mtDNA variation among bonobos from five localities, separated from one another by rivers, was conducted by Eriksson et al. (2004). Geographic structuring was apparent, and all localities were significantly different from one another based on genetic distances. Although recent gene flow between most localities was evident, genetic distances correlated with geographic distances measured around rivers, but not with straight-line distances, indicating that rivers constitute a partial barrier to gene flow between bonobo populations. A further study of both mitochondrial and Y-chromosome sequences from four bonobo localities, using the same male individuals for analyses of both kinds of data, found much greater differentiation between localities based on Y-chromosome variation than based on mtDNA variation (Eriksson et al., 2006). This result was as predicted for a species exhibiting female dispersal and male philopatry.

Genetic studies have found differences in patterns of geographic variation between *Pan* and *Gorilla*. These patterns can be used to reconstruct the

microevolutionary histories of the two genera, and the differences between them (e.g., Gagneux et al., 1999; Yu et al., 2004; Thalmann et al., 2007). They can also provide models for reconstructing the likely demographic characteristics of ancestral hominoid taxa (e.g., Jensen-Seaman et al., 2001; Yu et al., 2004). Genetic studies can contribute a valuable perspective to morphological studies, as they make explicit the relationship between patterns of variation and demography. Different patterns of philopatry and dispersal result in different patterns of variation. This is particularly useful to keep in mind when applying models of variation based on extant taxa to interpreting variation in the fossil record.

**Variation in hand and foot morphology**

The particular ability of hands and feet to reflect evolutionary diversity is noted by Lewis (1989:v): "In less than one hundred million years evolutionary diversification has produced a remarkable array of mammalian species, including some very bizarre forms, but on close examination it is apparent that these transformations have almost entirely affected the head region and the distal parts of the limbs." Among workers who have studied primate functional morphology, adaptations to different positional behaviors and substrates have been argued to be particularly evident in the hands (e.g., Napier, 1980) and feet (e.g., Schultz, 1963). More specifically, hominoid genera and species differ in features of the hand and foot which appear to correspond to differences in substrate/superstrate use and positional behavior (e.g., Morton, 1935; Susman, 1979; Stern and Susman, 1983; Gebo, 1992).

This section briefly reviews a selection of previous work on variation in hand and foot morphology among hominoids and its proposed relationships to variation in arboreal

and terrestrial locomotion. It is divided into separate subsections for the hand and the foot and also includes a subsection on the hand and foot of the mountain gorilla. It concentrates on the background literature that provided, or provided the basis for, most of the hand and foot bone measurement ratios analyzed in this study (also see Appendix 1).

### *Hand*

Although a number of regions of the forelimb have been argued to vary between hominoid taxa in relation to function, the hand stands out for its professed ability to reflect both arboreal and terrestrial locomotion.

The lengths of the hands and of the fingers have been frequently considered to be functionally significant for both arboreal and terrestrial locomotion in hominoids. It has been argued that longer fingers in more arboreal hominoids function to increase the hand's potential grasp diameter (e.g., Preuschoft, 1973; Susman, 1979). In a discussion of chimpanzees, Hunt (1991a) more specifically interpreted long fingers as an adaptation for grasping vertical weight-bearing structures, rather than for larger-diameter weight-bearing structures, pointing out that the fingers are placed diagonally when they grasp a vertical structure, increasing the effective diameter of the structure. In relation to forelimb length, the hand of *Pan* has been shown to be much longer than the hand of *Gorilla* (Napier and Napier, 1967; Jouffroy et al., 1993), but Jouffroy et al. (1993) argued that the shortness of the gorilla hand, rather than the length of the chimpanzee hand, is unusual when compared to other primates. Jouffroy et al. (1993) related this manual shortness to terrestrial walking, because this index was also especially small in *Papio* (the baboon) and was correlated with locomotor habits in primates in general. Sarmiento (1994) found that gorillas also have short hands relative to body weight, as compared to

chimpanzees, which he associated with terrestrial quadrupedal behavior. The shortness of gorilla hands, in his interpretation, functions to minimize bending moments. Tuttle (1970) gave the explanation that, in terrestrial contexts, long fingers are biomechanically inefficient and may be maladaptive. He wrote that this is because the extended digits are too long to act as propulsive levers without excessive stress and may catch on vegetation and other irregularities on the forest floor.

Inouye (1992, 1994) evaluated measurements of the metacarpals and hand phalanges in African apes from the perspective of ontogenetic allometry. She found that most measurements were ontogenetically scaled between *Gorilla* and *Pan*, with the exception of bone lengths, which were shorter in gorillas relative to their size (Inouye, 1992). She considered whether these differences in bone lengths could be due to differences in the amount of knuckle-walking or differences in the proportion of weight borne on the forelimbs, but, when comparisons between taxa were made at common sizes, these hypotheses were not supported by the literature (Inouye, 1994). She concluded that the explanation probably lies in differences in knuckle-walking kinematics or in adaptive compromises among multiple locomotor behaviors (Inouye, 1994).

Measurements of metacarpals and proximal phalanges seem especially likely to reflect the demands of knuckle-walking. Great compressive and bending forces must be resisted by these elements, and the hand must maintain the integrity of the metacarpophalangeal joint, which must function in hyperextension. Measurements of these elements, and functional interpretations of their variation, have been discussed in detail by Susman (1979). According to Susman (1979), for example, dorso-palmar midshaft diameters of the metacarpal and proximal phalanx relate to resistance to bending

forces; dorso-palmar head diameter of the metacarpal represents both extent of articular surface for hyperextension of the metacarpophalangeal joint and biomechanical advantage for resisting ground reaction forces at the joint; and joint-related ligament attachment sites in both metacarpals and proximal phalanges represent ligamentous resistance to hyperextension of the metacarpophalangeal joint. Susman (1979) found measurements of all of these features to array the hominoids along a terrestrial-arboreal continuum, with the highest values in *Gorilla* and the lowest values in *Pongo* and *Hylobates*.

While most morphological differences between hominoid taxa in the manual digital rays have been linked to frequencies of knuckle-walking, curvature of the proximal hand phalanges has been demonstrated to correlate with frequency of climbing and suspensory behaviors in hominoids. Various measurements of curvature have been used. Among the African apes, researchers have reported that the proximal phalanges of bonobos are the most curved, those of gorillas are the least curved, and those of chimpanzees are intermediate, with the proximal phalanges of the more arboreal orangutans and hylobatids being more curved than those of the African apes (Susman, 1979; Stern and Susman, 1983). Curvature of metacarpals in African apes has also been attributed to arboreal behaviors (Susman, 1979; Hunt, 1991a). Susman (1979) argued that increased curvature is a remodeling response to strong bending moments due to long fingers, and Richmond (2007) demonstrated with a finite element analysis that curved hand phalanges reduce strain associated with suspensory behaviors. In Hunt's (1991a) view, curved metacarpals and phalanges distribute tissue strain more evenly around the grasped structure and permit the hand to grip larger structures.

***Foot***

More than other regions of the hindlimb, the foot has been demonstrated to be a good source of measurements that distinguish African apes from one another in apparent relation to locomotor behavior.

Longer calcaneal tuberosities are thought to be adaptations to increased terrestrial quadrupedalism. The length of the calcaneal tuberosity is generally considered to be the power arm of the lever system used in pedal propulsion, while the rest of the foot minus the phalanges is the load (lever) arm (Schultz, 1963; Langdon, 1986; Sarmiento, 1994). Increased power arm length, relative to load arm length, provides greater power for plantarflexion, which provides propulsion during African ape quadrupedalism (Schultz, 1963; Langdon, 1986; Sarmiento, 1994). Schultz (1963) and Sarmiento (1994) measured calcaneal tuberosity length relative to the load arm of the foot, and both authors found the power arm to be greater in gorillas than in chimpanzees with no overlap in their ranges. Langdon (1986) found gorillas to have a much higher value than chimpanzees for calcaneal tuberosity length relative to calcaneus length. Gebo (1992) calculated a ratio of *distal* calcaneus length to calcaneus length and found chimpanzees to have a longer distal calcaneus (therefore presumably a shorter calcaneal tuberosity) than gorillas. In all of these studies that included *Pongo* (Schultz, 1963; Langdon, 1986; Gebo, 1992), chimpanzees fell between the larger-bodied orangutans and gorillas, strengthening the connection between tuberosity size and terrestriality without regard to body size.

Wider calcaneal tuberosities are also thought to be associated with increased terrestrial quadrupedalism. Many studies have found that gorillas have relatively wider calcaneal tuberosities than chimpanzees (e.g., Langdon, 1986; Gebo, 1992; Sarmiento,

1994), and the tuberosity of the less-terrestrial orangutan is narrower than that of the smaller-bodied chimpanzee (Langdon, 1986; Gebo, 1992). According to Langdon (1986), the function of a wider tuberosity is to increase the weight-bearing surface of the heel. More specifically, Gebo (1992) explained the bony buildup along the posterolateral region of the tuberosity, which is responsible for increased width in these taxa, as support for the inverted position of the calcaneus during locomotion on terrestrial or very broad substrates. Sarmiento (1994) stated that the wide tuberosity in gorillas is related to the wide area of insertion for a large triceps surae muscle.

Other foot proportions are argued to indicate arboreality. For example, in the calcaneus, the shape and depth of the cuboid facet are considered significant by Gebo (1992). A proportionally long and narrow cuboid facet corresponds to a high degree of mobility in the calcaneocuboid joint (Gebo, 1992). Cuboid facet shape has been found to array the African apes from bonobos to chimpanzees to gorillas, with the bonobo having the longest and narrowest facet (Gebo, 1992). *Pongo* has a longer and narrower facet than the bonobo, lending support to the apparent relevance of this feature for foot mobility and arboreal behaviors (Gebo, 1992). A deep cuboid facet also relates to foot mobility, and chimpanzees have been found to have a deeper facet than gorillas (Langdon, 1986; Gebo, 1992). Greater curvature of the proximal foot phalanges, as with the hand phalanges, has been considered to indicate a higher frequency of climbing and suspension. Stern and Susman (1983) found these bones in chimpanzees and bonobos to be more curved than those of gorillas. While chimpanzees and bonobos had nearly the same curvature, the bonobo mean was higher than the chimpanzee mean for all four lateral rays.

As with the hand, the length of the foot and its segments can be interpreted from the perspective of either arboreal or terrestrial behaviors. Long feet and pedal rays are interpreted as adaptations to climbing; short feet and pedal rays are interpreted as adaptations for terrestriality. In a study by Sarmiento (1994), gorillas had a shorter foot length relative to body weight than chimpanzees. Humans scaled with gorillas, and orangutans scaled beyond chimpanzees, leading Sarmiento (1994) to conclude that the short foot of the gorilla was associated with marked terrestriality. He interpreted the function of short feet in gorillas to be minimizing bending moments. Schultz (1963) showed that gorillas have shorter pedal ray III phalanges and metatarsals relative to foot length than do chimpanzees. He also related his findings to greater terrestriality in gorillas. From the other perspective, elongated toes in hominoids are frequently cited as arboreal features which improve grasping ability (Stern and Susman, 1983; Susman et al., 1984; Langdon, 1986; Gebo, 1992).

***Mountain gorilla hand and foot morphology***

Among anatomical regions closely involved with positional behavior, the hands and feet of mountain gorillas (*G. b. beringei*) have long been thought to particularly distinguish them from other populations. Schultz's (1934) examination of the mountain gorilla skeleton, in comparison to that of the western lowland gorilla, found ray I to be longer relative to ray III in both the hand and foot. Although he included all eastern gorillas in the group he called the "mountain gorilla", his sample of six eastern gorilla skeletons included only one specimen which would today be considered an eastern lowland gorilla rather than a mountain gorilla. His observations of external anatomy revealed the mountain gorilla (sample composition unclear) to have a relatively broader

hand and foot than the western lowland gorilla. Differences between eastern ("mountain") and western gorillas in the hand and foot were attributed by Schultz (1927) to greater terrestriality in the eastern gorilla. Groves and Stott (1979) reported that the big toe of the only mountain gorilla foot skeleton available to them was longer relative to foot length than in populations assigned to *G. g. graueri*.

Rather than saying that ray I is long relative to the hand and the foot, results from the studies by Schultz (1934) and by Groves and Stott (1979) could be restated to say that the mountain gorilla has a relatively short hand and foot. This is supported by Inouye (1992), who found that a number of measurements of the third metacarpal and proximal hand phalanx were ontogenetically scaled between mountain and western lowland gorillas, with the exception of third metacarpal length, which was shorter in mountain gorillas. In a study of features relating to terrestriality in gorillas, Sarmiento (1994) demonstrated that the mountain gorilla hand and foot are shorter and wider, and its foot has greater development of a transverse plantar arch, when compared to the more arboreal western lowland gorilla. Sarmiento et al. (1996) compared mountain gorillas from the Virungas to the gorilla population at Bwindi. The Bwindi gorillas, which live at lower altitudes with warmer temperatures and more fruiting trees, had longer hands and feet relative to body size and shorter thumbs and big toes relative to hand and foot lengths. They also had longer limbs in general. The authors interpreted the shorter appendages, including hands and feet, in the Virungas gorillas as an adaptation for greater heat retention at colder temperatures. As they explained it, longer appendages are an advantage for gorillas at Bwindi, increasing their range of possible supports as they climb trees to feed on fruit, while gorillas from the Virungas obtain little of their diet

from trees and can sacrifice appendage length to reduce heat loss. In this scenario, short hands and feet in the Virungas gorillas are not the result of selection for terrestriality but the result of a relaxation of selection for arboreality.

## Background: Positional behaviors and habitat

This section reviews the literature on African ape positional behaviors and habitat variation that relates to this study. Research on variation in arboreality and terrestriality and in habitat suggests that sufficient geographic variation exists in these ecological factors to potentially influence variation in limb bone morphology. Approaching the question from the opposite direction, this research also suggests that geographic variation found in limb bone morphology could potentially be explained by differences between geographic groups in arboreality and terrestriality and, by extension, in habitat. Literature on positional behaviors that best characterize and distinguish arboreal and terrestrial activity patterns, in combination with the literature on the functional significance of hand and foot morphology (reviewed above), permits the selection of hand and foot variables that appear most likely to reflect differences in arboreality and terrestriality. Literature on African ape locomotor and postural kinematics provides the basis on which selected hand and foot variables are proposed to reflect frequencies of arboreal and terrestrial positional behaviors.

This section is divided into subsections on variation in arboreality and terrestriality, positional behaviors that distinguish arboreality and terrestriality, kinematics, and variation in habitat.

### *Variation in arboreality and terrestriality*

Gorillas, chimpanzees, and bonobos all share a varied repertoire of positional (locomotor and postural) behaviors, including both terrestrial and arboreal activity patterns (e.g., Tuttle, 1986; Doran, 1996). Based on the differing proportions of these patterns in each taxon's profile, they are commonly arrayed along a terrestrial-arboreal continuum from gorillas to chimpanzees to bonobos (e.g., Tuttle, 1986; Hunt, 1991b; Doran, 1996). This generalization, however, obscures the variation in positional behavior found within each of these taxa. A growing body of observational data, particularly quantitative studies, increasingly permits comparisons to be made not only between genera and species but also between subspecies and populations.

Available quantitative and qualitative studies of arboreality (meaning amount of time spent in trees versus on the ground) in African ape species support a continuum with gorillas the least arboreal, chimpanzees intermediate, and bonobos the most arboreal (e.g., Doran and Hunt, 1994; Doran, 1996; Remis, 1998). Note that there is a direct and inverse relationship between degree of arboreality and degree of terrestriality; therefore, differences in arboreality imply differences in terrestriality, as well. Quantitative data also reflect geographic variation in arboreality within chimpanzees. Doran and Hunt (1994) demonstrated quantitative differences in arboreality between chimpanzee populations both from different subspecies and from within the same subspecies. They compared results from three chimpanzee study sites (one *P. t. verus* and two *P. t. schweinfurthii* sites) and determined that differences between males from each site and between females from each site were significant. Although comparable quantitative data on gorillas are not available due to the difficulty of continuously observing and following gorillas in the dense forests of west central Africa, western lowland gorillas are widely

agreed to be more arboreal than mountain gorillas based on long-term observations of their behavior (Doran, 1996; Doran and McNeilage, 1998; Remis, 1998).

Body size appears to be one factor affecting arboreality, at least within populations. Differences in degree of arboreality between males and females of a single study population have been reported in all African ape taxa for which applicable data have been collected: mountain gorillas (Tuttle and Watts, 1985; Doran, 1996), western lowland gorillas (Remis, 1995; Doran, 1996), *P. t. verus* (Doran, 1993a), and *P. t. schweinfurthii* (Doran and Hunt, 1994). All authors attribute these differences primarily to size dimorphism, with the smaller females always observed to be more arboreal. Additionally, in a study of adult male *P. t. schweinfurthii*, Hunt (1994) found that larger individuals climbed less often and fed on the ground more often than smaller individuals.

Habitat is also thought to be an important influence on arboreality. Remis (1998) attributed the greater arboreality of western lowland gorillas, as compared to mountain gorillas, to the higher canopy and more abundant tree foods in the western lowland gorilla habitat. Doran and Hunt (1994) suggested that greater male arboreality in a *P. t. verus* population, as compared to two *P. t. schweinfurthii* populations, was due to taller trees at the *P. t. verus* study site. In another example, Doran (1996) observed that bonobos from Lomako sometimes travel arboreally between trees, but Wamba bonobos travel only on the ground, which she explains by the greater prevalence of undisturbed primary forest at Lomako.

### *Positional behaviors that distinguish arboreality and terrestriality*

In order to attempt to identify skeletal morphology which has the potential to reflect geographic variation in arboreality and terrestriality, it is necessary to first

distinguish terrestriality and arboreality by identifying positional behaviors that characterize each of them and that are kinematically distinct.

Terrestrial locomotion in African apes is strongly characterized by knuckle-walking quadrupedalism (Schaller, 1963; Goodall, 1965; Reynolds and Reynolds, 1965; Susman et al., 1980; Susman, 1984; Tuttle and Watts, 1985; Doran, 1992, 1993b, 1997; Hunt, 1992). Quadrupedalism, including both knuckle-walking and palmigrady, also occurs in arboreal settings, but it does not dominate the arboreal positional repertoire. Quantitative studies show that most arboreal locomotion consists of climbing and suspension (Susman, 1984; Hunt, 1992; Doran, 1993b; Doran and Hunt, 1994; Doran, 1996; Remis, 1998), which are distinctively arboreal behaviors. Most postures are shared between terrestrial and arboreal settings, but suspensory postures are distinctively arboreal, as well (Kano and Mulavwa, 1984; Tuttle and Watts, 1985; Hunt, 1991b; Doran, 1993a, 1996; Remis, 1995). These arboreal behaviors are a kinematic contrast to knuckle-walking most notably in employing the forelimb in tension rather than in compression.

In summary, terrestrial locomotion is strongly characterized by knuckle-walking, and arboreal locomotion is distinguished from terrestrial locomotion by its reliance on climbing and suspension. Suspensory postures are also distinctively arboreal. On this basis, postcranial morphology which varies in relation to knuckle-walking would be likely to reflect differences between geographic groups in frequencies of terrestrial locomotion, and postcranial morphology which varies in relation to climbing, locomotor suspension, and postural suspension would be likely to reflect differences between geographic groups in frequencies of arboreal positional behavior.

***Kinematics***

As discussed in the above section, differences between African ape groups in frequencies of terrestrial and arboreal positional behaviors are most likely to be reflected in postcranial morphology related to knuckle-walking (for terrestrial behaviors), climbing (for arboreal behaviors), and suspension (for arboreal behaviors). In order to identify hand and foot variables which are most likely to reflect knuckle-walking, climbing and suspension, an understanding of the kinematics of these positional behaviors with regard to the hand and foot is necessary.

In knuckle-walking, the forelimbs bear weight with the dorsal surfaces of two to four of the intermediate finger phalanges flat on the substrate. Chimpanzees and bonobos have been described as bearing weight primarily or exclusively on digits III and IV (Tuttle, 1970; Susman and Stern, 1979; Inouye, 1994, 1995), while gorillas are observed to use digits II-V (Tuttle, 1970; Sarmiento, 1994; Inouye, 1994) or II-IV (Tuttle and Basmajian, 1974). The metacarpophalangeal joints are hyperextended (Tuttle, 1970 [chimpanzees]; Tuttle and Basmajian, 1974 [gorillas]; Sarmiento, 1994 [gorillas]). Gorillas are more likely to place the hand perpendicular to the line of progression, while chimpanzees and bonobos may place their hands parallel, angled, or perpendicular to the line of progression (Tuttle, 1970; Susman and Stern, 1979, 1980; Inouye, 1989).

During terrestrial knuckle-walking, the chimpanzee foot is basically plantigrade (Goodall, 1965; Reynolds and Reynolds, 1965; Tuttle, 1970; Gebo, 1992). The heel and posterior sole strike the ground first, followed by the lateral sole, then the medial sole to a lesser extent, and then the curled toes (Tuttle, 1970). The foot is usually lifted before the lateral four toes bear much weight, and no toe snap occurs at the end of a stride (Tuttle,

1970). The foot is slightly inverted, the proximal phalanges of digits II-V are extended or hyperextended, and the intermediate and distal phalanges are flexed (Tuttle, 1970). Comparable details for the bonobo are not available but are assumed here to be similar to those of the chimpanzee in the absence of published observations to the contrary. The gorilla foot is also plantigrade during terrestrial knuckle-walking (Schaller, 1963; Gebo, 1992; Sarmiento, 1994). Weight is also rolled along the lateral side of the foot (Tuttle and Watts, 1985; Gebo, 1992) before being partially transferred to the medial side (Gebo, 1992), but toe position sometimes differs from that of the chimpanzee. According to Sarmiento (1994), gorilla toes are not curled, and they dorsiflex at the metatarsus during toe-off; however, this may not always be the case, as Tuttle and Watts (1985) wrote that they sometimes tightly flex their pedal interphalangeal and metatarsophalangeal joints during knuckle-walking. During quadrupedal progression in an arboreal environment, the foot of all African apes may sometimes grasp the branches (Tuttle, 1970; Susman et al., 1980; Susman, 1984; Kano, 1992; Sarmiento, 1994); therefore, in contrast to the hand, foot kinematics during knuckle-walking may sometimes differ depending on whether the animal is on the ground or in the trees.

During climbing, the hands of African apes grasp the substrate; the forelimbs bear some of the body weight and provide at least some propulsion (Schaller, 1963; Tuttle and Watts, 1985; Hunt, 1992; Kano, 1992). Chimpanzees and bonobos appear to prefer narrower vertical substrates (vines and narrow trunks) to wider trunks, even as a method to reaching the branches of a tree with a wider trunk (Hunt, 1992; Kano, 1992). This suggests that they prefer substrates they can grasp more tightly. The foot grasps the substrate during climbing in chimpanzees (Reynolds and Reynolds, 1965), bonobos

(Kano, 1992), and gorillas (Sarmiento, 1994), with the tightness of the grasp depending on the size of the trunk or branch and with a looser grasp characteristic of gorillas.

The kinematics of the hand during suspension is most fully described for chimpanzees among the African apes. During suspensory locomotion and posture in chimpanzees the body is suspended from the hands which grip a superstrate. The feet may grasp small branches or vines at the same time (Goodall, 1965), or other parts of the body may contact weight-bearing structures (Hunt, 1992), but the majority, if not all, of the body's weight is supported by the forelimb. Suspensory locomotion in African apes includes: 1) hand-over-hand progression by means of pendulum-like swings ending with both hands contacting the superstrate and no period of free flight; 2) dropping from a branch to another branch or to the ground by means of hanging from a branch by both hands before releasing its grip, sometimes dropping to the ground and sometimes stopping the fall by grasping a lower branch with both hands; and 3) riding a small-diameter tree to the ground by clinging to it and then pulling it to a horizontal position with one's body weight before dropping off (Hunt, 1992; Doran and Hunt, 1994; Remis, 1995). Two kinds of suspensory grips used by chimpanzees were described by Marzke and Wullstein (1996). In the transverse hook grip, used on horizontal or slightly sloped supports, finger flexion may be limited to the interphalangeal joints for small supports and may include the metacarpophalangeal joints for larger supports (also see Susman and Stern, 1980; Sarmiento, 1988). In the diagonal hook grip, used on vertical or oblique cylindrical supports, flexion of the metacarpophalangeal joint is greatest for digits IV and V and least for digit II, but the hand may be adducted to allow digits II and III to increase their flexion. The thumb frequently opposes the fingers on larger supports. The palm

may be involved in either type of grip on a larger support. As the natures of gorilla and bonobo suspensory behaviors seem generally similar to those of chimpanzees (Susman et al., 1980; Doran and Hunt, 1994; Remis, 1995), the kinematics of suspension in all African apes will be assumed to be the same in this study, in the absence of information to the contrary.

This background information about hand and foot kinematics during African ape positional behaviors provides a foundation for the selection of hand and foot variables that appear likely to reflect relative frequencies of knuckle-walking, climbing, and suspension. Justifications and literature sources for the proposed relationships between positional behaviors and the selected hand and foot variables are given in Appendix 1.

***Variation in habitat***

Habitat variation between geographic groups of *Gorilla* and *Pan* has already entered into the above discussions of variation in morphology and positional behavior. In addition to references in those discussions, a limited overview of documented habitat variation within each of the African ape genera is provided here. As the intention is to demonstrate the existence of ecological variation relevant to the study of postcranial morphology, this review focuses specifically on variation which is likely to affect daily travel distance, degree of arboreality, and frequencies of arboreal positional behaviors.

Of the two African ape genera, habitat differences between groups of gorillas have received the most attention over time. Mountain gorillas and western lowland gorillas occupy two habitat extremes, as reviewed by Remis (1998) and Doran and McNeilage (1998, 2001). In the Virungas, the type locality of the mountain gorilla, trees of the montane forest are short and few gorilla foods grow in them. Instead, the mountain

gorilla diet relies heavily on densely-distributed terrestrial herbs. In contrast, western lowland gorillas live in lowland forests with high canopies and abundant tree foods, including many species of fruit. Terrestrial herb distribution is sparser. Not surprisingly, the western lowland gorilla is much more frugivorous and arboreal than the mountain gorilla. Another apparent consequence of this difference in ecology is that the mountain gorilla day range is much shorter, as mountain gorillas do not have to travel as far to reach their daily requirements of terrestrial herbage as western lowland gorillas have to travel to reach the patchily-distributed ripe fruits they prefer (Doran-Sheehy et al., 2004). Similarly, eastern lowland gorillas from a lowland forest habitat have been found to eat much more fruit and travel significantly farther every day than gorillas in the Virungas (Yamagiwa and Mwanza, 1994).

Some important ecological differences within the gorilla subspecies have been discovered, as well. For example, McNeilage (2001) compared the habitats of two mountain gorilla groups in the Virungas, one with a higher-altitude home range and the other with a lower-altitude home range. The higher-altitude group was from the Karisoke study site, where most mountain gorilla studies have taken place, while the ecology of the lower-altitude group was poorly known. McNeilage found that the lower-altitude habitat had a lower density of usable foods, and the gorillas traveled farther per day and farther between food sites. Within populations currently considered to belong to *G. b. graueri*, there are also altitude-related differences in ecology and behavior. Yamagiwa et al. (1992) found that the gorillas of Itebero (DRC, a "tropical forest" site of intermediate altitude) eat more kinds of fruit and have longer day ranges than the gorillas of Kahuzi, which overlaps the Virungas in altitude and is characterized by montane forest. As

previously discussed, ecological differences form one basis for the argument that the Bwindi gorillas do not belong to the same subspecies as those from the Virungas. Sarmiento et al. (1996) observed that there are more trees, and more fruiting trees, at Bwindi; accordingly, the Bwindi gorillas eat more fruit, spend more time in the trees, and have a longer day range than the gorillas of the Virungas.

Habitat variation between chimpanzee sites can be great, as well. Kortlandt (1972, 1974) was early in recognizing chimpanzee habitat diversity but did not initially provide any quantitative data. Since quantitative studies have been available, reviews of general habitat differences have been provided by McGrew et al. (1981), Kano (1983), Kortlandt (1983), and Fruth and Hohmann (1994). Chimpanzee populations live in a wide range of environments from dry grasslands to woodlands to rainforests. Although chimpanzees depend on trees to some extent at all sites, Mt. Assirik (Senegal) provides an extreme example of a dry chimpanzee habitat, being 55% grassland, 37% woodland, and only 3% forest (McGrew et al., 1981). Both wetter and dryer habitats occur across the chimpanzee range and do not seem to be correlated with subspecies. In a study of three groups of chimpanzees (*P. t. schweinfurthii*) in western Tanzania, Collins and McGrew (1988) found the sites to have significant vegetation differences related to differences in altitude and rainfall. From lowest to highest altitude/rainfall, Bilenge (in the Mahale Mountains) was mostly open woodland; Gombe had less open woodland and more "thicket woodland" (semideciduous forest); and Kasoje (also in the Mahale Mountains) was dominated by closed forest and vine tangle with less woodland.

The bonobo's range is much more restricted than that of either the chimpanzee or the gorilla. All bonobo populations live in the lowland forests of the Congo Basin within

a few degrees of the equator, and therefore the great contrasts in forest types seen among chimpanzee and gorilla sites are absent within the bonobo range. At the same time, ecological observation from several sites located across their range illustrate that bonobo habitats are not homogeneous, either within or between sites. Lomako, Wamba, Yalosidi, and Lake Tumba all include primary forest, secondary forest, and swamp forest, and all of these forest types are frequented by bonobos (White, 1992 [Lomako]; Kano and Mulavwa, 1984 [Wamba]; Kano, 1983 [Yalosidi]; Horn, 1980 [Lake Tumba]). Lomako is the only one of the sites which, at the time early studies were conducted, was far from human habitation and had not experienced any clearing of trees in many decades (Badrian and Malenky, 1984). At Wamba, Yalosidi, and Lake Tumba, recent habitation and cultivation have resulted in abundant secondary forest, which tends to have shorter trees and a less continuous canopy than primary forest (Kano and Mulavwa, 1984; Kano, 1983; Horn, 1980). The human practice of clearing trees was already in place in the Congo Basin when the bonobo skeletal collections available today were made, so secondary forest was probably a significant feature of some bonobo habitats at that time, as well. Lake Tumba is the most westerly of the four sites, and its forests differ from the others as a result. The western part of the Congo Basin, including Lake Tumba, is dominated by swamp forest, which is characterized by ground inundation and by shorter trees than found in "terra firma" primary forest (Horn, 1980). Also, primary "terra firma" forests in the western Congo Basin are semideciduous and do not have a continuous canopy, unlike the closed evergreen primary forests farther east (Horn, 1980). More recently, a study of bonobos at the southern limit of their range, in the forest/savanna

mosaic habitat at Lukuru, has recorded them moving through grasslands and feeding on several species of grassland fruits (Thompson, 2001, 2003).

Variation in habitat is well-documented for both *Gorilla* and *Pan* and extends to differences between populations of the same subspecies. This establishes the possibility that the variation among geographic groups of African apes in frequencies of arboreal and terrestrial positional behaviors may be a consequence of variation in habitat, particularly when habitats vary in the availability of tree fruits, height of trees, and continuity of the canopy. If geographic variation in postcranial morphology were found to relate to frequencies of distinctively arboreal and distinctively terrestrial positional behaviors, this might enable paleontologists to reconstruct habitats occupied by fossil hominoids.

## This study

### *Overview*

This study documents patterns of geographic variation in the forelimb and hindlimb skeletons of African apes. Previous work on craniodental morphology and genetics has demonstrated the existence of geographic variation at the levels of species, subspecies, and populations in both *Gorilla* and *Pan*. These studies have found that geographic structuring is stronger in *Gorilla* than in *Pan*, with respect to both the separation between groups at a given level and the hierarchical clustering of groups from one level into groups at the next level. These observed patterns of geographic variation have not yet been tested using postcranial data. Documentation of patterns of geographic variation in African ape forelimb and hindlimb skeletal morphology will provide a basis

for the taxonomic assessments of fossil limb bone specimens and contribute to reconstructing the evolutionary history of African apes and humans.

One part of the study focuses on geographic variation in a set of hand and foot variables and explores their potential functional significance. Variables of the hand and foot were chosen for this part of the study because multiple areas of the literature suggest hands and feet are especially likely to reflect potential functional and adaptive differences between geographic groups due to differences in habitat and positional behavior. If these variables are found to vary among geographic groups and also appear to vary with known differences in positional behavior profiles, these variables may constitute valuable tools in interpreting the behavior and ecology of fossil taxa. In addition, improved understanding of African ape hand and foot variation has applications to ongoing debates in paleoanthropology. Interpretation of variation in hand and foot bones plays an important role in several current controversies about locomotion and human evolution, involving questions about the locomotor mode that preceded bipedality, the context for the transition to bipedality, and the degree to which the earliest habitual bipeds engaged in arboreal behaviors (Ward, 2002; Harcourt-Smith and Aiello, 2004).

As species of *Gorilla* and *Pan* are allopatric, this study considers geographic variation in the African apes to include variation at the level of species as well as the levels of subspecies and populations.

The primary questions addressed in this study are:

1. Do African apes exhibit geographic variation, particularly at the levels of subspecies and populations, in forelimb and hindlimb skeletal morphology?
2. If so, how do *Gorilla* and *Pan* differ in the patterns and extents of such variation?

Previous studies of craniodental and genetic variation lead to the following major predictions:

1. *Gorilla* will show distinct separations between species, subspecies and populations, and populations will cluster according to subspecies.

2. *Pan* will show distinct separations between species, but subspecies and populations will be distinguished less clearly than in *Gorilla*, and populations of *P. troglodytes* will not cluster according to subspecies.

Based on previous studies, the following minor predictions are made:

1. *G. beringei* will be discriminated from *G. gorilla* at least as well as *P. paniscus* will be discriminated from *P. troglodytes*.

2. *G. b. graueri* will group with *G. b. beringei* rather than with *G. g. gorilla*.

3. *G. g. diehli* will be discriminated from other *Gorilla* subspecies and will group with *G. g. gorilla* rather than with the subspecies of *G. beringei*.

4. Gorillas from Kahuzi and Tshiaberimu will group with gorillas from Mwenga-Fizi and Utu (*G. b. graueri*) and not with gorillas from the Virungas (*G. b. beringei*).

5. *P. t. verus* will be the most distinct subspecies of *P. troglodytes*.

6. *P. t. vellerosus* will be discriminated from other *P. troglodytes* subspecies. Evidence from mtDNA suggests it will be most similar to *P. t. verus*. Evidence from dental morphology suggests it will be most similar to *P. t. troglodytes*.

7. Chimpanzees from the northwestern and the southeastern parts of the eastern chimpanzee range will be distinguishable from one another.

Secondary questions regarding patterns of variation are also addressed:

1. Are there patterns of differences between taxonomic levels, anatomical regions, and sexes in relative strength of group discrimination?

2. Are there patterns in which variables, and which *types* of variables, best differentiate groups?

3. Do selected variables of the hand and foot vary according to known differences in frequencies of positional behaviors characteristic of arboreal and terrestrial substrate use?

***Summary of chapters***

Chapter 2, Materials and Methods, provides details of the two major sets of analyses conducted for this study. One major set of analyses is based on raw measurements of forelimb and hindlimb bones, including bones of the hand and foot. The other major set of analyses is based on ratios of hand and foot bone measurements. This chapter also explains how the samples were sorted into geographic groups.

Chapter 3 contains the results of the analyses of forelimb and hindlimb bone raw measurements for *Gorilla* and *Pan*. Analyses include comparisons of means and principal components analyses. Comparisons of means at the levels of species and subspecies are reported. Principal components analyses are assessed with regard to variation at the levels of species, subspecies, and populations.

Chapter 4 contains the results of the analyses of hand and foot bone ratios for *Gorilla* and *Pan*. Analyses include comparisons of means, discriminant function analyses, and principal components analyses. Comparisons of means at the levels of genus, species, subspecies, and population are reported. Discriminant function analyses are conducted and discussed at the levels of genus, species, subspecies, and population. Principal components analyses are used to complement the subspecies-level discriminant

function analyses. At the end of the chapter, results are examined to look for further patterns that may contribute to better understanding the observed patterns of geographic variation in African ape hands and feet.

Chapter 5, Discussion and Conclusions, begins by directly addressing this study's questions and predictions. Major findings are that both *Gorilla* and *Pan* exhibit geographic variation in skeletal morphology of the forelimb and hindlimb at the levels of subspecies and populations, and the observed patterns of geographic variation are similar to those observed in studies of geographic variation in African ape craniodental morphology and genetics. Subspecies and populations of *Gorilla* are more distinct than those of *Pan*, and *Gorilla* populations cluster more consistently according to taxon. Although the sample offers only limited opportunities to investigate the relationship between limb bone morphology and ecology, patterns of geographic variation in limb bone morphology appear to reflect phylogeography rather than differences in habitat and arboreality. Models of geographic variation in *Gorilla* and *Pan* are presented that may be applied to the interpretation of variation in forelimb and hindlimb bones in fossil hominoids.

# CHAPTER 2

# MATERIALS AND METHODS

## Materials

The study sample is composed of forelimb and hindlimb bones from adult males and females belonging to the genera *Gorilla* (n = 266) and *Pan* (n = 274). All individuals were collected from the wild, and all species and subspecies assignments were made based on recorded localities of origin. Specimens are housed in the following museum collections: American Museum of Natural History, Department of Mammalogy (New York, NY); American Museum of Natural History, Department of Anthropology (New York, NY); Anthropological Institute and Museum, University of Zurich (Zurich, Switzerland); Cleveland Museum of Natural History (Cleveland, OH); Field Museum of Natural History (Chicago, IL); Museum of Comparative Zoology, Harvard University (Cambridge, MA); Natural History Museum (London, UK); Royal Museum of Central Africa (Tervuren, Belgium); Powell-Cotton Museum (Birchington, UK); U. S. National Museum of Natural History (Washington, DC); and Zoological Museum of Berlin, Humboldt University (Berlin, Germany).

The following ten bones of the forelimb and hindlimb are included in the study: humerus, radius, third metacarpal, third proximal hand phalanx, femur, tibia, calcaneus, first metatarsal, third metatarsal, and third proximal foot phalanx. Many specimens in the study sample do not preserve all elements in the study. As the study includes multiple analyses based on various combinations of elements, sample sizes vary among analyses. For any given analysis in this study, individuals were considered to be adult if the

epiphyses of all elements included in the analysis were fused. Sample sizes are tabulated by analysis in Appendix 2.

Species and subspecies are defined according to Groves (2001). See Table 1.1 for details. Representatives of all African ape taxa defined in Groves (2001) are included in the study sample, although some taxa are much better-represented than others. Note that all *Gorilla beringei beringei* specimens were collected from the type locality of the Virunga Volcanoes; therefore, uncertainty about the subspecific identity of the Bwindi population (Sarmiento et al., 1996) is not a concern with regard to the study sample.

**Definitions of populations**

Population-level analyses were conducted with two slightly different goals in mind. The first goal was to make a direct comparison between *Gorilla* and *Pan* of patterns of discrimination between populations. For this purpose, the populations of both genera needed to be geographically identical. Small sample sizes from many areas and differences in geographic representation between the genera limited the number of populations available for direct comparison. Ultimately, three geographic regions of west-central Africa were identified from which comparable populations with adequate sample sizes could be defined for both genera. Comparisons of means and discriminant function analyses were performed on hand and foot bone ratios from these three populations of *P. t. troglodytes* and three populations of *G. g. gorilla*. The second goal was to assess whether there are differences between *Gorilla* and *Pan* in the extent to which populations cluster into species and subspecies, in general, allowing that some samples are very small and some geographical regions are only represented by one genus. For this broad comparison of patterns, principal components analyses were performed on

forelimb and hindlimb bone raw variables from eleven populations of *Gorilla* and ten populations of *Pan*.

Geographic origins of specimens were obtained mostly from catalogs and accession records of museum collections, although additional information was sometimes gathered from field notes, correspondence, scientific publications, and popular accounts written by the collectors. Place names were located in gazetteers or on maps, if possible, in order to determine their geographic positions. Contemporary maps and geographic descriptions were sometimes consulted when place names had changed or become obscure over time.

***Populations for direct comparison***

Individuals belonging to *G. g. gorilla* and *P. t. troglodytes*, the west-central African subspecies of each genus, were sorted into smaller geographically-defined groups, hereafter called "populations", for the purpose of directly comparing patterns of population-level variation in *Gorilla* and *Pan*. The ranges of the two genera overlap extensively in west-central Africa, permitting direct comparisons of population-level patterns in this region. By contrast, there are no gorillas within the distribution of the western chimpanzee, and the eastern gorillas only overlap a portion of the eastern chimpanzee range. The Cross River gorilla and the Nigerian chimpanzee both occupy, or previously occupied, areas of northwestern Cameroon and southeastern Nigeria, but the available postcranial samples of these taxa are far too small to permit population-level study.

First, the *G. g. gorilla* specimens were sorted into the geographic groups analyzed by Groves (1970) in his study of skulls. Unfortunately, museum collections tend to

include many more gorilla skulls than gorilla postcranial skeletons, and some Groves localities were not well-represented by postcrania in the museum collections visited for this study. In order to address the problem of small sample sizes, some Groves localities were combined when ecologically and biogeographically justifiable. Pilbrow (2003) also combined some Groves localities to form new groups, and it would have been preferable to use her groups so results would be directly comparable, but her groupings were not well-suited to the available postcranial samples, either.

Next, the *P. t. troglodytes* specimens were sorted into the same geographic groupings used for *G. g. gorilla*. This is a departure from previous studies (Pilbrow, 2003; Shea et al., 1993), which have defined chimpanzee populations independently of gorilla populations. For this study, because so few populations had sample sizes which were large enough for analysis, it was preferable to compare patterns of variation between identically-defined populations of chimpanzees and gorillas, in order to reduce the number of confounding factors. As it happens, the largest west-central African samples of both chimpanzee and gorilla postcranial skeletons come from the same localities, and three geographic areas were identified that had samples of hands and feet that were sufficiently large to analyze in both *G. g. gorilla* and *P. t. troglodytes*.

The three geographic areas that define populations for the purposes of direct comparisons in this study are designated Coast, Cameroon Interior, and Ebolowa. Their correspondences with localities and regions defined in previous studies are given in Table 2.1. Sample sizes of the three populations are given in Appendix 2, Tables 7 and 8. Figure 2.1 shows their locations on a map, and they are described as follows:

Coast – coastal Cameroon, coastal Gabon, and all Equatorial Guinea

Cameroon Interior – inland Cameroon localities clustered around the Nyong River and between the Dja River and the upper Sanaga River

Ebolowa – inland Cameroon locality, south of the Nyong River and west of the Dja River

The Coast population includes all Groves (1970) localities within the area designated as the Atlantic Equatorial Coastal Forests ecoregion by the World Wildlife Fund's Terrestrial Ecoregions of the World project (Olson et al., 2001; http://www.nationalgeographic.com/wildworld/terrestrial.html), with the exception of Ebolowa. Ecoregions from the Terrestrial Ecoregions of the World project are identified according to both ecological and biogeographical criteria (Olson et al., 2001). Although the constituent Groves (1970) localities are separated by rivers, their combination into a Coast population for the purpose of this analysis is justified by their inclusion in the same ecoregion.

The Cameroon Interior population includes four Groves (1970) groups within the area designated as the Northwest Congolian Lowland Forest ecoregion (Olson et al., 2001; http://www.nationalgeographic.com/wildworld/terrestrial.html). The Groves (1970) groups of Abong Mbang and Metet are made up of a continuous array of inland localities along and around the Nyong River. The Groves (1970) groups of Batouri and Lomie appear to be continuous populations based on records from the Powell-Cotton Museum indicating that specimens were collected from many closely-spaced localities between Batouri and Lomie. Combination of these four groups into a single population is justified by their inclusion in the same ecoregion and by the apparent lack of biogeographic boundaries between Abong Mbang and Metet, on the one hand, and Batouri and Lomie, on the other.

The Ebolowa population is within the Atlantic Equatorial Coastal Forests ecoregion, but it is very close to this ecoregion's intergraded border with the Northwest Congolian Lowland Forest ecoregion (Olson et al., 2001; http://www.nationalgeographic.com/wildworld/terrestrial.html). It is analyzed separately because it has a large sample size and because it may be ecologically intermediate.

Table 2.1. Populations defined for this study (for direct comparison) and corresponding groups in other studies

| This study | Groves (1970) gorillas | Pilbrow (2003) gorillas | Shea et al. (1993) chimpanzees | Pilbrow (2003) chimpanzees |
|---|---|---|---|---|
| Coast | 2, 3, 4, 15 | 2, 3, 4 (part), 7 (part) | 6, 7, 13, 14, 19 | 5, 7 (part), 8 (part) |
| Cam Int | 10, 11, 12, 13 | 6, 7 (part) | 9, 10, 11 | 6 (part) |
| Ebolowa | 14 | 7 (part) | 8 | 6 (part) |

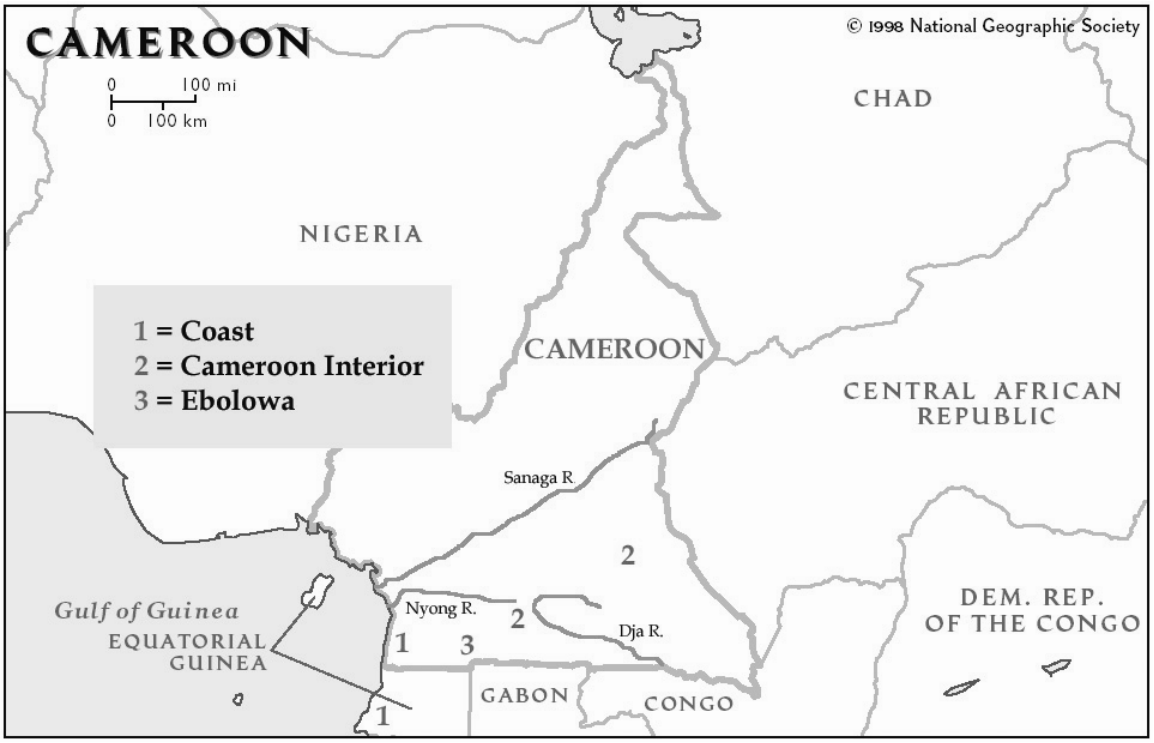


Figure 2.1. West-central African populations of *Gorilla* and *Pan*, for direct comparison between genera. Note that the Coast population includes coastal Gabon, not shown here. Adapted from a National Geographic Society map downloaded from http://www.nationalgeographic.com/xpeditions/.

***Populations for broad comparison***

For the purpose of making broad comparisons between the genera of the extent to which populations cluster into species and subspecies, eleven populations of *Gorilla* and ten populations of *Pan* were identified.

Populations of *Gorilla* are defined based on Groves (1970). The Groves (1970) populations of *G. g. gorilla* are consolidated into a smaller number of groups for this study, following ecological and biogeographical criteria (Olson et al., 2001). Correspondences between populations of *Gorilla* defined for this study and groups defined in previous studies are listed in Table 2.2. Sample sizes of each population of *Gorilla* are listed in Appendix 2, Table 3. Figure 2.2 shows their locations on a map.

Populations of *P. t. troglodytes* are defined according to population definitions used for *G. g. gorilla* (see Table 2.2). Populations of *P. t. schweinfurthii* are defined based on Groves (2005), who separates eastern chimpanzees into *P. t. schweinfurthii*, made up of the northwestern populations, and *P. t. marungensis*, made up of the southeastern populations. The subspecies *P. t. verus* and *P. t. vellerosus*, with small sample sizes, are each considered as a single population. Correspondences between populations of *Pan* defined for this study and groups defined in previous studies are listed in Table 2.3. Sample sizes for each population of *Pan* are listed in Appendix 2, Table 4. Figure 2.3 shows their locations on a map.

Table 2.2. *Gorilla* populations defined for this study (for broad comparison of clustering patterns) and corresponding groups in other studies. Also see maps in Figure 2.2.

| | Groves (1970) | Pilbrow (2003) |
|---|---|---|
| *G. b. beringei* | | |
| 1 – Virungas | 19 | 11 |
| *G. b. graueri* | | |
| 2 – Mwenga-Fizi | 17 | 9 |
| 3 – Kahuzi | B | 13 |
| 4 – Tshiaberimu | 18 | 10 |
| 5 – Utu | 16 | 8 |
| *G. g. gorilla* | | |
| 6 – Coast | 2, 3, 4, 15 | 2, 3, 4 (part), 7 (part) |
| 7 – Ebolowa | 14 | 7 (part) |
| 8 – Abong Mbang/Metet | 12, 13 | 7 (part) |
| 9 – Batouri/Lomie | 10, 11 | 6, 7 (part) |
| 10 – Sangha | 5, 6, 7, 8, 9 | 4 (part), 5 |
| *G. g. diehli* | | |
| 11 – Cross River | 1 | 1 |

Table 2.3. *Pan* populations defined for this study (for broad comparison of clustering patterns) and corresponding groups in other studies. Also see maps in Figure 2.3.

| | Shea et al. (1993) | Pilbrow (2003) |
|---|---|---|
| *P. t. schweinfurthii* | | |
| 1 – NW eastern | 22, 23, 24 | 10, 11, 12 (part) |
| 2 – SE eastern | 25, 26, 27, 28, 29, 31 | 12 (part), 13 |
| *P. t. troglodytes* | | |
| 3 – Coast | 6, 7, 13, 14, 19 | 5, 7 (part), 8 (part) |
| 4 – Ebolowa | 8 | 6 (part) |
| 5 – Abong Mbang/Metet | 9 | 6 (part) |
| 6 – Batouri/Lomie | 10, 11 | 6 (part) |
| 7 – Sangha | 12, 16, 17, 20 | 6 (part), 7 (part), 8 (part) |
| *P. t. vellerosus* | | |
| 8 – North of Sanaga River | 4, 5 | 4 |
| *P. t. verus* | | |
| 9 – Ivory Coast and Liberia | 1[1] | 1[1] |
| *P. paniscus* | | |
| 10 – South of Congo River | 33, 34 | 14, 15 (part) |

[1] Although both Shea et al. (1993) and Pilbrow (2003) each include Ivory Coast in Group 2, it is clear from the map in Shea et al. (1993) and the description in Pilbrow (2003) that their boundary between Groups 1 and 2 is the Sassandra River, in western Ivory Coast. All Ivory Coast specimens included in this study are from west of the Sassandra River and, therefore, would be included in Group 1 of either of the previous studies.

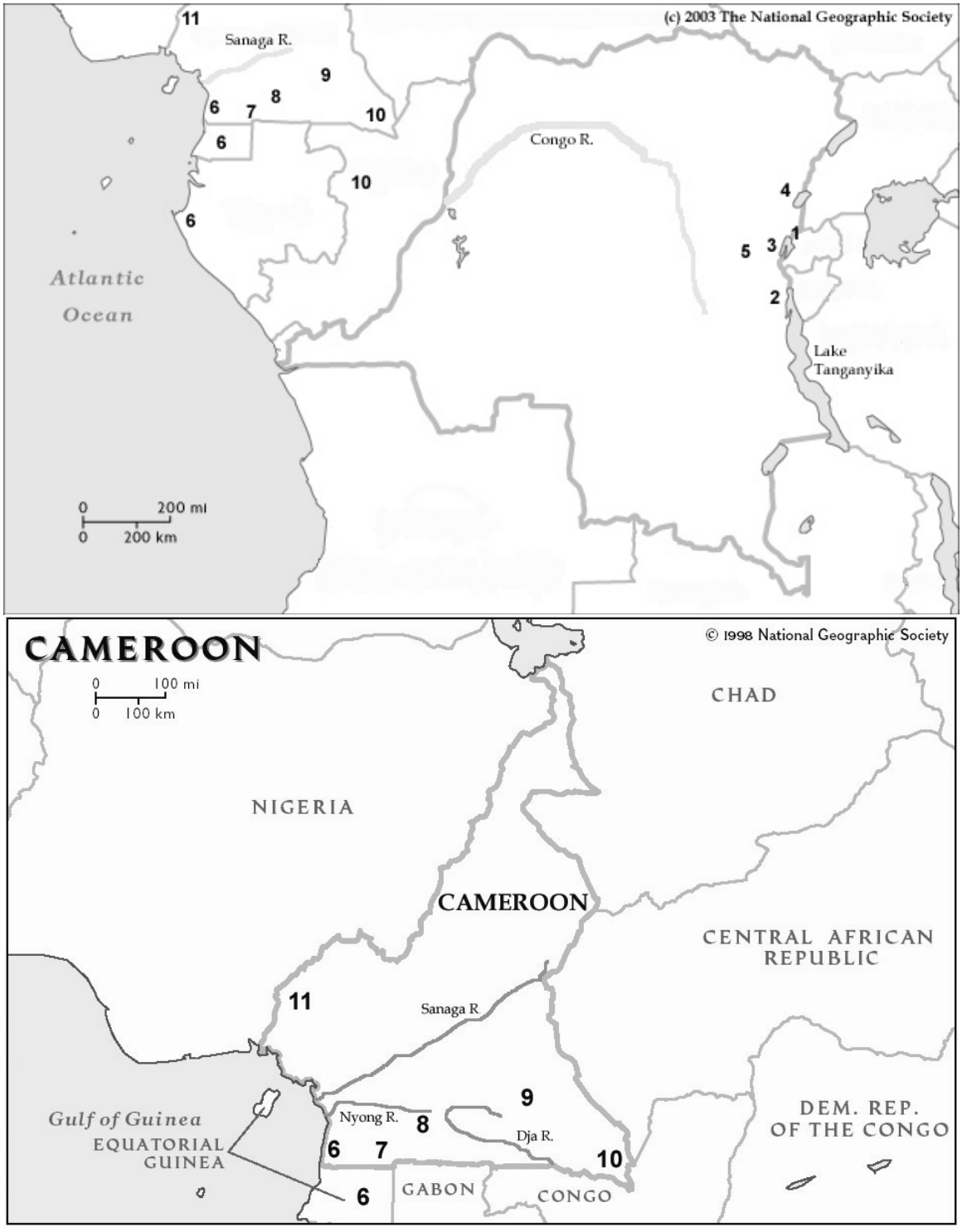


Figure 2.2. Upper image: central Africa, showing all populations of *Gorilla* defined for broad comparison of clustering patterns. Lower image: close-up of Cameroon and vicinity, showing west-central African populations. See Table 2.2 for correspondences between numbers and names of populations. Adapted from National Geographic Society maps downloaded from http://www.nationalgeographic.com/xpeditions/.


Figure 2.3. Upper image: Africa, showing populations of *Pan* defined for broad comparison of clustering patterns. Lower image: close-up of Cameroon and vicinity, showing west-central African populations (indicated with an asterisk in upper image). See Table 2.3 for correspondences between numbers and names of populations. Adapted from National Geographic Society maps downloaded from http://www.nationalgeographic.com/xpeditions/.

## Methods

Two large sets of analyses were conducted to address questions and predictions regarding geographic variation in African ape limb skeleton morphology. The first set of analyses examines geographic variation in raw measurements of all the forelimb and hindlimb bones included in the study. The second set of analyses focuses on geographic variation of the hand and foot bones, based on ratios of linear measurements.

### *Variables*

#### *Raw measurements*

Forty-three linear measurements of the forelimb and hindlimb skeleton, including the hand and foot, were analyzed in the set of analyses based on raw variables. These measurements were selected to generally describe the size and shape of the ten bones included in this study. Measurement definitions are given in Table 2.4, and measurements are illustrated in Figures 2.4 – 2.13.

Table 2.4. Definitions of measurements used in analyses of raw measurements

NOTE: Most measurements are defined for data collection using calipers, but some measurements of the humerus, radius, femur, and tibia are defined for data collection using a digitizer that collects 3D landmarks. These measurement definitions are followed by the parenthetical note "3D landmarks".

***Forelimb***

Humerus
**length** (HUM_LENGTH): distance between most proximal point of head and most distal point of trochlea (3D landmarks)
**medio-lateral midshaft diameter** (HUM_ML_MID): medio-lateral diameter of shaft taken at 40% of the length from the distal end (to avoid the deltoid tuberosity at midshaft), with medio-lateral axis defined as axis of distal end
**antero-posterior midshaft diameter** (HUM_AP_MID): antero-posterior diameter of shaft taken at 40% of the length from the distal end (to avoid the deltoid tuberosity at midshaft), with antero-posterior axis defined as perpendicular to axis of distal end
**head height** (HUM_SI_HEAD): maximum supero-inferior diameter of head, point-to-point, viewing head from anterior perspective and holding caliper so sides of jaws are visible
**distal articular width** (HUM_DISTARTWD): distance between most lateral point of distal capitulum and most distal point of trochlea (3D landmarks)
**biepicondylar width** (HUM_BIEPI): distance between most lateral point of lateral epicondyle and most medial point of medial epicondyle (3D landmarks)

Radius
**length** (RAD_LENGTH): distance between most lateral point of distal articular surface and most proximal point of posterior head (3D landmarks)
**medio-lateral midshaft diameter** (RAD_ML_MID): medio-lateral diameter at midshaft
**antero-posterior midshaft diameter** (RAD_AP_MID): antero-posterior diameter at midshaft
**medio-lateral head diameter** (RAD_ML_HEAD): distance between most medial point on medio-lateral head diameter and most lateral point on medio-lateral head diameter (3D landmarks)
**distal width** (RAD_DISTALWD): distance between most lateral point of distal articular surface and most medial point of the antero-medial region of the distal articular surface (3D landmarks)

Metacarpal 3
**length** (MC_LENGTH): maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**radio-ulnar midshaft diameter** (MC_RU_MID): radio-ulnar diameter at midshaft
**dorso-palmar midshaft diameter** (MC_DP_MID): dorso-palmar diameter at midshaft
**head width** (MC_RU_HEAD): maximum radio-ulnar diameter of head

**biepicondylar width** (MC_BIEPI): maximum distance across epicondyles, measured using flat surfaces of caliper jaws

Proximal hand phalanx 3
**length** (HP_LENGTH): maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**maximum shaft width** (HP_RU_MAX): maximum radio-ulnar shaft diameter
**minimum shaft width** (HP_RU_MIN): minimum radio-ulnar shaft diameter, measured using sharpened edges of caliper jaw points
**base width** (HP_RU_BASE): maximum radio-ulnar diameter of base region, not limited to articular surface
**trochlear width** (HP_RU_TROCH): maximum radio-ulnar width of trochlea, not including epicondyles

***Hindlimb***

Femur
**length** (FEM_LENGTH): distance between most proximal point on head and most distal point on medial condyle (3D landmarks)
**medio-lateral midshaft diameter** (FEM_ML_MID): medio-lateral diameter at midshaft
**antero-posterior midshaft diameter** (FEM_AP_MID): antero-posterior diameter at midshaft
**head height** (FEM_HEAD_HT): distance between most superior point of head on diameter perpendicular to neck and most inferior point of head on diameter perpendicular to neck (3D landmarks)
**bicondylar width** (FEM_BICON_WD): distance between point on medial border of medial condyle's articular surface at mid-height of condyle and point on lateral border of lateral condyle's articular surface at mid-height of condyle, as seen from posterior view (3D landmarks)

Tibia
**length** (TIB_LENGTH): distance between most proximal point of medial spine and most distal point of distal articular surface (3D landmarks)
**medio-lateral midshaft diameter** (TIB_ML_MID): medio-lateral diameter at midshaft
**antero-posterior midshaft diameter** (TIB_AP_MID): antero-posterior diameter at midshaft
**plateau width** (TIB_PLATEAU): maximum projected (not point-to-point) medio-lateral width of plateau, measured using flat surfaces of caliper jaws and holding caliper jaws perpendicular to medio-lateral axis of plateau

Calcaneus
Orientation: Calcaneus is placed on a table, or held as if it were resting on a table, so that the long axis of the calcaneal tendon facet is dorso-plantar and the fossa of the cuboid facet opens in a plantar or slightly medio-plantar direction. If use of these two features

results in contradictory orientations, use the one which appears to have a more typical orientation based on other landmarks.
**length** (C_LENGTH): maximum projected (not point-to-point) length from most posterior point of calcaneal tuberosity to most anterior point of dorsal cuboid facet, with caliper jaws held perpendicular to long axis of calcaneus
**tuberosity length** (C_TUB_LENGTH): measured with calcaneus in defined orientation and tuberosity against a vertical plane (such as a stiff-sided box), using outside-facing jaws of caliper to measure minimum distance between most posterior point of posterior talar facet and vertical plane
**tuberosity height** (C_TUB_HTADJ): measured with calcaneus resting on a metal ruler and held in researcher's hand, in defined orientation, measuring from bottom of ruler to dorsal-most tuberosity (thickness of ruler subtracted from measurement)
**tendon facet width** (C_TENDON_WD): maximum width of calcaneal tendon facet perpendicular to dorso-plantar axis, measured with points of caliper jaws (if tubercle has built up laterally and covered facet, lateral point of measurement may be projected onto tubercle)
**cuboid facet width** (C_CUB_WD): maximum diameter of cuboid facet in approximately medio-lateral direction, orienting facet so that fossa opens in a plantar direction
**cuboid facet depth** (C_CUB_DPADJ): depth of cuboid facet, measured with caliper depth gauge from stiff ruler placed across dorsal part of facet (thickness of ruler subtracted from measurement)

Metatarsal 1
**length** (MT1_LENGTH): maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher

Metatarsal 3
**length** (MT3_LENGTH): maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**head width** (MT3_ML_HEAD): maximum medio-lateral diameter of head
**biepicondylar width** (MT3_BIEPI): maximum distance across epicondyles, measured using flat surfaces of caliper jaws

Proximal foot phalanx 3
**length** (FP_LENGTH): maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**maximum shaft width** (FP_MAXSHAFT): maximum medio-lateral shaft diameter
**minimum shaft width** (FP_MINSHAFT): minimum medio-lateral shaft diameter, using sharpened edges of jaws

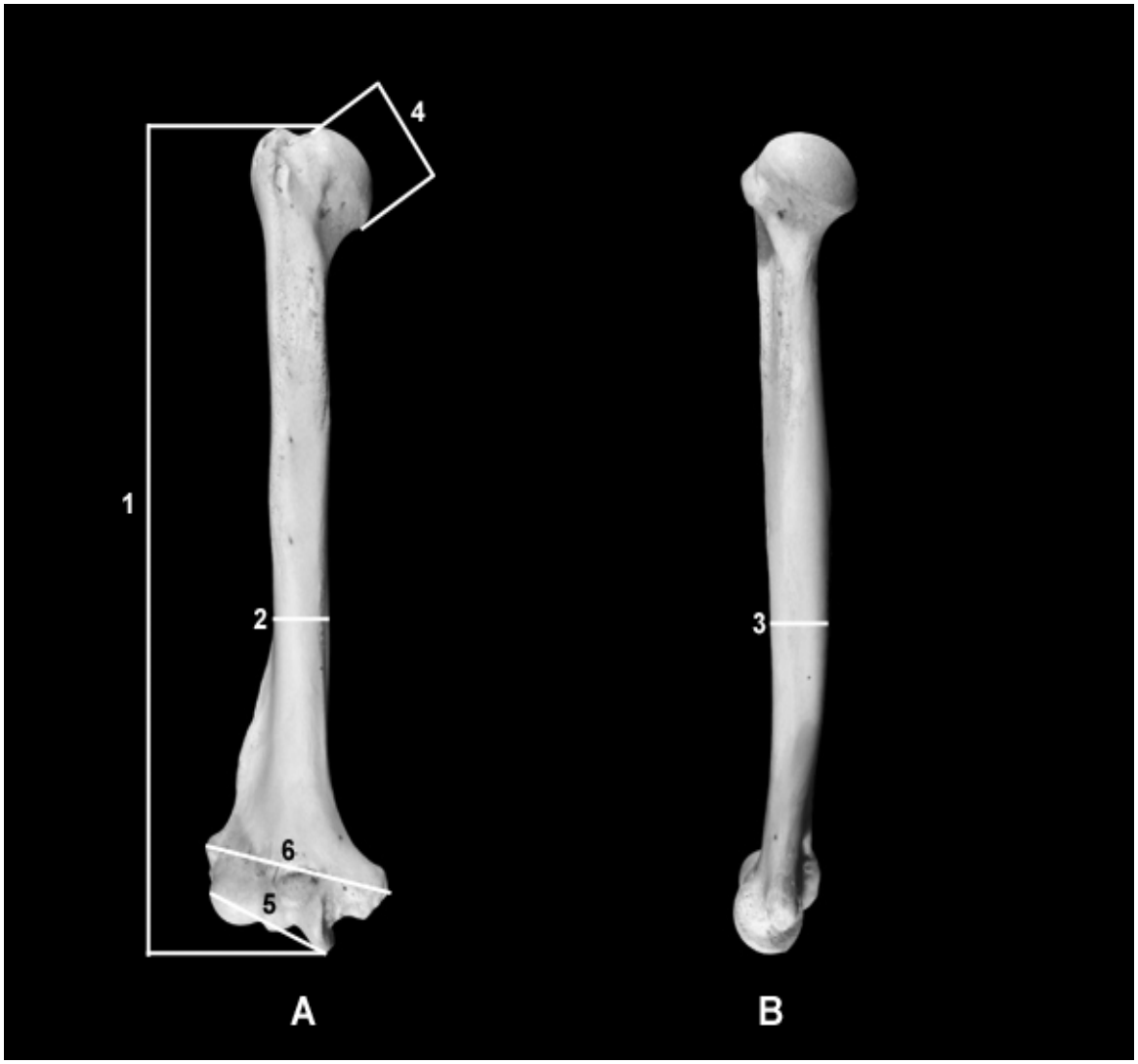


Figure 2.4. Measurements of the humerus, illustrated on *P. troglodytes*. A (anterior view): 1, length; 2, medio-lateral midshaft diameter; 4, head height; 5, distal articular width; 6, biepicondylar width. B (medial view): 3, antero-posterior midshaft diameter.

Measurements are defined in Table 2.4. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

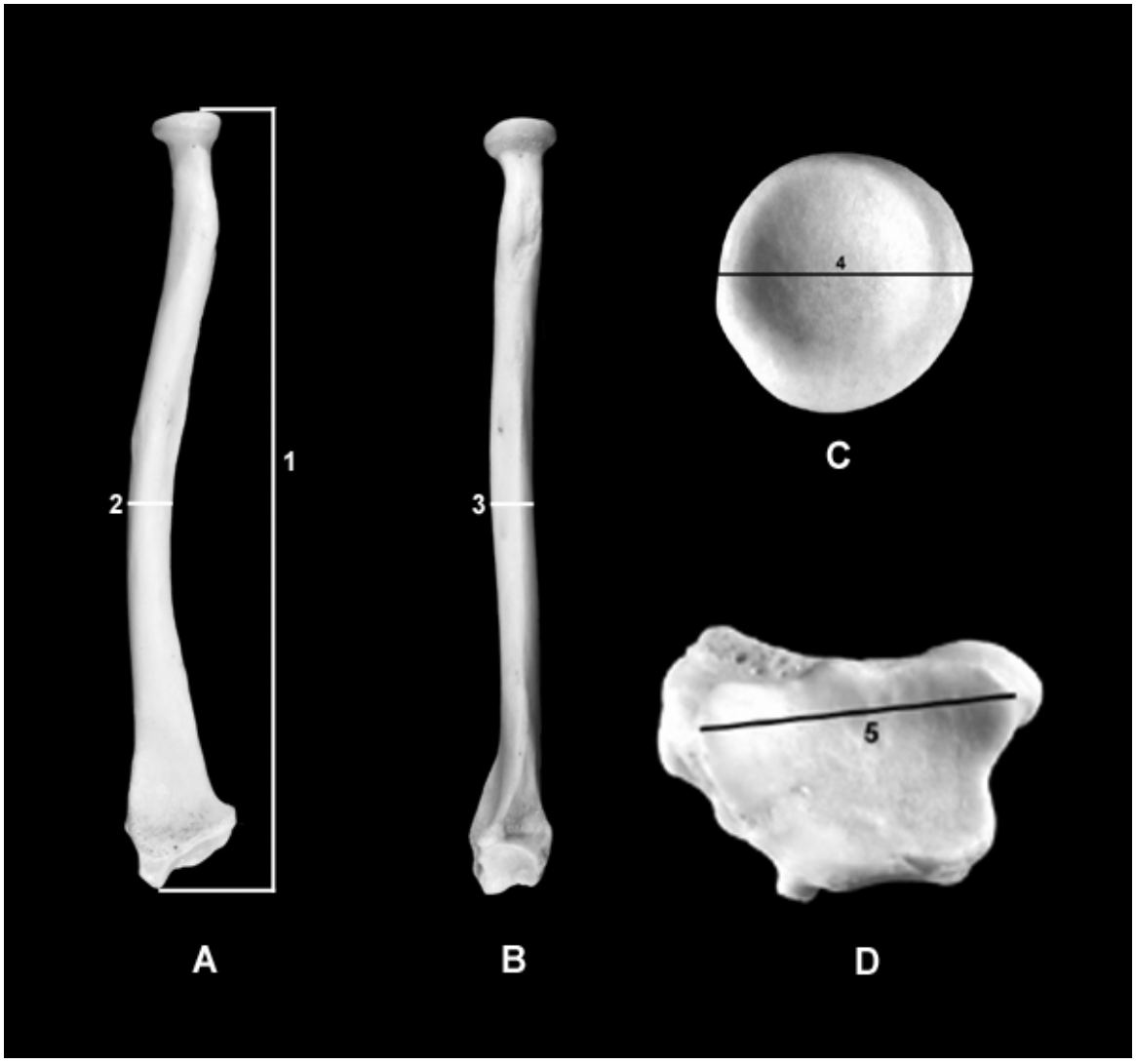


Figure 2.5. Measurements of the radius, illustrated on *P. troglodytes*. A (anterior view): 1, length; 2, medio-lateral midshaft diameter. B (medial view): 3, antero-posterior midshaft diameter. C (proximal view): 4, medio-lateral head diameter. D (distal view): 5, distal width.

Measurements are defined in Table 2.4. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

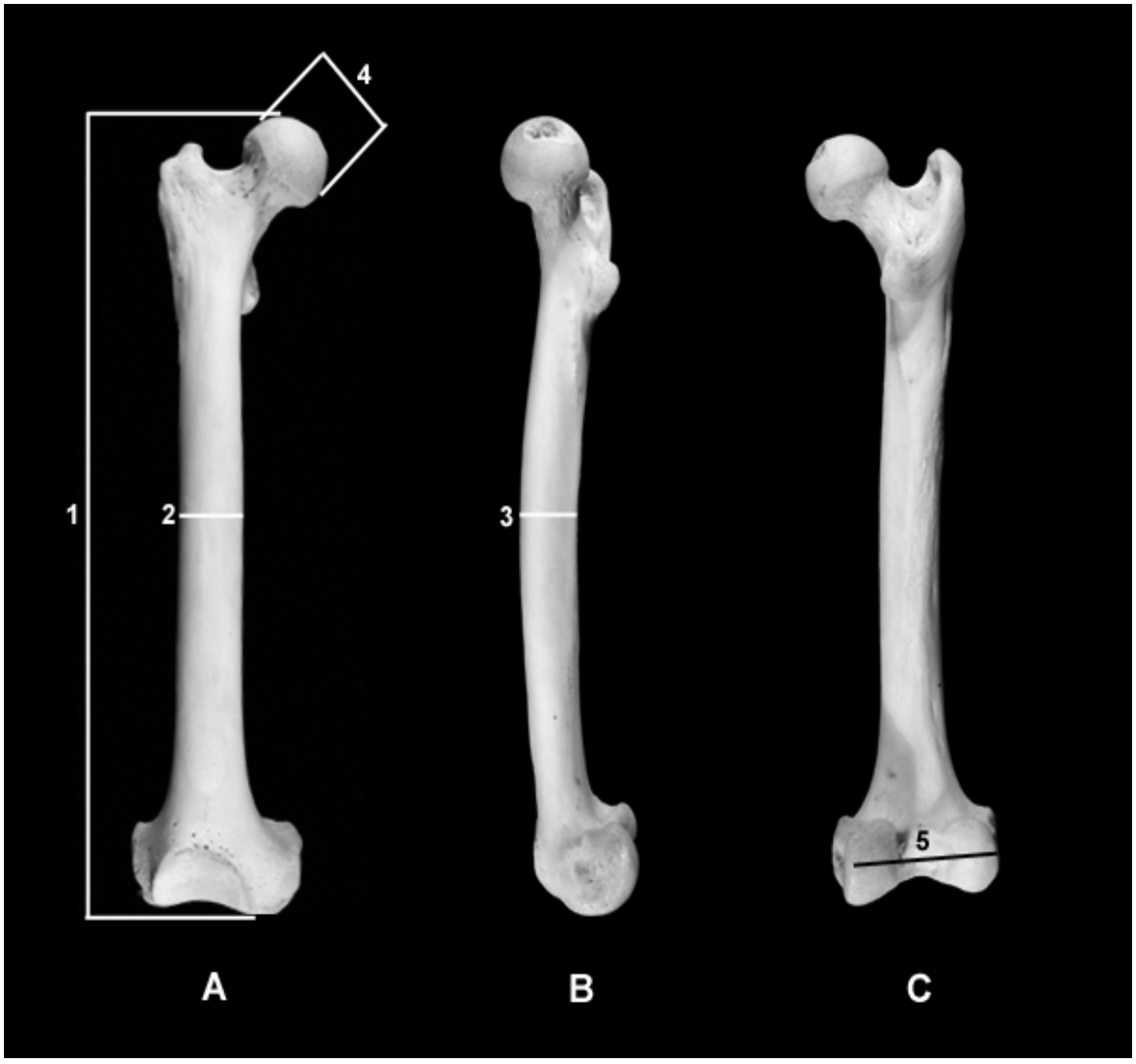


Figure 2.6. Measurements of the femur, illustrated on *P. troglodytes*. A (anterior view): 1, length; 2, medio-lateral midshaft diameter; 4, head height. B (medial view): 3, antero-posterior midshaft diameter. C (posterior view): 5, bicondylar width.

Measurements are defined in Table 2.4. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

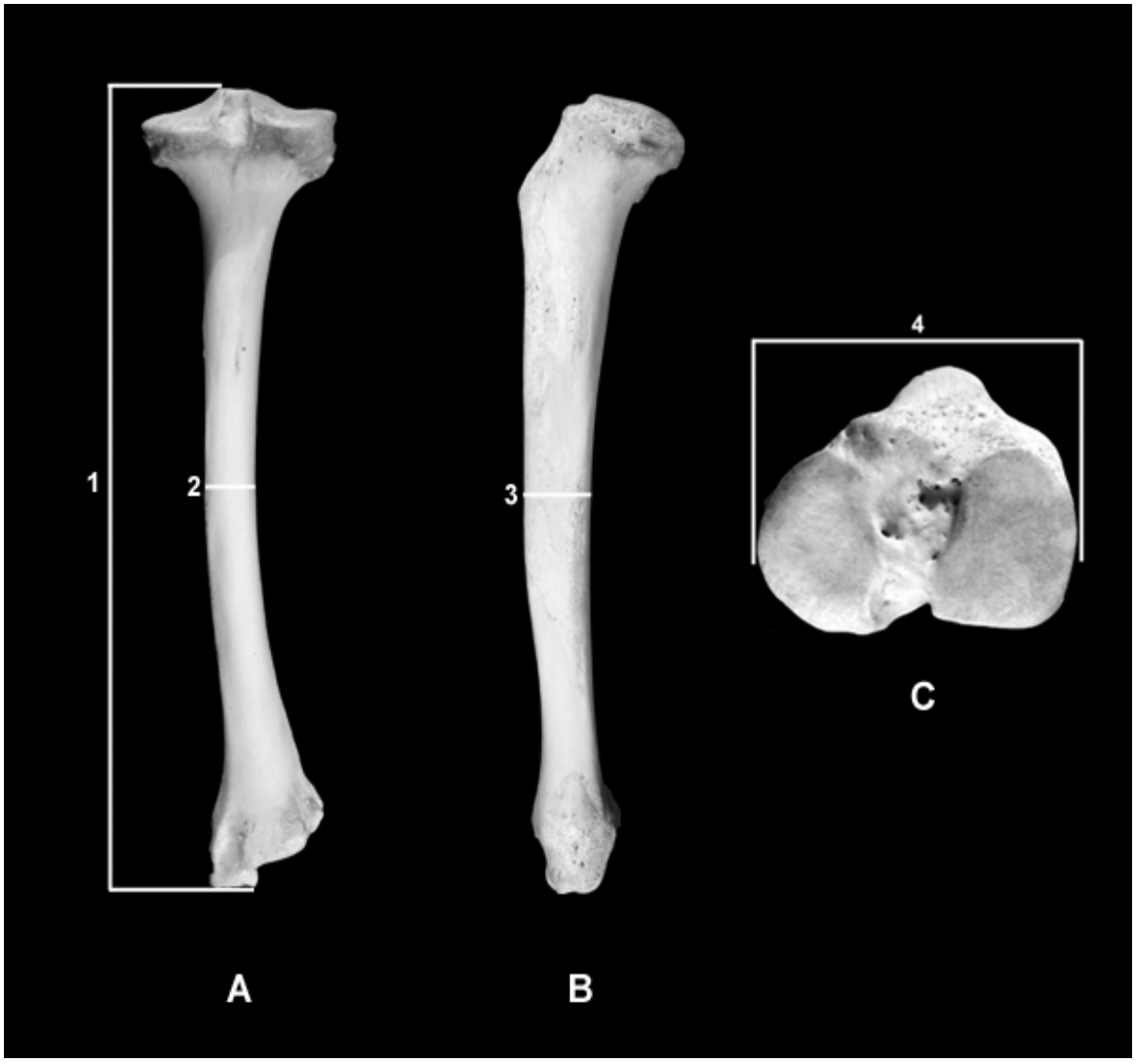


Figure 2.7. Measurements of the tibia, illustrated on *P. troglodytes*. A (posterior view): 1, length; 2, medio-lateral midshaft diameter. B (medial view): 3, antero-posterior midshaft diameter. C (proximal view): 4, plateau width.

Measurements are defined in Table 2.4. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

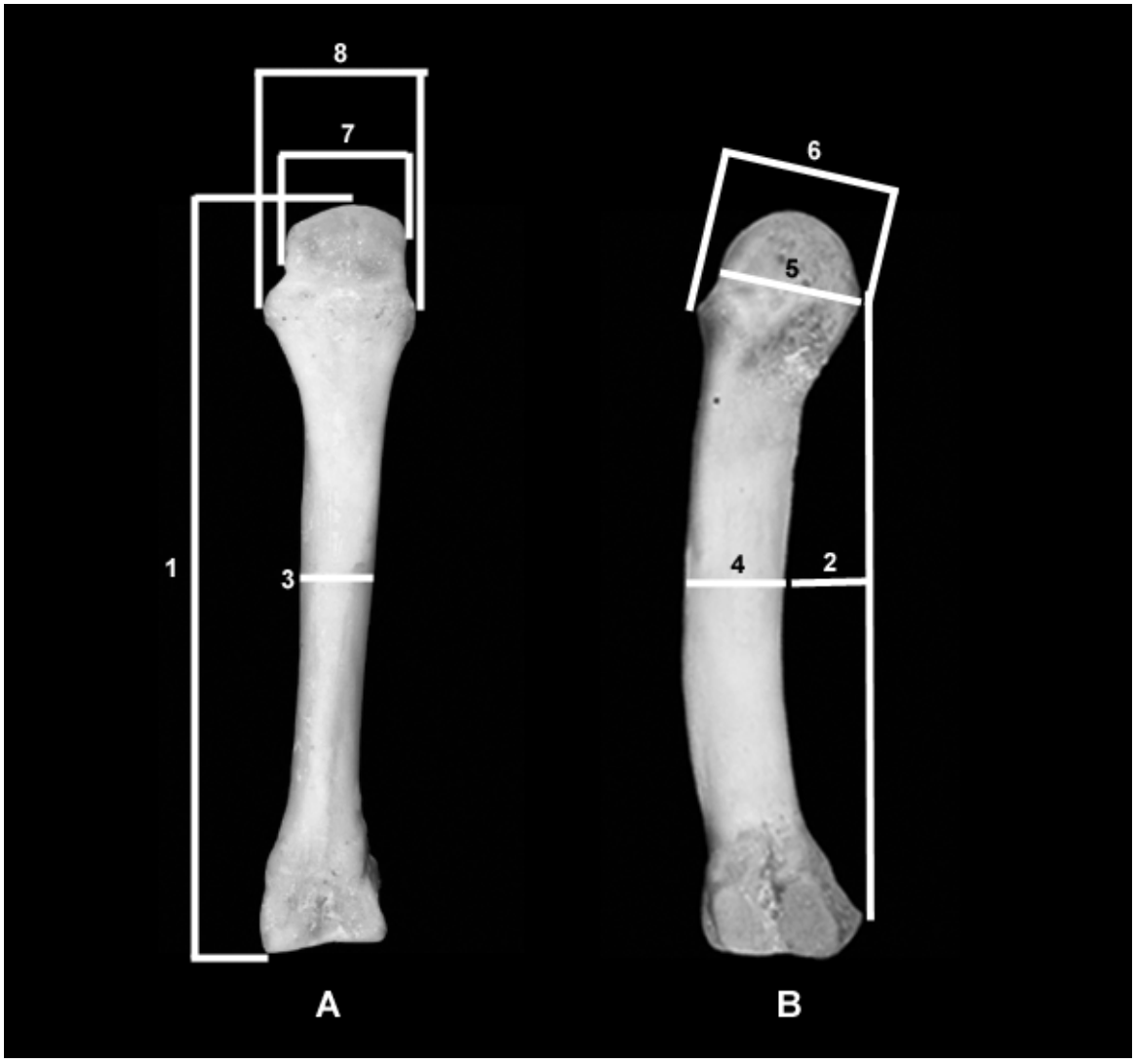


Figure 2.8. Measurements of the third metacarpal, illustrated on *P. troglodytes*. A (dorsal view): 1, length; 3, radio-ulnar midshaft diameter; 7, head width; 8, biepicondylar width. B (medial view): 2, height of arch; 4, dorso-palmar midshaft diameter; 5, head height; 6, head height plus ridge.

Measurements are defined in Tables 2.4 and 2.7. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

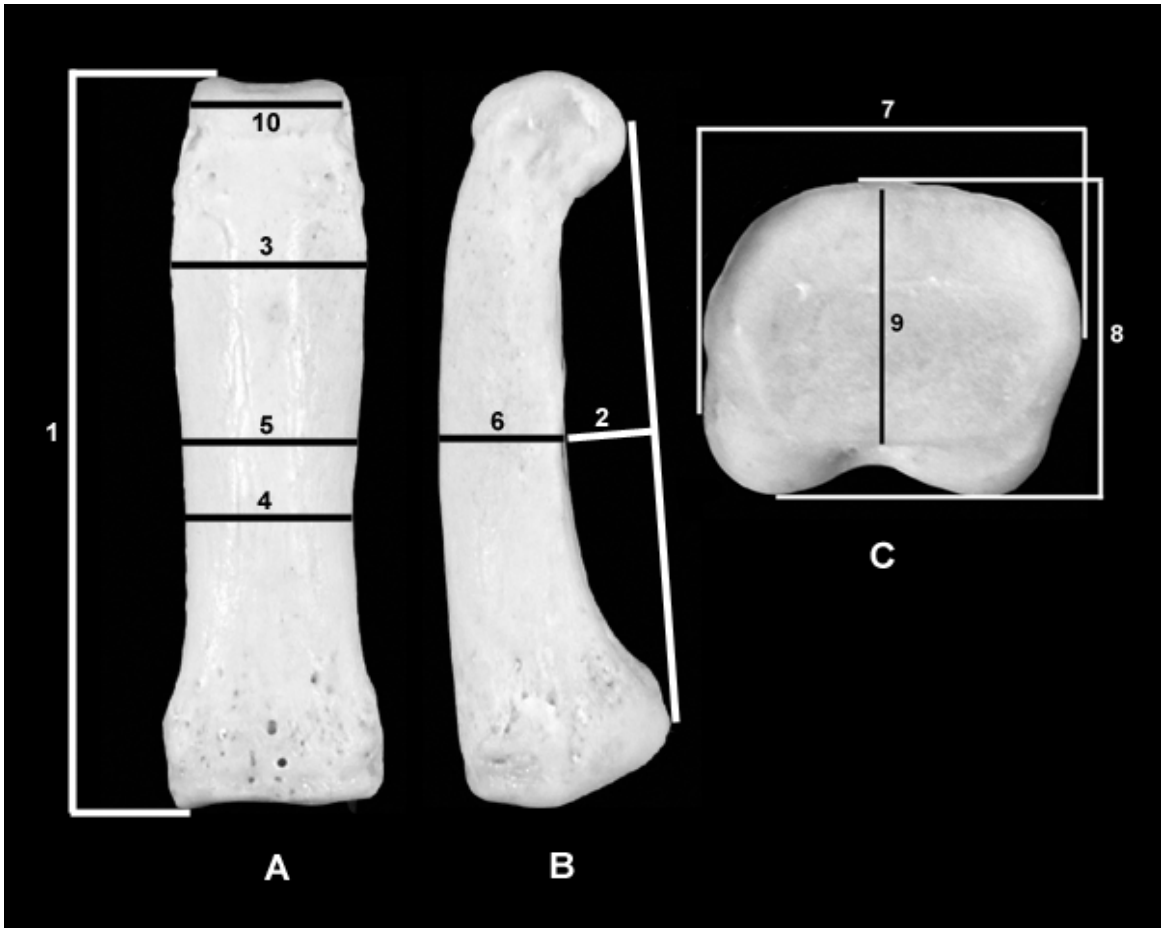


Figure 2.9. Measurements of the third proximal hand phalanx, illustrated on *P. troglodytes*. A (dorsal view): 1, length; 3, maximum shaft width; 4, minimum shaft width; 5, radio-ulnar midshaft diameter; 10, trochlear width. B (medial view): 2, height of arch; 6, dorso-palmar midshaft diameter. C (proximal view): 7, base width; 8, maximum base height; 9, articular base height.

Measurements are defined in Tables 2.4 and 2.7. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

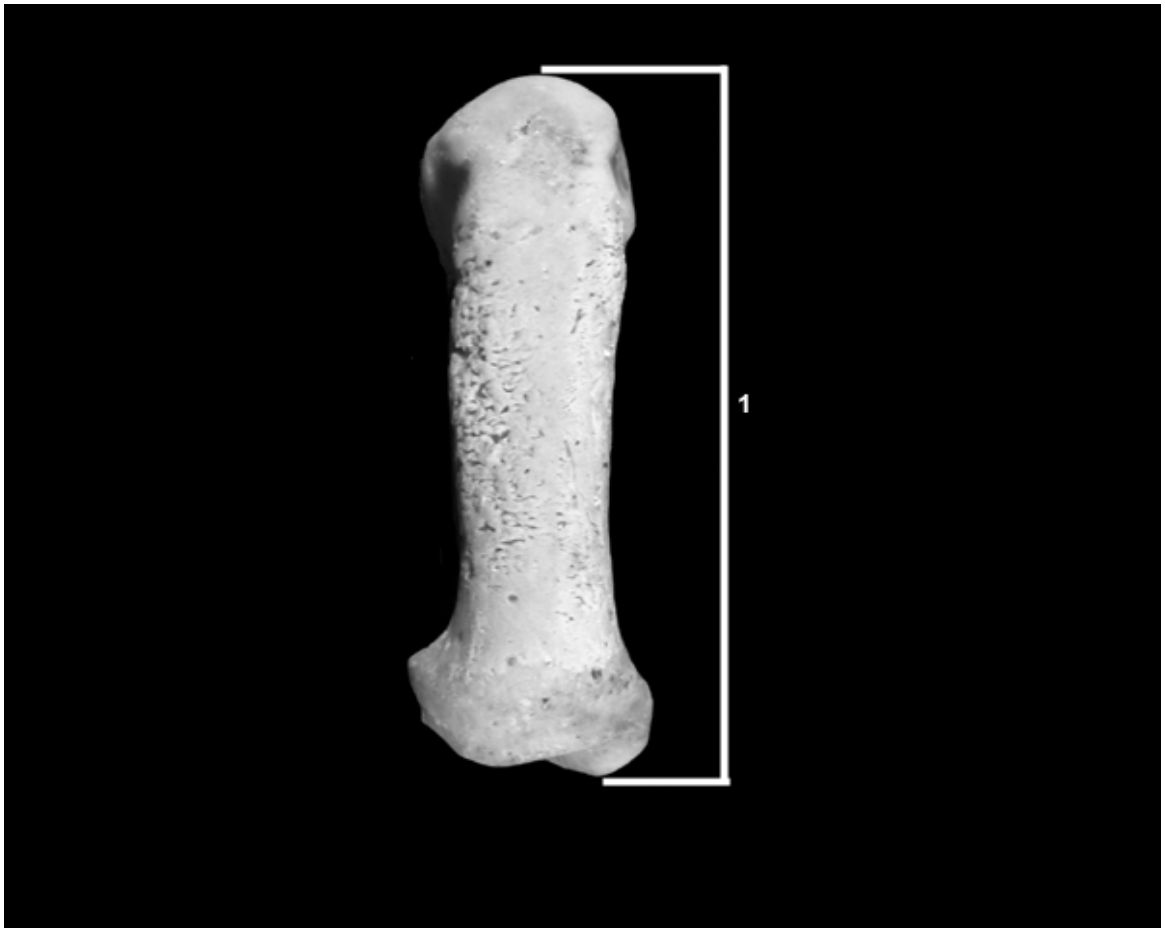


Figure 2.10. Measurements of the first metatarsal, illustrated on *P. troglodytes*. 1, length.

Measurement is defined in Table 2.4. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

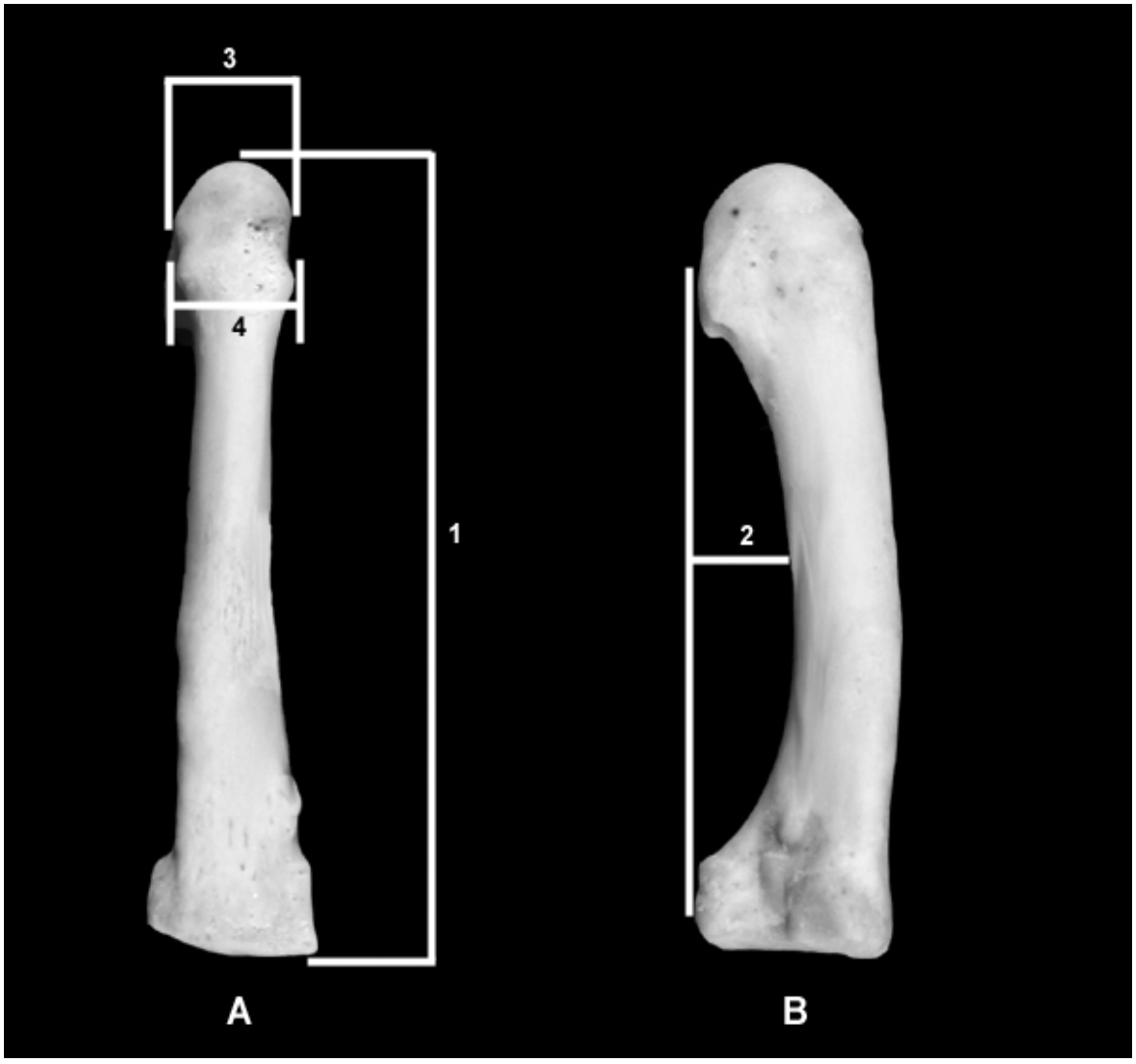


Figure 2.11. Measurements of the third metatarsal, illustrated on *P. troglodytes*. A (dorsal view): 1, length; 3, head width; 4, biepicondylar width. B (medial view): 2, height of arch.

Measurements are defined in Tables 2.4 and 2.7. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

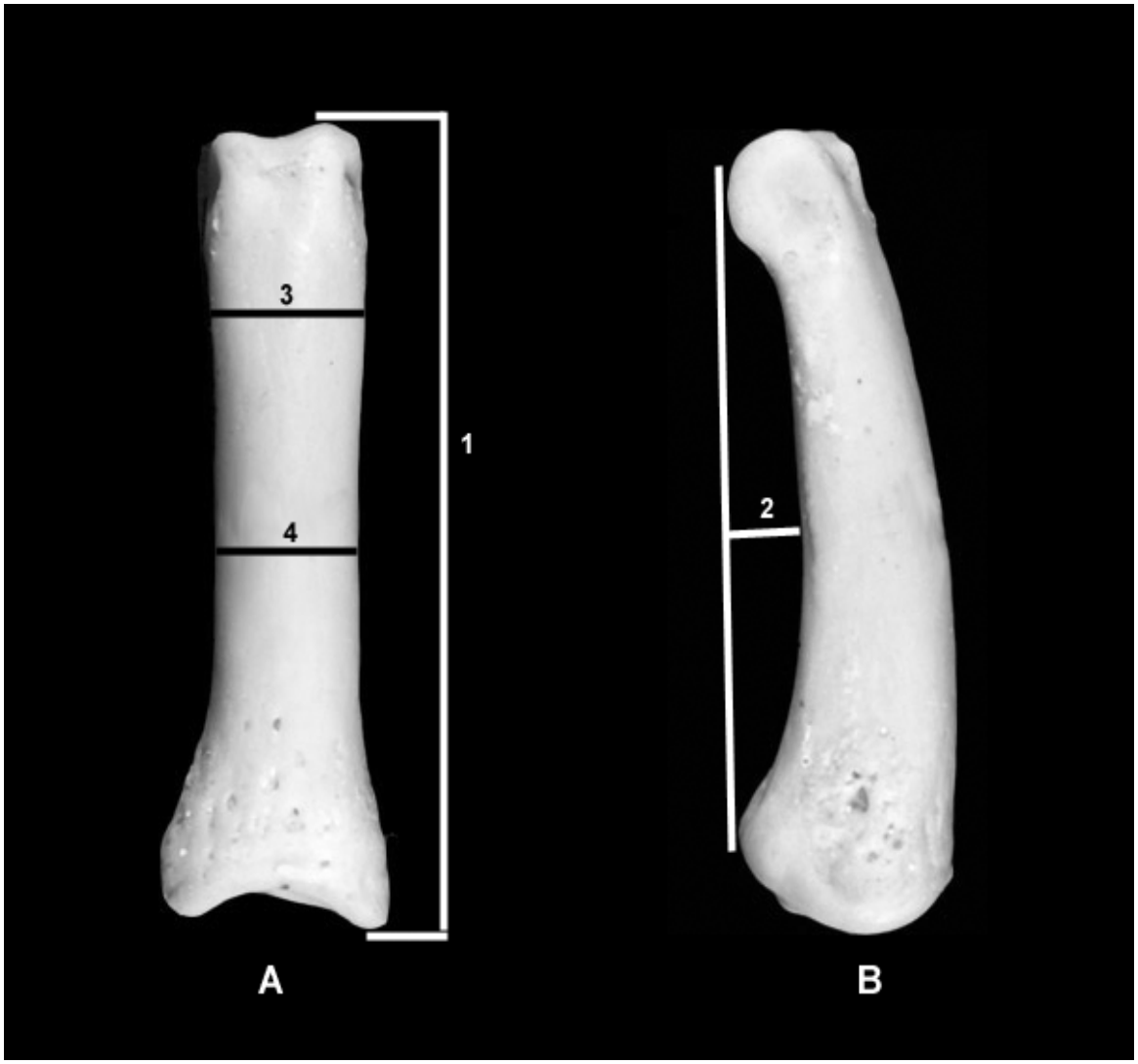


Figure 2.12. Measurements of the third proximal foot phalanx, illustrated on *P. troglodytes*. A (dorsal view): 1, length; 3, maximum shaft width; 4, minimum shaft width. B (medial view): 2, height of arch.

Measurements are defined in Tables 2.4 and 2.7. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

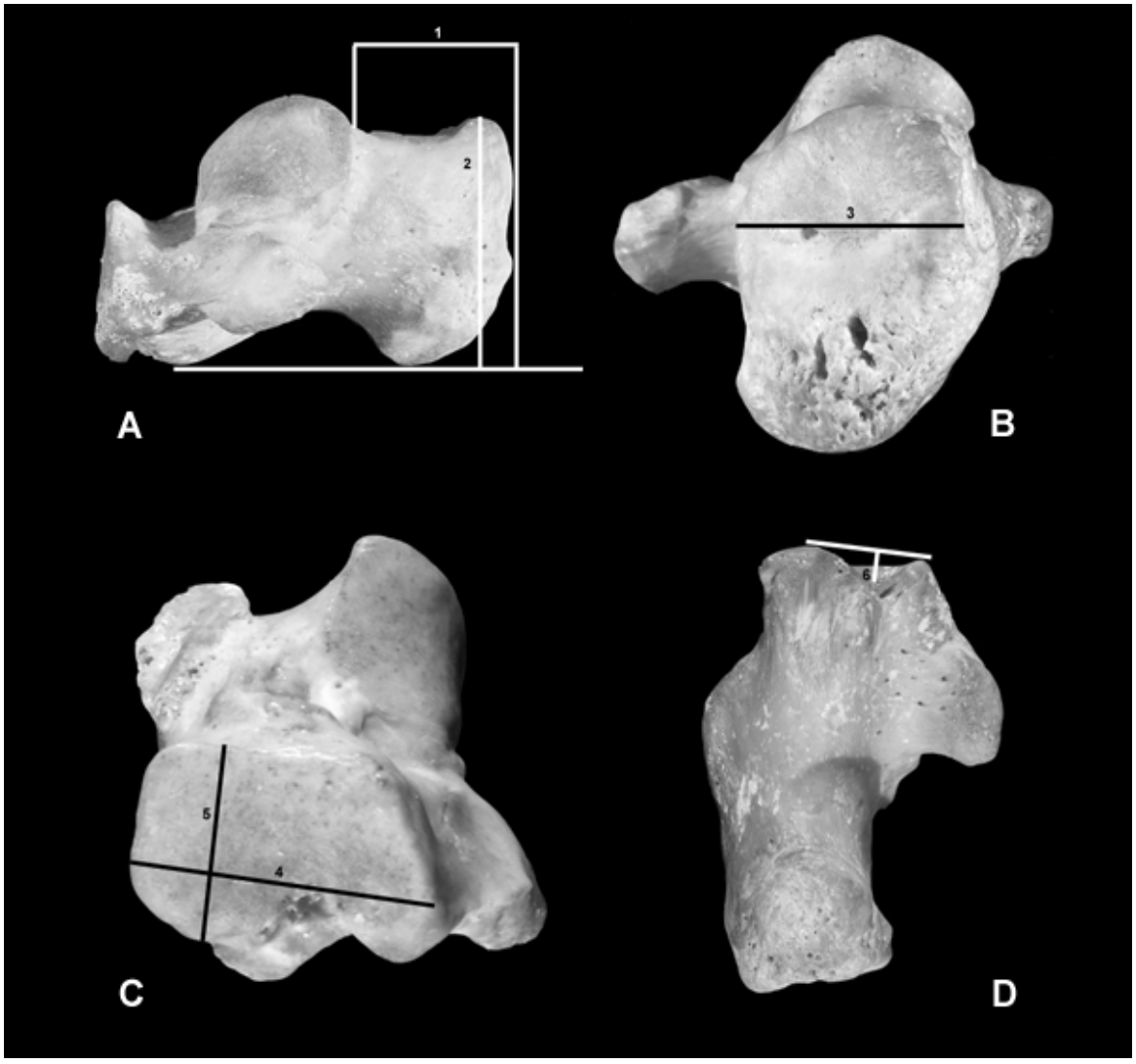


Figure 2.13. Measurements of the calcaneus, illustrated on *P. troglodytes*. A (medial view): 1, tuberosity length; 2, tuberosity height. B (proximal view): 3, tendon facet width. C (distal view): 4, cuboid facet width; 5, cuboid facet height. D (plantar view): 6, cuboid facet depth.

Measurements are defined in Tables 2.4 and 2.7. Illustrations serve only to aid in visualization. Illustrations are adapted from images made available by The eSkeletons Project (http://www.eskeletons.org/).

*Hand and foot ratios*

Twenty-two ratios, calculated from thirty-two linear measurements of the hand and foot bones, were analyzed in the second set of analyses. The list of ratios includes thirteen from the hand and nine from the foot. The primary goal of this set of analyses is to address the same questions about patterns of geographic variation that are addressed by the analyses of raw variables, using a different methodological approach; however, the use of variables with postulated functional significance allows this set of analyses to explore potential adaptive differences between groups, as well. These ratios were selected because they were thought likely to reflect the relative frequency of positional behaviors which are either characteristically arboreal (climbing and suspension) or characteristically terrestrial (knuckle-walking). The ratios are listed and defined in Tables 2.5 (listed by skeletal element) and 2.6 (listed by proposed functional significance), and the linear measurements on which they are based are listed and defined in Table 2.7. Most of these linear measurements are also among those included in the analyses of raw measurements, but the two sets of measurements are presented in separate tables to facilitate more targeted reference.

Variables of the hand and foot were chosen for this set of analyses because evidence from multiple areas of the literature suggests that hands and feet are especially likely to reflect potential functional and adaptive differences between geographic groups due to differences in habitat and positional behavior. During locomotor behaviors and many postural behaviors, the hands and feet interact directly with the behavioral substrate or superstrate, which places them under great functional stresses, exposing them both to selective pressures and also to the effectors of dynamic skeletal change. More

specifically, in the literature of hominoid functional morphology, the bones of the hand and foot have been thought to reflect varying locomotor adaptations more than other limb elements.

The list of ratios used in the analysis was developed by first searching the primate comparative morphology literature for hand and foot bone features which have been proposed to relate to relative arboreality and terrestriality and by then adding two original features to the list based on consideration of the anatomy and locomotor kinematics of African apes. If features had not already been described as measurement ratios or indices, ratios were designed to best reflect them, and new ratios were designed for some features which had been previously described as ratios or indices. The resulting list of ratios includes measures of inter-element length proportions, midshaft shapes, shaft curvatures (arch heights), articular surface shapes, and tendon and ligament attachments. The source or sources for each ratio and its proposed functional relevance are detailed and explained in Appendix 1.

Because many of these features were originally studied and published as ratios or indices, and ratios can provide indications of shapes or proportions which are sometimes more relevant to functional interpretation than linear measurements or scaled linear measurements, the decision was made to use ratios for a set of analyses exploring geographic variation in morphology that has been associated with variation in substrate use and positional behavior. Each ratio was designed so that a higher value of the ratio reflects a greater proposed amount of the associated functional activity (either climbing and suspension or knuckle-walking).

Although these ratios of the hand and foot were selected because they were thought likely to have functional significance, it is important to note that, even if they are not actually functionally significant, they reflect morphology that may vary between geographic groups. Analysis of these ratios serves primarily as a second approach to investigating patterns of geographic variation, regardless of whether or not the ratios vary in relation to habitat and positional behavior. The selection of these particular ratios, however, does permit this study to investigate the extent to which geographic groups can be distinguished on the basis of features that have been described as functionally significant. It also allows this study to explore the possibility that observed geographic variation in postcranial morphology may be related to differences in ecology.

Table 2.5. Definitions of hand and foot ratios, listed by skeletal element[1]

***Hand***

Metacarpal 3
arch height ratio (MCAH) = height of arch/length
midshaft diameter ratio (MCM) = dorso-palmar midshaft diameter/radio-ulnar midshaft diameter
dorsal ridge height ratio (MCDR) = head height plus ridge/head height
head shape ratio (MCHS) = head width/head height
biepicondylar width ratio (MCB) = biepicondylar width/head width

Proximal hand phalanx 3
flexor sheath ridge size ratio (HPFS) = maximum shaft width/minimum shaft width
arch height ratio (HPAH) = height of arch/length
midshaft diameter ratio (HPMD) = dorso-palmar midshaft diameter/radio-ulnar midshaft diameter
base width ratio (HPBD) = base width/minimum shaft width
trochlear width ratio (HPTW) = trochlear width/minimum shaft width
glenoid plate tubercle size ratio (HPGT) = maximum base height/articular base height

Inter-element
phalanx-metacarpal length ratio (XPMC) = proximal hand phalanx 3 length/metacarpal 3 length
hand power arm:load arm ratio (XHPL) = metacarpal 3 head height(1/2)/proximal hand phalanx 3 length

***Foot***

Metatarsal 3
arch height ratio (MTAH) = height of arch/length
biepicondylar width ratio (MTB) = biepicondylar width/head width

Proximal foot phalanx 3
flexor sheath ridge size ratio (FPFS) = maximum shaft width/minimum shaft width
arch height ratio (FPAH) = height of arch/length

Calcaneus
cuboid facet shape ratio (CCFS) = cuboid facet height/cuboid facet width
cuboid facet depth ratio (CCFD) = cuboid facet depth/cuboid facet width
calcaneal tendon facet width ratio (CCTW) = tendon facet width/tuberosity height

Inter-element
phalanx-metatarsal length ratio (XPMT) = proximal foot phalanx 3 length/metatarsal 3 length
calcaneal tuberosity-metatarsal length ratio (XCMT) = calcaneal tuberosity length/metatarsal 3 length

[1] Definitions of measurements are given in Table 2.7.

Table 2.6. Definitions of hand and foot ratios, listed by proposed functional significance[1,2,3]

***Hand***

Arboreal

MC3 arch height ratio (MCAH) = MC3 height of arch/length
HP3 flexor sheath ridge size ratio (HPFS) = HP3 maximum shaft width/minimum shaft width
HP3 arch height ratio (HPAH) = HP3 height of arch/length
phalanx-metacarpal length ratio (XPMC) = HP3 length/MC3 length

Terrestrial

MC3 midshaft diameter ratio (MCM) = MC3 dorso-palmar midshaft diameter/radio-ulnar midshaft diameter
MC3 dorsal ridge height ratio (MCDR) = MC3 head height plus ridge/head height
MC3 head shape ratio (MCHS) = MC3 head width/head height
MC3 biepicondylar width ratio (MCB) = MC3 biepicondylar width/head width
HP3 midshaft diameter ratio (HPMD) = HP3 dorso-palmar midshaft diameter/radio-ulnar midshaft diameter
HP3 base width ratio (HPBD) = HP3 base width/minimum shaft width
HP3 trochlear width ratio (HPTW) = HP3 trochlear width/minimum shaft width
HP3 glenoid plate tubercle size ratio (HPGT) = HP3 maximum base height/articular base height
hand power arm:load arm ratio (XHPL) = MC3 head height(1/2)/HP3 length

***Foot***

Arboreal

MT3 arch height ratio (MTAH) = MT3 height of arch/length
FP3 flexor sheath ridge size ratio (FPFS) = FP3 maximum shaft width/minimum shaft width
FP3 arch height ratio (FPAH) = FP3 height of arch/length
CALC cuboid facet shape ratio (CCFS) = CALC cuboid facet height/cuboid facet width
CALC cuboid facet depth ratio (CCFD) = CALC cuboid facet depth/cuboid facet width
phalanx-metatarsal length ratio (XPMT) = FP3 length/MT3 length

Terrestrial

MT3 biepicondylar width ratio (MTB) = MT3 biepicondylar width/head width
CALC calcaneal tendon facet width ratio (CCTW) = CALC tendon facet width/tuberosity height
calcaneal tuberosity-metatarsal length ratio (XCMT) = CALC tuberosity length/MT3 length

[1] Definitions of measurements are given in Table 2.7.
[2] Variables described as "arboreal" are proposed to reflect arboreal positional behaviors. Variables described as "terrestrial" are proposed to reflect terrestrial positional behaviors.

[3] Skeletal elements are abbreviated as follows: MC3 = third metacarpal, HP3 = third proximal hand phalanx, MT3 = third metatarsal, FP3 = third proximal foot phalanx, CALC = calcaneus.

Table 2.7. Definitions of measurements used in hand and foot ratios

***Hand***

Metacarpal 3

**length**: maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher

**height of arch**: distance between most palmar point at midshaft and a chord connecting the most palmar points of head and base, measured by resting palmar surfaces of head and base on a stiff ruler and using upper jaws of caliper to measure distance between the ruler and the shaft

**radio-ulnar midshaft diameter**: radio-ulnar diameter at midshaft

**dorso-palmar midshaft diameter**: dorso-palmar diameter at midshaft

**head height**: maximum dorso-palmar diameter of head, not including dorsal ridge

**head height plus ridge**: maximum dorso-palmar diameter of head including dorsal ridge

**head width**: maximum radio-ulnar diameter of head

**biepicondylar width**: maximum distance across epicondyles, measured using flat surfaces of caliper jaws

Proximal Hand Phalanx 3

**length**: maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher

**height of arch**: distance between most palmar point of shaft at midshaft and a chord connecting the most palmar points of proximal and distal ends, calculated by adding flexor sheath ridge projection to unadjusted height of arch

- **unadjusted height of arch**: distance between most palmar point at midshaft (whether on shaft or ridges) and a chord connecting the most palmar points of proximal and distal ends, measured by resting palmar surfaces of proximal and distal ends on a stiff ruler and using upper jaws of caliper to measure distance between the ruler and the most palmar point
- **flexor sheath ridge projection**: projection of flexor sheath ridges beyond palmar surface of shaft at midshaft, measured using caliper depth gauge

**maximum shaft width**: maximum radio-ulnar shaft diameter

**minimum shaft width**: minimum radio-ulnar shaft diameter, measured using sharpened edges of caliper jaw points

**radio-ulnar midshaft diameter**: radio-ulnar diameter at midshaft

**dorso-palmar midshaft diameter**: dorso-palmar diameter at midshaft, calculated by subtracting flexor sheath ridge projection from d-p midshaft diameter plus ridges

- **dorso-palmar midshaft diameter plus ridges**: dorso-palmar diameter at midshaft, including projection of flexor sheath ridges, measured using flat surfaces of caliper jaws
- **flexor sheath ridge projection**: projection of flexor sheath ridges beyond palmar surface of shaft at midshaft, measured using caliper depth gauge

**base width**: maximum radio-ulnar diameter of base region, not limited to articular surface

**maximum base height**: maximum dorso-palmar diameter of base region, not limited to articular surface, measured holding caliper jaws perpendicular to long axis of shaft and using flat surfaces of caliper jaws
**articular base height**: maximum dorso-palmar diameter of articular surface of base, measured using points of caliper jaws
**trochlear width**: maximum radio-ulnar width of trochlea, not including epicondyles

***Foot***

Metatarsal 3
**length**: maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**height of arch**: distance between most plantar point at midshaft and a chord connecting the most plantar points of head and base, measured by resting plantar surfaces of head and base on a stiff ruler and using upper jaws of caliper to measure distance between the ruler and the shaft
**head width**: maximum medio-lateral diameter of head
**biepicondylar width**: maximum distance across epicondyles, measured using flat surfaces of caliper jaws

Proximal Foot Phalanx 3
**length**: maximum length, measured using flat surfaces of caliper jaws, with long axis of bone perpendicular to caliper jaws and dorsal surface of bone facing researcher
**height of arch**: distance between most plantar point of shaft at midshaft and a chord connecting the most plantar points of proximal and distal ends, calculated by adding flexor sheath ridge projection to unadjusted height of arch

> **unadjusted height of arch**: distance between most plantar point at midshaft (whether on shaft or ridges) and a chord connecting the most plantar points of proximal and distal ends, measured by resting plantar surfaces of proximal and distal ends on a stiff ruler and using upper jaws of caliper to measure distance between the ruler and the most plantar point
> **flexor sheath ridge projection**: projection of flexor sheath ridges beyond plantar surface of shaft at midshaft, measured using caliper depth gauge

**maximum shaft width**: maximum medio-lateral shaft diameter
**minimum shaft width**: minimum medio-lateral shaft diameter, using sharpened edges of jaws

Calcaneus
Orientation: Calcaneus is placed on a table, or held as if it were resting on a table, so that the long axis of the calcaneal tendon facet is dorso-plantar and the fossa of the cuboid facet opens in a plantar or slightly medio-plantar direction. If use of these two features results in contradictory orientations, use the one that appears to have a more typical orientation based on other landmarks.
**tuberosity length**: measured with calcaneus in defined orientation and tuberosity against a vertical plane (such as a stiff-sided box), using outside-facing jaws of caliper to

measure minimum distance between most posterior point of posterior talar facet and vertical plane

**tuberosity height**: measured with calcaneus resting on a metal ruler and held in researcher's hand, in defined orientation, measuring from bottom of ruler to dorsal-most tuberosity (thickness of ruler subtracted from measurement)

**tendon facet width**: maximum width of calcaneal tendon facet perpendicular to dorso-plantar axis, measured with points of caliper jaws (if tubercle has built up laterally and covered facet, lateral point of measurement may be projected onto tubercle)

**cuboid facet width**: maximum diameter of cuboid facet in approximately medio-lateral direction, orienting facet so that fossa opens in a plantar direction

**cuboid facet height**: maximum diameter of cuboid facet in approximately dorso-plantar direction, orienting facet so that fossa opens in a plantar direction

**cuboid facet depth**: depth of cuboid facet, measured with caliper depth gauge from stiff ruler placed across dorsal part of facet (thickness of ruler subtracted from measurement)

***Data collection***

Individuals were only included in the study sample if geographic origin was known, epiphyses were fused, and sex was recorded or could be determined with confidence. As some individuals were incomplete and did not preserve all skeletal elements included in the study, individuals were considered adult as long as epiphyses were fused on the skeletal elements included in any given analysis. Visible epiphyseal lines did not exclude a bone from analysis if the epiphyses appeared to be fully closed. If original catalog records did not include sex, sex determinations were made from the skull and dentition or, in the case of the extremely size-dimorphic gorilla, from the size of the postcranial skeletal elements.

Each skeleton was carefully inspected for major pathologies and anomalies. Decisions on whether to include or remove pathological and anomalous specimens were made on a case by case basis, paying particular attention to whether (and to what extent) observed pathologies and anomalies directly impacted the measurements to be collected and were likely to have affected locomotor behavior. Data were collected from the right side, if possible. If the right side was absent, pathological, or damaged, the left side was used.

Because measurements from the hand and foot were to be analyzed as ratios, as well as raw variables, efforts were made to use elements from one side only for each hand or foot. In four individual cases (2 *Gorilla* and 2 *Pan*), a complete measurement set for a hand or foot bone was obtained by combining measurements from the two sides, as both the right and the left element were damaged in different places. In each of these

four cases, although right and left measurement sets were combined, each of the resulting ratios was calculated from a numerator and denominator from the same side.

While identification and siding of most skeletal elements in the study was straightforward, identification and siding of third proximal hand and foot phalanges was quite challenging. Susman (1979) previously determined that the third proximal hand phalanges of gorillas and chimpanzees are longer and more symmetrical than the proximal phalanges of other hand rays, but he did not publish siding criteria, and no comparable published work was found on proximal foot phalanges. A study of articulated and disarticulated gorilla and chimpanzee hands was made, confirming and expanding the third proximal hand phalanx identification criteria given by Susman (1979) and permitting the development of siding criteria. A study of articulated and disarticulated gorilla and chimpanzee feet permitted the development of identification and siding criteria for third proximal foot phalanges. Because few specimens were available that were both naturally articulated, to verify ray number and side, and also prepared so the joint region morphology was clearly visible, these methods could not be tested on a large sample. Nevertheless, application of identification criteria to a complete set of right and left proximal hand or foot phalanges almost always permitted one pair of elements to be distinguished from the rest. While it is possible that the method did not always successfully identify the third proximal phalanges, the criteria were consistently applied to select the elements measured for this study. When the set of proximal phalanges was incomplete, interfering with seriation, identification was more difficult. Once two antimeric elements were identified as third proximal phalanges, siding criteria usually distinguished the two from one another, but idiosyncratic variation was high, and

some specimens could not be confidently sided. Difficulties in applying identification and siding criteria arose more frequently with foot phalanges than with hand phalanges.

Identification criteria used in this study for third proximal hand and foot phalanges (abbreviated HP3 and FP3, respectively), when seriated with other proximal phalanges of the hand or foot (as appropriate), are as follows:

*Gorilla* HP3 – longest, widest shaft

*Pan* HP3 – longest, widest shaft

*Gorilla* FP3 – longest, widest shaft

OR same length as FP4 but FP3 shaft is widest

[possible confusion with HP5, which is longer and is usually wider and less symmetrical]

*Pan* FP3 – longest, widest shaft

[possible confusion with HP5, which is longer and is usually less robust and more arched]

Siding criteria used in this study for third proximal hand and foot phalanges are based on the observation that third metacarpals and third metatarsals, which can be easily sided, almost always have asymmetrical heads. In the *Gorilla* and *Pan* third metacarpal and the *Gorilla* third metatarsal, the head projects further distally (bulges out more) on the ulnar/lateral side. In the *Pan* third metatarsal, the head leans laterally. The bases of the third proximal phalanges, which articulate with the metacarpal and metatarsal heads, have corresponding asymmetries that can be used to side isolated elements. Siding criteria used in this study are as follows:

*Gorilla* and *Pan* HP3

- The shorter and steeper side of the basal articular surface is ulnar.
- The deepest point of the basal articular surface is ulnar.
- The side of the base which points in a more proximal direction is ulnar.
- The palmar border of the base is angled disto-ulnarly.

*Gorilla* and *Pan* FP3

- The shorter and steeper side of the basal articular surface is lateral.
- The deepest point of the basal articular surface is lateral.
- The side of the base which points in a more proximal direction is lateral.

These siding criteria should be applied together as a suite of features and considered as a whole, keeping in mind that they all relate to the articulation of the phalanx with the asymmetrical head of the third metacarpal or third metatarsal. If double-checking is desired, each third proximal phalanx can be articulated with each third metacarpal or third metatarsal to find the best fit, if all four elements are present. For the hand, it is best to do this with the metacarpophalangeal joint in the hyperextended position.

Of the fifty-four linear measurements of forelimb and hindlimb bones required for the two sets of analyses (of raw measurements and of ratios), forty-four were collected using a Mitutoyo 150mm digital pointed jaw caliper (accurate to ±0.02 mm as reported by the manufacturer). Caliper measurements, which were taken to the nearest 0.01 mm, were recorded to an Excel spreadsheet using a Mitutoyo digital input tool. All measurements of the hand and foot bones, as well as half of the long bone measurements, were collected using calipers.

The remaining ten linear measurements, all from long bones, were calculated from three-dimensional landmarks collected with a MicroScribe 3DX digitizer from Immersion Corporation (accurate to ±0.23 mm as reported by the manufacturer). Coordinates for each landmark (point) were downloaded to an Excel spreadsheet using Immersion MicroScribe Utility Software. For each measurement, the Pythagorean Theorem was used to calculate the distance between two points. These ten measurements are indicated in Table 2.4 with the parenthetical note "3D landmarks".

Among the caliper measurements are midshaft diameters of the humerus, radius, femur and tibia. Before midshaft diameters could be collected from these bones, midshaft had to be located. This was done using an improvised and highly portable substitute for an osteometric board. A measuring tape was taped to a tabletop to serve as the horizontal measuring board. The bone was lined up at “zero” using a metal ruler held vertically at the “zero” end of the measuring tape. The length was then measured using a metal ruler lined up vertically at the other end of the bone. This length measurement was used only for determining the location of midshaft on these four bones and was not the same as the length measurement collected for analysis. In the case of the humerus, the deltoid tuberosity strongly influences the diameters at true midshaft; therefore, “midshaft” diameters of the humerus were taken at 40% of humeral length from the distal end, following Ruff (2002).

***Data analysis***

All data analysis was performed with SYSTAT 11 for Windows (2004). Data analysis included univariate and multivariate statistics to investigate variation among groups and Pearson correlations to examine the potential influence of size differences on

the results of the multivariate analyses. Significance levels were set at $p \leq 0.05$ for all analyses.

Multivariate analyses used in this study included principal components analysis (PCA) and discriminant function analysis (DFA). Both can be used to study patterns of geographic variation, but PCA is based on the total variance in the sample, blind to the group memberships of the individuals, while DFA relies on known group membership and is based on maximizing the differences between groups.

Principal components analysis works by finding a weighted combination of variables, known as a "component" (or factor), that accounts for the greatest amount of the total variance in the sample, without regard to group memberships. It then finds further components, each uncorrelated to previous components, that account for successively smaller amounts of the total variance. Individual specimens, labeled by group, can then be plotted on a graph according to their individual scores on components of interest (presumably high-numbered ones), with each axis of the graph representing a single component, and the amount of group separation and/or overlap on the various components can be visually assessed. This method is useful for exploring the extent to which group differences are reflected on the axes that account for the greatest amounts of total variance, from all sources, within the sample. It is also valuable for revealing patterns of clustering among groups. The correlation of each variable to a given component, referred to as its loading, indicates the extent to which it contributes to the positions of the cases on the component.

Discriminant function analysis also works by producing a weighted combination of variables, but this equation is essentially an attempt to classify as many cases as

possible into their correct groups by maximizing the differences between groups, and it is called a discriminant function. It can be used to compare how well different groups can be discriminated from one another when the objective of the analysis is specifically to separate groups and not to account for variance from other sources. Individual cases can be plotted on a graph according to their discriminant function scores to permit visual assessment of patterns of variation between groups. The coefficients of the variables can be compared to determine which variables contribute most to separating the groups.

The set of analyses based on raw linear measurements included comparisons of means and PCAs. Males and females were analyzed separately for comparisons of means and analyzed together for PCAs. Comparisons of means were conducted at the levels of species and subspecies. Principal components analyses were run separately for *Gorilla* and *Pan*, and results were plotted by species, subspecies, and population in order to explore patterns of geographic variation. Pearson correlation analyses were used to demonstrate the strong relationship between the first principal component and overall size, as measured by the geometric mean, permitting subsequent components to be interpreted as describing shape variation.

The set of analyses based on ratios of linear measurements from hand and foot bones included comparisons of means, DFAs, and PCAs. For all analyses, males and females were analyzed separately, and hands and feet were analyzed separately. Comparisons of means and DFAs were conducted at the levels of genus, species, subspecies, and population. Pearson correlation analyses were used to demonstrate that the subspecies-level discrimination revealed in the DFAs is probably unrelated or only

weakly related to body size. Principal components analyses were used to complement the DFAs at the subspecies level.

Two types of univariate analysis were employed for comparisons of means: two-sample t-tests and analysis of variance. Two-sample t-tests were used when only two samples were being compared. The two-sample t-test probabilities are based on separate variances, which is recommended when sample sizes are unequal (e.g., Zimmerman, 2004), and are reported both as uncorrected values and as Bonferroni-corrected values. Determinations of significance are based on Bonferroni-corrected values, but uncorrected values are also discussed. Analysis of variance (ANOVA) was used when three groups were being compared. In order to determine which pairs of means were significantly different in ANOVAs, probabilities were generated by post hoc tests using the Bonferroni method.

All PCAs were based on the correlation matrices. Although rotation of factor loadings is sometimes useful for refining PCA results, results from unrotated factor loadings were found to be adequate for the purposes of identifying broad patterns in the structuring of the data; all results reported in this study are from unrotated factor loadings. Note that the axes of PC score plots in Chapter 3 are labeled "factors" rather than "components". These plots are output from SYSTAT, which considers "factors" and "components" to be equivalent terms, although many workers do not.

In the set of analyses of raw measurements, PCA is the only multivariate method used to explore patterns of geographic variation. *Gorilla* and *Pan* were analyzed separately. For each genus, separate analyses were run for each of six sets of variables, with some variables overlapping between sets. The six sets of variables can be described

as follows: all variables, forelimb, hindlimb, long bones, hand, and foot. Forelimb variables include all measurements of the humerus, radius, third metacarpal, and third proximal hand phalanx. Hindlimb variables include all measurements of the femur, tibia, calcaneus, first metatarsal, third metatarsal, and third proximal foot phalanx. Long bone variables include all measurements of the humerus, radius, femur, and tibia. Hand variables include all measurements of the third metacarpal and third proximal hand phalanx, and foot variables include all measurements of the calcaneus, first metatarsal, third metatarsal, and third proximal foot phalanx.

In the set of analyses of hand and foot ratios, PCAs were used to assess variation among subspecies only. At the subspecies level, PCAs complement the DFAs, as groups are not predefined in PCAs, permitting a comparison between the structuring of predefined groups revealed by DFA and the structuring of ungrouped data revealed by PCA. In addition, it permits a comparison of which variables contribute most to the structuring revealed by each method. When reporting in the text the variables with the highest loadings (correlations to the component) on each component, all variables are included that have loadings with absolute values of 0.40 (an arbitrary cut-off value) or greater. This method is used as a complement to the subspecies-level DFAs, but not the genus-level or species-level DFAs, because differences between genera and species are clear from univariate comparisons of means alone, whereas univariate differences between subspecies (within a single species) are not as strong and usually not significant in more than one sex. Population-level DFAs are not complemented by PCAs, as separations between groups are already weak using DFAs, which maximize the differences between groups; group separation using PCAs would be as weak or weaker.

Discriminant function analysis (DFA) is employed only in the set of analyses of hand and foot ratios. The classical linear discriminant analysis option available in SYSTAT was used. Prior probabilities were set as equal for all groups. Variables were selected using three models: complete, backward stepwise, and forward stepwise. The complete model includes all variables. For stepwise models, the program automatically removes the variable least useful for discriminating between groups (backward stepwise) or enters the variable that contributes the most to discriminating between groups (forward stepwise) at each step, according to specified threshold criteria, until the final model is reached. The matrix inversion tolerance limit was set to the default of 0.001. For the stepwise procedures, the thresholds for removing or entering variables were both set to the default probability value of 0.15. The model with the best rate of correct classification in the jackknifed classification matrix was chosen for each analysis. Reported rates of correct classification are from the jackknifed classification matrix and are rounded to the nearest whole-number percentage. When reporting in the text the variables which contribute the most to each canonical discriminant function, all variables are included which have coefficients with absolute values of 0.40 (an arbitrary cut-off value) or greater in the standardized function, and they are listed in order of descending coefficient magnitude.

The small sample sizes available for some groups analyzed in the study posed a challenge in the effort to follow the usual DFA sample size guidelines. According to convention, a DFA should include no more variables than the number of cases in the smallest group. Unfortunately, in six analyses in the study, the model with the best rate of correct classification, using the jackknifed classification matrix, had more variables

than the number of cases in one of the analyzed groups. If this study were more limited in scope, there would be a simple solution to this problem: remove the variables which make the smallest contributions to discriminating the groups, and re-run the analysis with fewer variables. This is the solution used in a recent study of eastern chimpanzees by Groves (2005). As the current study, however, depends on comparing the results of many different analyses to one another and looking for patterns in the results, removing variables from a few analyses to address sample size concerns would make the results of the various analyses less directly comparable.

Fortunately, this sample size rule is only a rule of thumb (Colin Groves, pers. comm.). Large sample sizes relative to the number of variables are always preferred, but no statistical rule is violated if the rule of thumb is broken. The one firm rule on sample size, based on actual mathematical limits, is that the number of variables may not be larger than the degrees of freedom of the within-groups covariance matrix, which is calculated as the sum of all sample sizes minus the number of groups (F. James Rohlf, pers. comm.). Breaking this rule results in a singular covariance matrix and undefined computations. No analysis in this study violates this statistical rule of minimum sample size.

As a further reassurance, cross-checks on each analysis are built into the study design. Study questions are addressed by comparing the results of multiple analyses, across sexes, across hands and feet, across taxonomic levels, and across taxa, in order to detect broad patterns of variation. Major conclusions do not rest on the results of any one analysis.

Pearson correlation analysis is used in the set of analyses of raw measurements to address the potential effects of size on the PCAs. In all PCAs, the first principal component (Component 1) appeared to reflect the effects of size by separating males and females and, in the case of *Pan*, by separating species. Pearson correlation analyses of Component 1 scores and geometric means found very high Pearson correlation coefficients and very low probability values for all PCAs, suggesting that Component 1 could be considered to account for size differences in the sample. Shape differences (meaning non-size-correlated morphology) could then be assessed on the basis of the other principal components.

In the set of analyses of hand and foot ratios, Pearson correlation analysis was conducted at the subspecies level only. This analysis is used to investigate the possibility of a relationship between body size and the morphology-based discrimination between subspecies obtained from the DFAs. Because direct measurements of body size are not available for the vast majority of specimens, a geometric mean of a set of measurements from the forelimb and hindlimb was used as a body size proxy. This geometric mean was calculated from all variables defined for the principal components analyses of raw measurements (listed in Table 2.4). Pearson correlation coefficients were calculated for the associations between canonical scores from the DFAs and the body size proxy (geometric mean), and the significance of the correlations was tested with Bonferroni-corrected probabilities. The Pearson correlation coefficients are considered to indicate a strong relationship between the variables at $r > 0.7$ (absolute value), following Harcourt-Smith (2002), with the justification that a correlation coefficient with a smaller absolute

value indicates that the body size proxy accounts for less than half of the variance of the DFA score, because $r^2 < 0.49$.

***Distributions of ratio data***

Due to the concerns of some authors about the statistical properties of ratio data (e.g., Atchley et al., 1976), the distributions of ratio data in this study were investigated and considered. The Shapiro-Wilks test, which is appropriate for all sample sizes in the study, was used to explore how well the distribution of each variable fits the normal distribution. Distributions were tested for each variable in each sample at the levels of genus and species, with males and females sampled separately. Most variables were found to have a poor fit to the normal distribution ($p \leq 0.05$) in at least one of the samples tested, and multiple variables with poor fits were found even in the largest samples.

These results might be expected, whether the variables are linear measurements or ratios. The nested hierarchical structure of the biological groups being studied would suggest that the upper levels of the hierarchy would not exhibit normal distribution of variables, even though the sample sizes are large, because each genus-level sample is made up of two species which are predicted to have different group means, and each species-level sample is made up of multiple subspecies which are predicted to have different group means. In other words, because each upper-level group is made up of multiple populations, geographically and reproductively distanced from one another, there is no reason to expect the variables in these upper-level groups to display the statistical properties of variables in single populations. Because we would not necessarily expect variables to be normally distributed under these circumstances, poor

fits of variables to the normal distribution in a study sample should not be taken as an indication that the sample is unrepresentative of the group from which it is drawn.

Aside from this theoretical consideration, attempting to weed out non-normally distributed variables would lead to a practical problem. In order to compare the results of analyses in *Gorilla* and *Pan*, and in males and females, the list of variables must be the same for each analysis. If each variable which showed a poor fit to the normal distribution in a single sample were removed from all of the analyses, even at a single hierarchical level of the analysis (e.g., species-level), few variables would remain. For example, for the species-level analyses of hand variables, 10 out of 13 variables would have to be removed. If the analyses at the different hierarchical levels were to be made comparable, as well, even more variables would be lost.

One possible cause of a non-normal distribution is the presence of outliers. A complication of working with multivariate analyses, however, is that one outlying variate cannot be removed without removing the entire case from the analysis. For this reason, it was appropriate to explore whether individuals with an extreme value for one variable were otherwise unusual. In one exploration of this question, univariate outliers for all hand and foot variables were identified using box plots of data grouped at the species level. Out of nine outlying values, only two were from the same individual. To put it another way, out of eight individuals with outlying values, only one individual had more than one outlying value. In another exploration of the question, variables were identified which do not show a good fit to the normal distribution (according to the Shapiro-Wilks test) for a given species and sex, and individuals with the minimum and maximum values for those variables were located. All values for these individuals were inspected,

demonstrating that individuals with minimum or maximum values for one variable tend to have non-extreme values for all or almost all other variables. In summary, specimens at the extremes of variation for any given variable appear to be normal individuals with a single extreme variate, and, overall, there is no reason to think they are not representative of the groups from which they were drawn.

Of course, the assumption of normality is ultimately a mathematical issue, and the above discussion is not relevant if non-normally distributed variables will prevent the analyses from producing useful results. Fortunately, the potential impact of non-normally distributed variables on this study appears to be low. First, discriminant function analysis, which forms the core of the set of analyses based on ratios, has been found to be robust to non-normality (e.g., Lestrel, 2000; Klecka, 1980). Although computed probabilities may not be exactly correct if the assumption of normality is violated, results may still be useful if exact probabilities are not required (Klecka, 1980). As outliers are a potential cause of non-normal distribution, and discriminant function analysis is less robust to outliers than to other sources of non-normality, a small test was conducted of the impact of outliers in this study. All species-level discriminant function analyses were run both with and without the outliers identified by the box plots, and the results were quite similar, both in the rate of correct classification and in which variables contributed the most to discrimination between groups. Second, an experiment with subspecies-level ANOVAs for this study suggests that univariate outliers in this dataset have only a minor impact on the results. Each subspecies-level ANOVA which both showed a significant difference ($p \leq 0.05$) between at least one pair of groups and identified one or more outliers was re-run without the outlier(s). Out of 12 such analyses,

all still showed significant differences between the same pairs of groups after the outliers were removed.

If this study had a much narrower focus, it might be worthwhile to report results with and without non-normally distributed variables or with and without outliers; however, given the large number of analyses on which results are based and the small apparent impact of these data issues, overall results are unlikely to differ. Since the goal of this study is to reveal broad patterns in the data and not to set up precise models, the use of non-normally distributed variables and the inclusion of outliers appears to be justified.

# CHAPTER 3

## RESULTS: Analyses of raw measurements

This chapter includes results of the analyses of raw measurements. Measurement definitions can be found in Table 2.4. The chapter is organized into two main sections, one for the comparisons of means and one for the principal components analyses. Each main section is divided into a section for *Gorilla* results and a section for *Pan* results. Results of the comparisons of means are reported for species-level and subspecies-level analyses. Results of the principal components analyses are reported in relation to variation at the levels of species, subspecies, and populations.

Tables in this chapter use abbreviations to refer to variables. Table 2.4 includes abbreviations, but variables are listed by their descriptive names. For the reader's ease of reference, variables are listed by their abbreviations, with descriptive names following the abbreviations, in Appendix 3, Table 1.

### Comparisons of means

Comparisons of means at the species level were conducted using two-sample t-tests. Results include both uncorrected and Bonferroni-corrected p-values. As forty-three measurements were compared between species, the Bonferroni correction is rather large, and many uncorrected p-values that are less than or equal to 0.05 are above this significance level once the correction is applied. Consequently, both uncorrected and corrected p-values are discussed, because the goal of these comparisons is not to conduct strict tests of significant differences between groups but to identify, based on the study sample, which measurements vary the most between species and which measurements

exhibit large differences between species in both males and females. At the same time, differences are described as "significant" only when Bonferroni-corrected p-values are less than or equal to 0.05. References to "low uncorrected p-values" describe uncorrected p-values less than or equal to 0.05. Results of comparisons of means provide a foundation for discussing the differences between the species and for interpreting the principal components analyses.

Comparisons of means at the subspecies level were accomplished with one-way ANOVAs. Results are based on post hoc significance tests of pairwise comparisons.

Descriptive statistics for raw measurements, by species and by subspecies, are tabulated in Appendix 4.

### *Gorilla*

#### Species

Results of the two-sample t-tests for raw measurements of forelimb and hindlimb elements in the two species of *Gorilla*, *G. beringei* and *G. gorilla*, are summarized in Table 3.1. Descriptive statistics for these raw measurements in the two *Gorilla* species are tabulated in Table 1 of Appendix 4.

##### Forelimb

In evaluating forelimb differences, it is useful to consider the humerus and radius separately from the hand elements. Eleven measurements of the humerus and radius were assessed, separately for males and females, and a significant difference between species was found in only one comparison. One measurement of the radius, the antero-posterior midshaft diameter, is significantly greater in *G. gorilla* females than in *G.*

*beringei* females. In males, this measurement is also greater, although non-significantly so, in *G. gorilla*, with a low uncorrected p-value. In addition, the distal width of the radius is greater in *G. gorilla* to the extent that the uncorrected p-values are low in both sexes, although the difference is not significant in either sex when Bonferroni corrections are applied. No measurements of the humerus are significantly different between species.

Differences between the species are more marked in the two hand elements than in the humerus and radius. Two measurements of the third metacarpal are significantly greater in *G. gorilla* than in *G. beringei* in both sexes. These two measurements are length and biepicondylar width. In addition, third metacarpal head width is greater in *G. gorilla*, with low uncorrected p-values in both sexes, although this difference is not significant in either sex. Four measurements of the third proximal hand phalanx are significantly greater in *G. gorilla* in both sexes: length, minimum shaft width, base width, and trochlear width.

In sum, six forelimb measurements are significantly different in both sexes, and they are all measurements of the hand. One further measurement, which is not from the hand, is significantly different in females only. In all of these comparisons, the *G. gorilla* mean is significantly greater than that of *G. beringei*. Further, of the twenty-one forelimb measurements, the *G. beringei* mean is (non-significantly) greater for only three measurements based on the male sample and five measurements based on the female sample. Only one of these measurements for which *G. beringei* has the greater mean is a hand bone measurement, and *G. beringei* has the greater mean for this measurement in one sex only.

The measurements of the third metacarpal and third proximal phalanx that are significantly different between the species seem to reflect a pattern across the two elements. In both hand bones, bone lengths and most widths of articular regions differ significantly between species in both sexes. The one articular measurement that does not differ significantly between the species, third metacarpal head width, has low uncorrected p-values for both sexes. In contrast, shaft measurements of these hand bones are not consistently different between species. Neither shaft measurement of the third metacarpal is significantly different, and only one of two phalangeal shaft measurements is significantly different.

Hindlimb

Similarly to the forelimb, it is useful to discuss the femur and tibia separately from the elements of the foot. Of the nine measurements of the femur and tibia, only two are significantly different between species. One measurement of the femur, antero-posterior midshaft diameter, is significantly greater in *G. beringei* males than in *G. gorilla* males; in females, it is non-significantly greater in *G. beringei*, with a low uncorrected p-value. One measurement of the tibia, tibia length, is significantly greater in *G. gorilla* in both sexes.

Differences between species are more dramatic in the foot. All seven measurements of the pedal ray bones are significantly greater in *G. gorilla* in both sexes. These measurements are first metatarsal length; third metatarsal length, head width, and biepicondylar width; and third proximal foot phalanx length, maximum shaft width, and minimum shaft width. Of the six calcaneus measurements, three are significantly different in one or both sexes. Calcaneus tendon facet width and cuboid facet depth are

significantly greater in *G. gorilla* in both sexes. In males, cuboid facet width is significantly greater in *G. gorilla*; it is non-significantly greater in *G. gorilla* females, with a low uncorrected p-value. Additionally, low uncorrected p-values for comparisons of calcaneus length call attention to greater values for this measurement in both sexes of *G. gorilla*.

Ten hindlimb measurements are significantly different between species in both sexes, and all but one are measurements of foot elements. Two further measurements, one of which is from the foot, are significantly different in males only. Every significantly different measurement from the foot is greater in *G. gorilla*. Only one measurement of the foot is (non-significantly) greater in *G. beringei*. As with the hand, bone lengths and articular regions show strong differences between the species. Results from shaft measurements of the foot bones cannot be directly compared with results from the hand, as there are no metatarsal shaft measurements to compare with metacarpal shaft measurements, but the third proximal foot phalanx shaft measurements are both significantly different between species, whereas only the minimum shaft width was significantly different in the third proximal hand phalanx. Of all the foot measurements, calcaneus tuberosity length and height showed the weakest differences between the species.

In the femur and the tibia, the size differences between the species, while not great, run in opposite directions in the two elements. In the tibia, the one significantly different measurement, tibia length, is greater in *G. gorilla* for both sexes. Of the remaining tibia measurements, two out of three in each sex are non-significantly greater in *G. gorilla* than in *G. beringei*, including one measurement, medio-lateral midshaft

diameter, which has a low uncorrected p-value in females. In contrast, the femur appears to be slightly larger in *G. beringei*. The antero-posterior midshaft diameter of the femur is significantly greater in *G. beringei*, and the *G. beringei* mean for this measurement is also greater in females, with a low uncorrected p-value. Femoral head height in males also has a low uncorrected p-value, and the *G. beringei* mean for this measurement is greater in both males and females. Overall, four of the five femoral measurements have a greater mean, in both sexes, in *G. beringei*.

Summary

The clearest difference between *G. gorilla* and *G. beringei* that presents itself in comparisons of means of forelimb and hindlimb measurements is that the hand and foot elements of *G. gorilla* are larger than the hand and foot elements of *G. beringei*. In particular, the third metacarpal, first and third metatarsals, and third proximal phalanges are all significantly longer in both sexes of *G. gorilla*. Calcaneal length also follows this pattern, but differences are not great enough to be significant after the Bonferroni correction is applied. Most measurements of articular regions in hand and foot elements are also significantly larger in *G. gorilla*.

Patterns are more difficult to detect in comparisons of means of measurements of the humerus, radius, femur, and tibia. Three measurements are significantly different, in one or both sexes, in these elements. *Gorilla gorilla* has the greater mean for only two of these three significantly different measurements. Taking into consideration both significant and non-significant differences in this sample for each element, *G. gorilla* appears to have slightly larger measurements, in general, of the humerus, radius, and tibia, but *G. beringei* appears to have slightly larger measurements of the femur. Two of

the three significantly different measurements are antero-posterior midshaft diameters, but even these measurements do not agree in their direction of variation. In the radius, antero-posterior midshaft diameter is significantly greater in *G. gorilla*; in the femur, it is significantly greater in *G. beringei*. Aside from the hand and foot, size differences between species of *Gorilla* in the forelimb and hindlimb skeleton cannot be easily characterized; the two species are generally similar, and overlap greatly (see Table 1 of Appendix 4), in their measurements.

**Subspecies**

Three subspecies of *Gorilla* have adequate samples for statistical comparisons of means: *G. b. beringei, G. b. graueri,* and *G. g. gorilla*. These three subspecies represent both species of *Gorilla*. As there is not yet broad consensus on whether two species of *Gorilla* should be recognized, subspecies-level comparisons of means include comparisons both within *G. beringei* and between *G. beringei* and *G. gorilla*.

Comparisons of means for *Gorilla* subspecies were accomplished with one-way ANOVAs including all three of the subspecies for which samples are adequate for analysis: *G. b. beringei, G. b. graueri*, and *G. g. gorilla*. Results of post hoc significance tests of pairwise comparisons are reported in Tables 3.2 – 3.4. Descriptive statistics for raw measurements, by subspecies of *Gorilla*, are tabulated in Table 2 of Appendix 4.

This study also includes data from three specimens of *G. g. diehli*, two males and an apparent female. One of the males only includes four study elements, and the female only includes one. Measurement data from these three specimens are discussed in comparison with the ranges of measurements from the other three subspecies of *Gorilla*. Raw data for *G. g. diehli* specimens are reported in Table 3 of Appendix 4.

Subspecies comparisons across species:

*G. g. gorilla* vs. *G. b. beringei* and *G. g. gorilla* vs. *G. b. graueri*

As the two subspecies of *G. beringei* share many differences with *G. g. gorilla*, results of comparisons of means between *G. g. gorilla* and each of the *G. beringei* subspecies are discussed together. Comparisons of measurement means between *G. g. gorilla* and *G. b. beringei* and between *G. g. gorilla* and *G. b. graueri* are summarized in Table 3.2 and Table 3.3, respectively.

Similarities between the two subspecies of *G. beringei* in their differences with *G. g. gorilla* are particularly evident in the hand and foot. In all significant differences of the hand and foot, the mean for *G. g. gorilla* is greater than the mean for the *G. beringei* subspecies. Six measurements of the hand and nine measurements of the foot are significantly different between *G. g. gorilla* and both subspecies of *G. beringei* (in at least one sex): third metacarpal length and biepicondylar width; third proximal hand phalanx length, minimum shaft width, base width, and trochlear width; calcaneus tendon facet width, cuboid facet width, and cuboid facet depth; first metatarsal length; third metatarsal length and biepicondylar width; and third proximal foot phalanx length, maximum shaft width, and minimum shaft width. This list is almost identical to the list of hand and foot measurements that are significantly different (in at least one sex) between the species *G. gorilla* and *G. beringei*; the latter list also includes third metatarsal head width.

The remaining two measurements, outside of the hand and foot, that are significantly different between *G. g. gorilla* and both subspecies of *G. beringei* (in at least one sex) are also significantly different (in at least one sex) between *G. gorilla* and

*G. beringei*. They are femur antero-posterior midshaft diameter, which is significantly smaller in *G. g. gorilla*, and tibia length, which is significantly greater in *G. g. gorilla*. One further measurement, radius antero-posterior midshaft diameter, is significantly different when the two species means are compared but is only significantly different in one subspecies-level comparison.

There are three other measurements that are significantly different in both sexes between *G. g. gorilla* and one of the *G. beringei* subspecies but not in either sex when *G. g. gorilla* is compared to the other *G. beringei* subspecies; *G. b. graueri* is the *G. beringei* subspecies in all of these significant differences. These measurements are third metacarpal head width, calcaneus tuberosity height, and third metatarsal head width. In each case, the greater mean is found in *G. g. gorilla*. Note that two of these measurements, head widths of the third metacarpal and third metatarsal, are homologous measurements of the hand and foot. Measurements that are significantly different between subspecies in only one sex of one pairwise comparison are not listed here, but some are discussed below in order to inform discussion of significant differences between *G. b. beringei* and *G. b. graueri*.

Subspecies comparisons within *G. beringei*:

*G. b. beringei* vs. *G. b. graueri*

Comparisons of measurement means between *G. b. beringei* and *G. b. graueri* are summarized in Table 3.4.

Significant differences between the two subspecies of *G. beringei* are found in only six variables, five of which show significant differences in only one sex. Sample sizes are somewhat small in both of these subspecies, which may limit the ability of the

tests to identify true differences between them. The six variables are humerus distal articular width, third metacarpal radio-ulnar midshaft diameter, femur head height, tibia medio-lateral midshaft diameter, calcaneus tuberosity height, and third metatarsal head width.

The one measurement that is significantly different in both sexes is calcaneus tuberosity height. This is one of the three measurements that are significantly different in both sexes between *G. g. gorilla* and *G. b. graueri* but not between *G. g. gorilla* and *G. b. beringei*. Male and female *G. b. graueri* have smaller means for this measurement than do males and females of the other subspecies.

Four of the remaining five measurements, which show significant differences in only one sex, also show a significant difference between *G. g. gorilla* and one of the *G. beringei* subspecies. These measurements are humerus distal articular width, femur head height, tibia medio-lateral midshaft diameter, and third metatarsal head width. Bringing together the results of the different pairwise comparisons for each of these measurements clarifies which subspecies among the three is unusual. For humerus distal articular width, *G. b. beringei* is significantly smaller than both *G. b. graueri* and *G. g. gorilla* in males. It is non-significantly smaller than the other subspecies in females. For femur head height, *G. b. graueri* is significantly larger than both of the other subspecies in males and non-significantly larger in females. For tibia medio-lateral midshaft diameter, *G. b. graueri* is significantly smaller than the other subspecies in females, but the subspecies are very similar in males. Finally, for third metatarsal head width, *G. b. graueri* is significantly smaller than both other subspecies in males, significantly smaller than *G. g. gorilla* in females, and non-significantly smaller than *G. b. beringei* in females.

*G. g. diehli*

The three *G. g. diehli* specimens in this study include one male with all study elements present; one male with only humerus, radius, and femur; and one apparent female with only a radius. The apparently female radius is one of three radii included with the incomplete male specimen (ZMB 12791); all three radii are marked with what appears to be the specimen's original number (perhaps a field or accession number), "Gorilla 5 Oboni", and the apparently female radius is much smaller than the other two radii. Oboni is the locality from which the specimen was collected.

*Gorilla gorilla diehli* would be predicted to be closest to the *G. g. gorilla* sample in its measurements, as these two subspecies are geographically proximate and are generally considered to belong to the same species. In fact, the measurements of the three *G. g. diehli* specimens always fall within the range of the *G. g. gorilla* sample, while they sometimes fall either below or above the range of *G. b. beringei* and/or *G. b. graueri*. Of course, it must be kept in mind that the sample sizes for the *G. beringei* subspecies are much smaller than those for *G. g. gorilla*, so it is possible that the ranges within the *G. beringei* samples are sometimes smaller than the ranges that would be seen if the samples for these subspecies were as large as those for *G. g. gorilla*.

Given the limitations of *G. g. diehli* sample sizes, concentrating on measurements that differ significantly between the two species may better focus the comparisons. Interestingly, bones of the manual and pedal rays show a different pattern than other skeletal elements with regard to where *G. g. diehli* measurements fall within the *G. g. gorilla* range. For each of the thirteen ray bone measurements that are significantly different between the two gorilla species, the one *G. g. diehli* specimen with hand and

foot bones, which is a male, falls at the low end of the *G. g. gorilla* range. The *G. gorilla* mean is greater than the *G. beringei* mean for each of these measurements, and the value of the *G. g. diehli* measurement is almost always closer to the *G. beringei* subspecies means. Outside of the ray bones, the *G. g. diehli* specimens, both the males and the apparent female, fall within the midrange of *G. g. gorilla* values for every measurement that is significantly different between species. For males, these significantly different measurements occur in the femur, tibia, and calcaneus. For females, only the single significantly different measurement of the radius was compared, as the *G. g. diehli* sample includes only a radius.

Summary

Not surprisingly, the differences between *G. g. gorilla* and each of the two *G. beringei* subspecies are greater than the differences between the two *G. beringei* subspecies. These differences reflect, to a large extent, the differences already observed between *G. gorilla* and *G. beringei*. The strongest signal that comes across in comparisons between *G. g. gorilla*, *G. b. beringei*, and *G. b. graueri* is that *G. g. gorilla* has significantly larger hand and foot skeletons than the two subspecies of *G. beringei*, while other elements are more similar in size. Interestingly, the very small sample of *G. g. diehli* hints at the possibility that differences between *G. g. gorilla* and its congener may follow the same pattern, although more data are clearly needed. At the very least, the apparent differences observed between *G. g. gorilla* and the very small sample of *G. g. diehli* serve as a reminder that the *G. gorilla* sample in this study is made up almost entirely of *G. g. gorilla* specimens, and differences observed between the two gorilla

species in this study may be more accurately described as differences between the species *G. beringei* and the subspecies *G. g. gorilla*.

To summarize, *G. g. gorilla* is significantly larger than both *G. b. beringei* and *G. b. graueri*, in at least one sex for each comparison of subspecies, in the following measurements of the hand and foot: third metacarpal length and biepicondylar width; third proximal hand phalanx length, minimum shaft width, base width, and trochlear width; calcaneus tendon facet width, cuboid facet width, and cuboid facet depth; first metatarsal length; third metatarsal length and biepicondylar width; and third proximal foot phalanx length, maximum shaft width, and minimum shaft width. In measurements outside of the hand and foot, *G. g. gorilla* is significantly larger than the two subspecies of *G. beringei* in tibia length and significantly smaller in femur antero-posterior midshaft diameter, in at least one sex for each comparison. In addition, a few measurements are significantly greater or smaller in one of the *G. beringei* subspecies in comparison with both *G. g. gorilla* and the other *G. beringei* subspecies, in at least one sex for each comparison of subspecies. Based on these results, *G. b. beringei* has an especially narrow distal articular width of the humerus, *G. b. graueri* has an especially large femoral head height, and *G. b. graueri* has an especially small calcaneal tuberosity height, medio-lateral midshaft diameter of the tibia and head width of the third metatarsal.

The two subspecies of *G. beringei* do not differ in the same ways that *G. gorilla* differs from *G. beringei*. Only one of the six measurements that are significantly different, in at least one sex, between *G. b. beringei* and *G. b. graueri* is among the measurements that are significantly different between the two species of *Gorilla*. This measurement is third metatarsal head width. The other five measurements are humerus

distal articular width, third metacarpal radio-ulnar midshaft diameter, femur head height, tibia medio-lateral midshaft diameter, and calcaneus tuberosity height. Unlike the pattern of differences between *Gorilla* species, differences between the *G. beringei* subspecies are not concentrated in the hands and feet.

## *Pan*

### Species

Results of the two-sample t-tests for raw measurements of forelimb and hindlimb elements in the two species of *Pan*, *P. paniscus* and *P. troglodytes*, are summarized in Table 3.5. Descriptive statistics for these raw measurements in the two *Pan* species are tabulated in Table 4 of Appendix 4.

#### Forelimb

Means were compared for twenty-one measurements of the forelimb, and the two species of *Pan* were found to be significantly different, in one or both sexes, in nineteen of them. For every significant difference, in either sex, *P. troglodytes* has the greater mean. Further, the *P. troglodytes* mean is greater for every forelimb measurement, in either sex, whether the difference is significant or not.

Of the four forelimb elements in the study, the third proximal hand phalanx is the most different between the two species; every measurement, in both sexes, is significantly larger in *P. troglodytes*. In the humerus, every measurement is significantly different in males, but two measurements are not significantly different in females, although they both have low uncorrected p-values. These two measurements are length and biepicondylar width. Differences in the radius and third metacarpal are less

consistently strong. In the radius, distal width is not significantly different in either sex, and length is not significantly different in females. In the third metacarpal, length is not significantly different in either sex, biepicondylar width is significantly different in both sexes, and three further measurements are significantly different in one sex only.

Two patterns are apparent upon examination of the non-significant differences. The first is that, when differences are significant for one sex and not the other, the females are usually the sex without a significant difference. This is the case even though the sample sizes of *P. paniscus*, which are small enough that they might be thought to limit the potential for significant results, are larger for females than for males for every measurement. The second is that, among females, the two species of *Pan* are poorly differentiated by bone lengths, with the exception of the third proximal hand phalanx, in which all measurements are significantly different between species.

Hindlimb

Of twenty-two measurements of the hindlimb, seven are significantly different, in one or both sexes, in the two species of *Pan*, and *P. troglodytes* has the greater mean in every significant difference. *Pan paniscus* has the greater mean in only five of the non-significant comparisons (in one sex for each of three measurements and in both sexes for one measurement). Further, four of these five comparisons are of calcaneus measurements, and the fifth, which is from the tibia, has nearly identical means for the two species. *Pan troglodytes* has the greater mean for every measurement, in both sexes, in the femur, first metatarsal, third metatarsal, and third proximal foot phalanx.

The femur is significantly different between species, in one or both sexes, in two measurements. Medio-lateral midshaft diameter is significantly greater in *P. troglodytes*

in both sexes. Head height is significantly greater in *P. troglodytes* males and is non-significantly greater, with a low uncorrected p-value, in *P. troglodytes* females. Low uncorrected p-values in both sexes for bicondylar width suggest this measurement may also be different between species, with greater means in *P. troglodytes*.

No measurement is significantly different between species in the tibia. Only the interspecific difference in tibial plateau width is great enough that the uncorrected p-values are low in both sexes, with the greater mean in *P. troglodytes*.

Of the six measurements of the calcaneus, only tuberosity height is significantly different between species. The mean for *P. troglodytes* is significantly greater in females and nonsignificantly greater, with a low uncorrected p-value, in males. The width of the tendon facet is also greater in *P. troglodytes*, with low uncorrected p-values in both sexes.

*Pan troglodytes* has a greater mean than *P. paniscus*, in both sexes, for every pedal ray bone measurement. First metatarsal length is significantly greater in *P. troglodytes*, in both sexes. No significant differences, however, are found in the third metatarsal, although low uncorrected p-values in both sexes suggest a potential difference in head width. All three measurements of the third proximal foot phalanx are significantly different, in one or both sexes, with a non-significant difference (having a low uncorrected p-value) found only in maximum shaft width in females.

As with the hand, the third proximal phalanx of the foot differentiates the two species particularly strongly. Another pattern seen in the forelimb is seen more strongly in the hindlimb. While forelimb bone lengths, with the exception of third proximal hand phalanx length, poorly differentiate species in females, hindlimb lengths poorly

differentiate species in both sexes, with the exception of third proximal foot phalanx and first metatarsal lengths.

Summary

Significant differences in limb bone measurements of *P. troglodytes* and *P. paniscus* all indicate that *P. troglodytes* has larger forelimb and hindlimb skeletons than *P. paniscus*. More significant size differences are observed in the forelimb than in the hindlimb. Non-significant differences reinforce the observations that *P. troglodytes* has larger limb bones and that the two species are more different in the forelimb than in the hindlimb. Differences are particularly strong in the third proximal phalanges of the hand and foot. As bone length is such a frequently-employed metric, it is worth noting that, although this study indicates that *P. troglodytes* has larger limb bones overall than *P. paniscus*, forelimb and hindlimb bone lengths do not consistently reflect this.

**Subspecies**

Subspecies-level comparisons of means for *Pan* are conducted only within *P. troglodytes*, as no subspecies of *P. paniscus* have been recognized. Three subspecies of *P. troglodytes* are represented by both males and females in this study's dataset: *P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus*. *Pan troglodytes vellerosus* is only represented by females, and only six specimens are included in this study's dataset; further, the sample size for this subspecies is as small as three specimens for some measurements.

Comparisons of means for *Pan* subspecies were accomplished with one-way ANOVAs including all three of the subspecies for which both male and female samples

are available: *P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus*. Results of post hoc significance tests of pairwise comparisons are reported in Tables 3.6 – 3.8. Descriptive statistics for raw measurements in these three subspecies of *P. troglodytes* are tabulated in Table 5 of Appendix 4.

As the comparisons of means are discussed in terms of results for both sexes, the *P. t. vellerosus* sample does not fit into this analysis. Further, including the all-female *P. t. vellerosus* sample in the ANOVAs would result in different numbers of groups in the male and female ANOVAs, leading to unbalanced Bonferroni corrections in the results for the two sexes. For these reasons, and because of small *P. t. vellerosus* sample sizes, observations are made on the relationship of female *P. t. vellerosus* means to the means of females of the other subspecies, but differences in means are not statistically analyzed. Descriptive statistics for raw measurements in *P. t. vellerosus* are tabulated in Table 6 of Appendix 4.

*P. t. verus* vs. *P. t. schweinfurthii*

As *P. t. verus* and *P. t. schweinfurthii* have more geographic distance between them than any other pair of *P. troglodytes* subspecies, and might be surmised on that basis to have accumulated the most differences, results of comparisons of measurement means are assessed for this pair of subspecies first and are summarized in Table 3.6. In fact, of forty-three measurements, only one shows a significant difference between these two subspecies. Humerus medio-lateral midshaft diameter is significantly greater in *P. t. schweinfurthii* males than in *P. t. verus* males. This measurement is non-significantly greater in *P. t. schweinfurthii* females.

It is possible that the virtual absence of significant differences between the samples is an effect of small sample sizes in both subspecies being compared. In any case, there is no strong tendency in either sex for one subspecies to have larger measurements than the other, suggesting that overall sizes are similar. At the same time, for any given measurement, there is a tendency for the mean to be greater in the same subspecies for both sexes, suggesting that small sample sizes have not obscured the signal and shape differences between the subspecies may be present.

*P. t. verus* vs. *P. t. troglodytes*

When mean measurements for *P. t. verus* and *P. t. troglodytes* are compared (Table 3.7), it is clear that the forelimb and hindlimb skeletons of *P. t. troglodytes* are larger overall. The *P. t. troglodytes* mean is greater in every significant difference between the two subspecies, and it is non-significantly greater in most of the remaining comparisons, especially in males.

Of the forty-three measurements, ten are significantly different in at least one sex. Significant differences are found in the humerus, radius, third proximal hand phalanx, femur, tibia, and third proximal foot phalanx. No significant differences are found in the third metacarpal, calcaneus, first metatarsal, and third metatarsal.

Four measurements are significantly different in both sexes: humerus medio-lateral midshaft diameter, third proximal hand phalanx maximum shaft width, femur antero-posterior midshaft diameter, and tibia antero-posterior midshaft diameter. Six additional measurements are significantly different in one sex but not the other: radius medio-lateral midshaft diameter, third proximal hand phalanx length, femur head height, tibia length, and third proximal foot phalanx length and minimum shaft width. In each of

these six cases, the *P. t. troglodytes* mean is also greater, but non-significantly so, in the other sex. The *P. t. verus* mean is greater, but not significantly greater, in only two of the forty-three male comparisons and nine of the forty-three female comparisons.

In addition to the observations that *P. t. troglodytes* limb bones appear to be larger, three interesting patterns present themselves. The first relates to the midshaft diameters of the large long bones (as opposed to the small long bones in the hand and foot). In the forelimb, both the humerus and the radius show significant differences in medio-lateral midshaft diameter, while in the hindlimb, both the femur and tibia show significant differences in the antero-posterior midshaft diameter. Second, the phalanges are the only hand and foot bones with significant differences in measurements. Third, both the hand and foot phalanges show significant differences in length.

*P. t. schweinfurthii* vs. *P. t. troglodytes*

Results of comparisons of means between *P. t. schweinfurthii* and *P. t. troglodytes* are summarized in Table 3.8. As with comparisons between *P. t. verus* and *P. t. troglodytes*, it is clear that the forelimb and hindlimb skeletons of *P. t. troglodytes* are larger overall. Once again, in every significant difference, *P. t. troglodytes* has the greater mean, and the *P. t. troglodytes* mean is non-significantly greater in most of the remaining comparisons. On the other hand, many of the measurements in which *P. t. schweinfurthii* differs from *P. t. troglodytes* are different from the measurements in which *P. t. verus* and *P. t. troglodytes* differ.

Differences between *P. t. schweinfurthii* and *P. t. troglodytes* are more pronounced in males. No hindlimb measurements are significantly different in females.

A number of significantly different measurements of the humerus and the hand and foot phalanges are found in males, but none are found in females.

Significant differences between *P. t. schweinfurthii* and *P. t. troglodytes*, in one or both sexes, are seen in nineteen of the forty-three measurements. At least one significant difference is found in every element except the first and third metatarsals.

Only one measurement, radius medio-lateral head diameter, is significantly different in both sexes. Eighteen more measurements are significantly different in one sex. The *P. t. troglodytes* mean is also greater, but not significantly greater, in the other sex for all but two of those eighteen measurements. In those remaining two measurements, the *P. t. schweinfurthii* mean is only very slightly greater than the *P. t. troglodytes* mean in the other sex.

The nineteen measurements that differ significantly between *P. t. troglodytes* and *P. t. schweinfurthii* are listed here by element. In the humerus, they include antero-posterior midshaft diameter, head height, distal articular width, and biepicondylar width. In the radius, they include the medio-lateral head diameter. In the third metacarpal, they include radio-ulnar midshaft diameter, head width, and biepicondylar width. In the third proximal hand phalanx, they include length, maximum shaft width, minimum shaft width, and base width. In the femur, they include medio-lateral midshaft diameter and bicondylar width. In the tibia, they include medio-lateral midshaft diameter and plateau width. In the calcaneus, they include tendon facet width. Finally, in the third proximal foot phalanx, they include length and minimum shaft width.

There is very little overlap between the measurements that are significantly different in *P. t. schweinfurthii* and *P. t. troglodytes* and those that are significantly

different in *P. t. verus* and *P. t. troglodytes*. The only elements in which these measurements overlap are the phalanges. The *P. t. troglodytes* mean is significantly greater than the means of both other subspecies, in at least one sex, for the following measurements: third proximal hand phalanx length and maximum shaft width, and third proximal foot phalanx length and minimum shaft width.

*P. t. vellerosus*

As explained above, because only female *P. t. vellerosus* individuals are included in the study sample, and sample sizes for some measurements are very small, observations are made here on the relationship of female *P. t. vellerosus* means to the means of females of the other subspecies, but differences in means are not statistically analyzed.

The mean of the *P. t. vellerosus* sample is smaller than the mean of the female *P. t. troglodytes* sample for all but nine of the forty-three measurements. Six of those nine exceptions are measurements of the foot. When the *P. t. vellerosus* sample is compared to the *P. t. troglodytes* sample for the phalangeal measurements that are significantly larger in the latter taxon compared to both *P. t. schweinfurthii* and *P. t. verus* (third proximal hand phalanx length and maximum shaft width, and third proximal foot phalanx length and minimum shaft width), it has the smaller mean for all four measurements, but the only measurement for which it is markedly smaller is the maximum shaft width of the hand phalanx. Measurements from the *P. t. vellerosus* sample do not tend to be consistently smaller or consistently larger than those from either *P. t. schweinfurthii* or *P. t. verus*. The only measurement for which the mean of the *P. t. vellerosus* sample appears exceptional in relation to all three of the other subspecies samples is the cuboid facet

depth of the calcaneus. The *P. t. vellerosus* mean is greater than the means of the other subspecies, and especially greater than the *P. t. verus* mean, for this measurement.

Summary

The clearest signal from the subspecies-level comparisons of means is that *P. t. troglodytes* has slightly larger forelimb and hindlimb skeletons, overall, than *P. t. schweinfurthii* and *P. t. verus*. *Pan troglodytes schweinfurthii* and *P. t. verus* do not appear to differ in overall limb bone size, although it must be kept in mind that the sample sizes for these two subspecies are much smaller than those for *P. t. troglodytes*. Means from the small, all-female sample of *P. t. vellerosus*, while not statistically compared to those of the other subspecies, suggest that the limb skeletons of this subspecies may be similar in overall size to those of *P. t. schweinfurthii* and *P. t. verus* and smaller than those of *P. t. troglodytes*.

Two shared patterns are observed when comparing significant differences between *P. t. troglodytes* and each of the subspecies *P. t. schweinfurthii* and *P. t. verus*. The first is that the only measurements that are significantly larger in *P. t. troglodytes*, in at least one sex, in comparison to *both* of the other two subspecies are certain measurements of the phalanges. The second is that phalangeal length is among those measurements for both the third proximal hand phalanx and the third proximal foot phalanx.

When the significant differences among this study's samples of these three subspecies are all compared to one another, and the sexes are examined separately, the following measurement means stand out for being exceptional in one subspecies (but only in males in each case): humerus medio-lateral midshaft diameter is particularly

narrow in *P. t. verus* males; third proximal hand phalanx maximum shaft width is particularly large in *P. t. troglodytes* males; and third proximal foot phalanx minimum shaft width is particularly large in *P. t. troglodytes* males. While significant differences between *P. t. troglodytes* and the other two analyzed subspecies (*P. t. schweinfurthii* and *P. t. verus*) are also found in phalangeal lengths, these are not listed here because the significant differences are not found in the same sex for both pairwise comparisons; these measurements are significantly larger in *P. t. troglodytes* females when compared with *P. t. verus* females and in *P. t. troglodytes* males when compared with *P. t. schweinfurthii* males.

It is informative to compare the patterns observed in the differences between *Pan* species to the patterns observed in the differences between *P. troglodytes* subspecies. First, more significant differences between species are seen in the forelimb than in the hindlimb. This pattern is not generally seen in subspecies-level comparisons. Second, differences between species are particularly evident in the third proximal phalanges of the hand and foot. This pattern is also seen when subspecies are compared. Finally, although *P. troglodytes* limb bones have greater dimensions than *P. paniscus* limb bones, in general, this difference is not clearly seen in bone lengths. Similarly, although *P. t. troglodytes* has greater limb bone dimensions than the other subspecies, in general, bone lengths do not clearly reflect this difference. A notable exception in both the species-level and subspecies-level comparisons is that phalangeal lengths differ significantly between taxa.

These comparisons must be qualified by pointing out that *P. t. troglodytes* makes up most of the *P. troglodytes* sample. Comparisons between *P. troglodytes* and *P.*

*paniscus* are heavily weighted toward differences between *P. t. troglodytes* and *P. paniscus*. In this light, it is not surprising to find similarities in the ways in which taxa differ at both the species and subspecies levels, as differences at both levels are heavily influenced by any ways in which *P. t. troglodytes* is especially different from all other *Pan* groups.

## Principal components analyses

Principal components analyses were conducted on six separately-analyzed sets of variables, which can be described as follows: all variables, forelimb, hindlimb, long bones, hand, and foot. Results of each analysis are discussed with regard to variation at the levels of species, subspecies, and populations.

Effects of size must be considered and set aside before shape differences between groups can be assessed. As explained in Chapter 2, Pearson correlation analysis of principal component (PC) scores and geometric means is used in this set of analyses to address the potential effects of size on the principal components analyses.

### *Gorilla*

Tables 3.9 – 3.14 report eigenvalues, percent of total variance explained, and component loadings for the first five components of each of the six principal components analyses of *Gorilla* measurements.

In all six principal components analyses of the *Gorilla* sample, Component 1 separates males and females. Due to the great size dimorphism between the sexes of *Gorilla* (see Table 1 of Appendix 4), separation on the basis of sex can be reasonably suggested to reflect separation on the basis of size. In fact, for every one of the six

principal components analyses, Pearson correlation analysis of Component 1 scores and geometric means results in a very high Pearson correlation coefficient (the lowest value of the six analyses is $r = 0.9935$) with a probability of $p < 0.0001$ (Table 3.15). On the basis of these results, Component 1 can be considered to account for size differences within the *Gorilla* sample in each principal components analysis, and shape differences can be assessed using the other components.

**Species and subspecies**

Variation at the levels of species and subspecies is discussed in this section, while variation at the population level is discussed in the next section. Preliminary inspection of scatterplots indicated that all analyses of *Gorilla* measurements separate both species and subspecies within the first several components after Component 1 and separation between taxa tends to diminish greatly after the fourth or fifth component. Consequently, the first five components of each analysis were inspected carefully for patterns of species-level and subspecies-level variation, and results reported in this section include observations from these components only.

All variables

Table 3.9 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of all limb variables together.

Component 1 explains 78.70% of the total variance. Within the cluster for each sex, the *G. beringei* specimens cluster toward the lower PC scores but remain almost entirely within the range of *G. gorilla* (Figure 3.1). As the females have lower PC scores than the males and the female measurements are generally smaller than the male

measurements, the position of the *G. beringei* specimens within each sex cluster can be interpreted to mean that this species has smaller measurements, in general, than *G. gorilla* for the variables in this study.

Examination of the shape components, meaning the components following the size-correlated Component 1, reveals separation of the two species of *Gorilla* on Component 2 (Figure 3.2), which explains 4.40% of the total variance. The variables with the highest loadings on Component 2 are minimum shaft width of the third proximal foot phalanx, cuboid facet depth of the calcaneus, biepicondylar width of the third metatarsal, and antero-posterior midshaft diameter of the femur. These variables are all among the hindlimb variables that are significantly different between the two species in both sexes. The variables with the next highest loadings, after the four listed above, are the lengths of the third metatarsal and third metacarpal, homologous measurements of the hindlimb and forelimb that are also significantly different between the two species in both sexes.

Components 3 and 4 both achieve some separation of the two subspecies of *G. beringei* (Figures 3.3 and 3.4), while Component 5 does not. Component 3 explains 2.72% of the total variance, and Component 4 explains 2.00% of the total variance. A large number of variables in Component 3 have loadings in a similar range to one another, and it is not possible to select a few that appear to make particularly great contributions in comparison to the others, but the higher loadings tend to be for bone lengths and shaft diameters, while the lower loadings tend to be for articular dimensions. It is much clearer which variable drives Component 4; cuboid facet depth of the calcaneus has a much higher loading on this component than any other variable. The

variables that contribute the most to these two components are not predictable from the comparisons of means. Only one variable, tuberosity height of the calcaneus, is significantly different between the two subspecies in both sexes, and its loading is very low on both components. The variable with the highest loading on Component 3 is medio-lateral midshaft diameter of the tibia, which is significantly different between the two subspecies in females only, but the other four variables that are also significantly different between subspecies in one sex are not among those that contribute most greatly to Component 3. Cuboid facet depth of the calcaneus, which strongly drives Component 4, is not significantly different between subspecies in either sex. This variable is discussed further in the section below on hindlimb variables.

The single specimen of *G. g. diehli* in this analysis falls within *G. gorilla* on Component 2, which separates the two species. It is among the *G. gorilla* specimens that lie closest to *G. beringei* along this component. When Components 3 and 4 are plotted against one another, the *G. g. diehli* specimen is located among the *G. gorilla* specimens that are overlapped by the *G. b. graueri* cluster and not by the *G. b. beringei* cluster (Figure 3.5).

Forelimb

Table 3.10 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of forelimb variables.

Component 1 explains 82.71% of the total variance. As in the analysis of all variables, the *G. beringei* specimens appear to be smaller than the *G. gorilla* specimens (Figure 3.6), clustering toward the lower PC scores within each sex cluster while remaining almost entirely within the range of *G. gorilla*.

Among the shape components, Component 2 separates the two species of *Gorilla* (Figure 3.7) and explains 3.31% of the total variance. The variables with the highest loadings on Component 2 include both of the third metacarpal measurements that are significantly different between species in both sexes: length and biepicondylar width. They also include third proximal hand phalanx length, which is significantly different between species in both sexes, but other phalangeal measurements that are also significantly different in both sexes have lower loadings on Component 2. Two midshaft diameters, medio-lateral midshaft diameter of the radius and antero-posterior midshaft diameter of the humerus, are among the variables with higher loadings on Component 2 but are not significantly different between species in either sex.

Component 3, which explains 2.59% of the total variance, separates the two subspecies of *G. beringei* somewhat (Figure 3.8). In addition, it clusters the *G. beringei* specimens at one end of the *G. gorilla* distribution. The *G. b. beringei* cluster is nearer the center of the *G. gorilla* distribution than is the center of the *G. b. graueri* cluster. The three variables with the highest loadings are a mix of those that distinguish the three *Gorilla* subspecies sampled here from one another, but none of them is significantly different when the two *Gorilla* species are compared. Humerus length, with the highest loading, is significantly greater in *G. g. gorilla* males than in *G. b. beringei* males; radio-ulnar midshaft diameter of the third metacarpal is significantly greater in *G. b. beringei* females than in *G. b. graueri* females; and radius length is significantly greater in *G. g. gorilla* females than in *G. b. graueri* females. Of the two forelimb measurements that are significantly different between the two *G. beringei* subspecies, each in only one sex, one (radio-ulnar midshaft diameter of the third metacarpal) has the second-to-highest loading

on Component 3, while the other (distal articular width of the humerus) has only a moderate loading in relation to the other variables.

The subspecies of *G. beringei* do not separate on Component 4 but do separate to some extent on Component 5, which explains 1.39% of the total variance. The variable that dominates Component 5 is the radio-ulnar midshaft diameter of the third metacarpal, which also has a high loading on Component 3.

When components 2 and 3 are plotted together (Figure 3.8), the single *G. g. diehli* specimen is among a small number of *G. gorilla* specimens overlapped by the *G. beringei* cluster and one of an even smaller number of *G. gorilla* specimens overlapped by the *G. b. graueri* cluster.

Hindlimb

Table 3.11 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of hindlimb variables.

Component 1 explains 76.84% of the total variance. Once again, the *G. beringei* specimens cluster toward the lower PC scores within each sex cluster, indicating smaller size in *G. beringei*, but remain almost entirely within the range of *G. gorilla* (Figure 3.9).

Inspection of shape components shows that this analysis separates the two species of *Gorilla* on Component 2 (Figure 3.10), which explains 6.33% of the total variance. The variables that load most highly on Component 2 are cuboid facet depth of the calcaneus, minimum shaft width of the third proximal foot phalanx, antero-posterior midshaft diameter of the femur, and biepicondylar width of the third metatarsal, followed at a distance by maximum shaft width of the third proximal foot phalanx. The four foot bone measurements are all significantly different between species in both sexes, and the

femur measurement is significantly different between species in males only, although the comparison of female means has a low uncorrected p-value.

The subspecies of *G. beringei* separate from one another on Component 3, which explains 3.69% of the total variance (Figure 3.11); little separation of subspecies is seen on Components 4 and 5. One variable, cuboid facet depth of the calcaneus, has a much higher loading on Component 3 than any other variable (as it also does on Component 4 of the analysis including all limb variables together and on Component 2 of the analysis of foot variables). Interestingly, this variable also has the highest loading on Component 2; it is significantly different between the species in both sexes, but it is not significantly different between the subspecies of *G. beringei* in either sex. Perhaps its effect on the arrangement of taxa on Component 3 can be understood by considering that this measurement is significantly greater in *G. g. gorilla* than in *G. b. beringei* in both sexes but significantly greater in *G. g. gorilla* than in *G. b. graueri* in males only. Also, the *G. b. graueri* mean for this variable is greater than the *G. b. beringei* mean in both sexes, although the difference is not significant. These observations suggest that Component 3 is not simply separating the two *G. beringei* subspecies but is placing each of the *G. beringei* subspecies in a different position relative to *G. gorilla* along its axis.

The single specimen of *G. g. diehli* falls comfortably within the *G. gorilla* cluster on Component 2, on the side of the *G. gorilla* cluster that is closer to the *G. beringei* cluster. Its position on Component 3 places it among the *G. g. gorilla* specimens that are overlapped by the *G. b. graueri* cluster and not by the *G. b. beringei* cluster.

Long bones

Table 3.12 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of variables from long bones (including humerus, radius, femur, and tibia but not hand and foot bones).

Component 1 explains 85.39% of the total variance. In contrast to the pattern seen in the other five analyses, the distribution of *G. beringei* cannot be readily distinguished from the distribution of *G. gorilla* within each sex cluster on Component 1 (Figure 3.12).

The shape components also indicate that differences between the species of *Gorilla* are responsible for a smaller portion of the total variance in the long bone analysis than they are in the other five analyses. The long bone analysis does not separate the two species of *Gorilla* on Component 2 but instead separates the two subspecies of *G. beringei* on this component (Figure 3.13), which explains 3.76% of the total variance. Among the females, there is very little overlap between the two subspecies, but there is much more overlap between male *G. b. beringei* and male *G. b. graueri*. Although Component 2 separates the two species of *Gorilla* in all of the other analyses, all of which include hand and foot bones, it does not separate species in the analysis of long bone variables. Although no variables have high loadings on Component 2, the pattern of loadings is clear. All lengths and midshaft diameters have higher loadings, and the loadings of all articular dimensions are lower.

Component 3, which explains 2.19% of the total variance, separates the two species of *Gorilla* (Figure 3.14). Two variables, antero-posterior midshaft diameters of the femur and radius, have markedly greater loadings than the other variables, although

no variables are very highly loaded. These two variables are two of the three long bone measurements that are significantly different between the species in at least one sex.

Although the species and subspecies of *Gorilla* are not distinguished on Component 4, Component 5 separates the subspecies of *G. beringei* to a similar extent as Component 2 (and explains 1.07% of the total variance). The antero-posterior midshaft diameter of the femur has the greatest loading. This is the same variable with the greatest loading on Component 3. The antero-posterior midshaft diameter of the tibia and the medio-lateral midshaft diameter of the radius also have high loadings on this component. None of these three variables are significantly different between the two *G. beringei* subspecies.

The *G. g. diehli* specimen falls near the center of the *G. gorilla* distribution on Component 3, which separates the *Gorilla* species. On Component 2, which separates the subspecies of *G. beringei*, it is within the *G. g. gorilla* and *G. b. graueri* ranges but outside of the *G. b. beringei* range.

Hand

Table 3.13 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of hand variables.

Component 1 explains 85.22% of the total variance. Within the cluster for each sex, the *G. beringei* specimens cluster toward the lower PC scores but remain almost entirely within the range of *G. gorilla* (Figure 3.15). The position of *G. beringei* specimens on Component 1 indicates that they have smaller hand bone measurements, in general, than specimens of *G. gorilla*.

Component 2, the first of the shape components, separates the two species of *Gorilla* (Figure 3.16) and explains 4.19% of the total variance. The variables that load more heavily on this component are third metacarpal length and radio-ulnar midshaft diameter and third proximal hand phalanx length, maximum shaft width, and minimum shaft width. In other words, the lengths and shaft widths of the two hand bones in this study drive the separation of the two species in this analysis, although some of them are not significantly different between the species, while articular measurements contribute very little.

Component 3 does not separate groups on the basis of either species or subspecies, but Components 4 and 5 (explaining 3.09% and 2.45% of the total variance, respectively) both somewhat separate the subspecies of *G. beringei* (Figures 3.17 and 3.18). Component 5 also clusters *G. beringei* on one side of the *G. gorilla* range. The four variables that load most highly on Component 4 are the four hand bone shaft diameters. The variable with the highest loading is third metacarpal radio-ulnar midshaft diameter, which is the one hand bone variable that is significantly different (in females only) between the two *G. beringei* subspecies. Component 5, which achieves some separation between both the species and the *G. beringei* subspecies, is more difficult to interpret. Variables that load most highly on Component 5 are, in descending order, third proximal hand phalanx length, third metacarpal biepicondylar width, third proximal hand phalanx maximum shaft width, third metacarpal head width, and third proximal hand phalanx base width. Perhaps there is some significance to the inclusion of the three measurements that are directly related to the metacarpophalangeal joint. Although some of these variables are significantly different when the two species are compared, none of

them are significantly different between *G. b. beringei* and *G. b. graueri*. The separation of these taxa on Component 5 may be explained by the contribution of third metacarpal head width, which is significantly different between *G. g. gorilla* and *G. b. graueri*. Perhaps Component 5 separates *G. g. gorilla* and *G. b. graueri*, which effectively separates the two *G. beringei* subspecies, as well.

The *G. g. diehli* specimen falls in the middle of the *G. gorilla* distribution along Component 2, which separates the two *Gorilla* species. When Components 4 and 5, which separate the subspecies, are plotted against one another, the *G. g. diehli* specimen falls among the *G. g. gorilla* specimens that are overlapped by the *G. b. graueri* cluster (Figure 3.19).

Foot

Table 3.14 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of foot variables.

Component 1 explains 77.13% of the total variance. Within each sex cluster, the *G. beringei* specimens occupy the lower range of PC scores and only partially overlap the range of *G. gorilla* specimens (Figure 3.20). The *G. beringei* foot bone measurements appear to be smaller than the *G. gorilla* foot bone measurements, in general, and this size difference is more marked than the size difference observed between species in the other five sets of variables analyzed.

The first of the shape components, Component 2, separates both the species of *Gorilla* and the subspecies of *G. beringei* (Figures 3.21 and 3.22). This component explains 6.25% of the total variance. The *G. beringei* sample is clustered at one end of the *G. gorilla* distribution on Component 2. Within the *G. beringei* cluster, the *G. b.*

*beringei* cluster is farther from the center of the *G. gorilla* cluster than is the *G. b. graueri* cluster. As a result, the overlapping subspecies clusters are arrayed from *G. b. beringei* to *G. b. graueri* to *G. g. gorilla*. One variable, cuboid facet depth of the calcaneus, has a high loading on Component 2, and all other variables contribute far less. This variable also strongly drives components in the analyses of all variables and of hindlimb variables. Differences between taxa in cuboid facet depth of the calcaneus are discussed in the section above on the analysis of hindlimb variables.

Component 3, which explains 5.39% of the total variance, primarily separates the two species of *Gorilla*; very slight separation of the *G. beringei* subspecies is also present (Figure 3.22). The variable with the highest loading on this component is calcaneus tuberosity length, which is not significantly different between species. It is not clear how to interpret its relationship to the other variables that make moderate contributions to this component, some of which are significantly different between species, but the contributions of the ray bone lengths are all very small. Component 4, which explains 2.64% of the total variance, also achieves some separation of the two species, although the separation is moderate in comparison to that of Component 3. Component 4 is driven by the lengths of the three ray bones of the foot, all of which are significantly different between species. Component 5 does not separate the species and only slightly separates the subspecies of *G. beringei*.

When Components 2 and 3 are plotted against one another, the *G. g. diehli* specimen falls among the *G. gorilla* specimens but near the *G. b. graueri* cluster.

Summary

In principal components analyses of *Gorilla* variables, Component 1, which is strongly correlated with size (as measured by the geometric mean), explains between 77% and 85% (approximately) of the total variance in the six sets of analyzed variables. Analyses of foot and hindlimb variables explain a smaller percentage of the total variance on Component 1 than do analyses of long bone, hand, and forelimb variables, and the analysis of all variables explains an intermediate percentage of the total variance. Component 1 strongly separates males and females in all analyses. Differences between the two *Gorilla* species, within each sex cluster, are also evident on Component 1 of every analysis except the analysis of long bone variables. This result suggests that the long bones of the two species are of similar overall sizes within each sex; results from the comparisons of means support this interpretation. The set of variables that best separates the two species on Component 1 is the set of foot variables, which suggests a greater size difference between *Gorilla* species in foot variables than in other analyzed variables of the limb elements.

After size differences are accounted for on Component 1, differences between the two species of gorilla explain a large portion of the remaining variance in all six sets of variables. Each set of variables has at least one component in its principal components analysis that primarily separates the two species. In four of the six analyses, Component 2 primarily separates the species. In the analysis of long bone variables, the first component to separate the species is Component 3, while Component 2 primarily separates the subspecies of *G. beringei*. In the analysis of foot bone variables, Component 2 arrays the subspecies from *G. g. gorilla* to *G. b. graueri* to *G. b. beringei*, which has the effect of separating the species as well as the subspecies, while Component

3 primarily separates the species. In sum, species-level differences appear to explain more of the total variance than any factor except sex in four of the six sets of variables; however, subspecies-level differences, whether between the two *G. beringei* subspecies or between all three sampled subspecies of *Gorilla*, explain more of the total variance in analyses of long bones and foot bones.

When PC scores for Components 2 and 3 are plotted for each set of variables (Figures 3.2, 3.7, 3.10, 3.14, 3.16, and 3.21) and the plots are compared, focusing only on the axis on which the species are best separated, the sets of variables clearly differ in how well they separate the species of *Gorilla*. Analyses based on all variables and on hindlimb variables both separate the two species with very little overlap. In each of these analyses, the species separate on Component 2, and similarities in these second components are not surprising, as Component 2 of the analysis of all variables strongly emphasizes variables of the hindlimb. The sets of forelimb variables and of long bone variables separate the species with moderate overlap, and the species overlap the most in analyses of hand and foot variables.

In addition to differences between the two species of *Gorilla*, differences between the two subspecies of *G. beringei* also appear responsible for a large portion of the total variance remaining after size differences are accounted for, in all six sets of variables. In fact, in the analyses of every set of variables except hand variables, species differences and subspecies differences explain Components 2 and 3, although not necessarily in that order. If Component 2 separates species, then Component 3 separates subspecies, and vice versa. Only in the analysis of hand variables is a situation found where Component 3 does not separate either species or subspecies. In this case, subspecies-level separation

is seen on Component 4. In some analyses, subspecies-level separation is apparent on an additional component, as well, and these higher-numbered components sometimes separate the subspecies as well as (or better than) the lower-numbered components.

Principal components analyses of the set of all variables and the set of hindlimb variables separate the two subspecies of *G. beringei* better than others sets of variables. These are the same two sets of variables that best separate the two species of *Gorilla*, but the subspecies are not separated as well as the species in these analyses. In the analysis of all variables, the two subspecies of *G. beringei* are separated on both Component 3 and 4, but less overlap is seen on Component 4. The overlap on Component 3 of the analysis of all variables is comparable to that seen in analyses of other sets of variables that separate the subspecies less well. Figures 3.4, 3.8, 3.11, 3.13, 3.17, and 3.22 show PC scores for the component or components of each analysis that best separate the subspecies of *G. beringei* plotted against the PC scores for the component that best separates the species of *Gorilla*. The component that separates species is always plotted as the X-axis, even if it has a higher number than the component on the Y-axis, in order to facilitate visual comparisons.

The principal components analyses offer an opportunity to compare the single specimen of *G. g. diehli* that includes all study elements with the other *Gorilla* subspecies in multivariate space. As expected based on taxonomy and geography, this specimen consistently falls among the specimens of *G. gorilla* on components that separate the species. Further, as expected based on the results of the comparisons of means, most of these components place it on the side of the *G. gorilla* cluster that is closer to the *G. beringei* cluster. Exceptions are found in the analysis of long bone variables, which

would be predicted based on the comparisons of means, and the analysis of hand bone variables, which was unexpected. Its position in the analysis of hand bone variables is probably explained by the large overlap between *G. gorilla* and *G. beringei* on the component that separates species, allowing it to fall both at the center of the *G. gorilla* distribution and at the extreme edge of the *G. beringei* distribution. On components that separate the subspecies of *G. beringei*, the *G. g. diehli* specimen tends to be located within or nearer to the distribution of *G. b. graueri*.

When component loadings of individual variables are examined for all analyses and for all components that best separate species and subspecies of *Gorilla*, a number of patterns can be detected both within and between analyses. In analyses of forelimb, hand, and long bone variables, almost all the components that best separate either species or subspecies emphasize bone lengths and shaft diameters and do not emphasize articular surface dimensions. In analyses of hindlimb and foot variables, measurements of the calcaneus make large contributions to most components that separate species and/or subspecies; the analysis of the hindlimb emphasizes other foot variables, as well, in the component that separates species. Cuboid facet depth of the calcaneus plays a particularly large role in separating both species and subspecies in both of these analyses. In the analysis of all variables, the component that separates species emphasizes hindlimb variables, mostly from the foot. Cuboid facet depth has the highest loading on this component. Of the two components that separate subspecies when all variables are analyzed, Component 3 is dominated by lengths and shaft diameters of both forelimb and hindlimb elements, while Component 4 is driven by cuboid facet depth of the calcaneus.

Interestingly, the two components that best separate the subspecies of *G. beringei*,

Component 3 of the analysis of hindlimb variables and Component 4 of the analysis of all variables, are both driven by cuboid facet depth of the calcaneus, but the subspecies of *G. beringei* do not differ significantly in this measurement. As discussed in the results for the hindlimb analysis, perhaps components driven by cuboid facet depth of the calcaneus that separate the two subspecies of *G. beringei* pull the two subspecies apart by positioning them differently with regard to *G. g. gorilla*.

Three analyses include, among the components that best separate taxa, a component that separates both the species of *Gorilla* and the subspecies of *G. beringei* on the same axis. These components can also be understood as separating the three sampled subspecies while still reflecting the closer relationship between the two subspecies of *G. beringei*. The three analyses including these components are those of the forelimb, hand, and foot. No consistent pattern is apparent in which variables, or which types of variables, are most heavily weighted on these components.

**Populations**

Variation at the population level, based on principal components analyses, is discussed in this section. The most important aspect of population-level variation to be described is the extent to which the populations of *Gorilla* cluster into the species and subspecies to which they are assigned. For this reason, only two components of each analysis are inspected, using a scatterplot, for the discussion of population-level variation: the component that best separates the species of *Gorilla* (which is plotted on the x-axis) and the component that best separates the subspecies of *G. beringei* (which is plotted on the y-axis). These two components are identified based on the preceding discussion of variation at the species and subspecies levels. Plots of PC scores on these

two components of each analysis, grouped by population, are presented in Figures 3.23 – 3.28.

The populations of *Gorilla* considered here are the eleven populations listed in Table 2.2. When they are considered by species, six populations belong to *G. gorilla* and five populations belong to *G. beringei*. When they are considered by subspecies, five populations belong to *G. g. gorilla*, four populations belong to *G. b. graueri*, and *G. g. diehli* and *G. b. beringei* are represented by one population each.

The single specimen from the Cross River population, which is also the single specimen of *G. g. diehli*, is discussed in the preceding section on species and subspecies patterns; as no further patterns are observed in its population-level clustering, it will not be discussed further in this section.

Once the sole specimen of *G. g. diehli* is removed from discussion, the species *G. gorilla* is represented entirely by populations of *G. g. gorilla* in these analyses.

All variables

Population-level patterns in the analysis of all variables are explored on Component 2 (which best separates species) and Component 4 (which best separates subspecies of *G. beringei*) (Figure 3.23).

Four of the five populations of *G. g. gorilla* cluster tightly together on these components, while the Sangha population differs in its distribution. The four Sangha specimens all have low values on Component 4, making them more similar to *G. b. graueri* than to *G. b. beringei*. In addition, their distribution on Component 2 is unusual, as one of the four has a very low value and another has one of the highest *G. gorilla* values on this component.

The five populations of *G. beringei* cluster as predicted by taxonomy, for the most part, despite the limitations of some very small samples. The two specimens from Kahuzi and the two specimens from Tshiaberimu lie within or near the Mwenga-Fizi cluster, as predicted by their membership in *G. b. graueri*. One Tshiaberimu specimen has the lowest PC score on Component 4 of any *G. beringei* specimen. The three specimens from the Utu population of *G. b. graueri* appear intermediate to *G. b. graueri* and *G. b. beringei* on Component 4, lying entirely within the overlap between the Mwenga-Fizi and Virungas populations. The Utu population's position on Component 2 is also interesting, as two of its three specimens are the *G. beringei* specimens with the lowest PC scores, placing them closest to the *G. gorilla* distribution.

Forelimb

Population-level patterns in the analysis of forelimb variables are explored on Component 2 (which best separates species) and Component 3 (which best separates subspecies of *G. beringei*) (Figure 3.24).

The distributions of the five *G. g. gorilla* populations are very similar on Component 2. The only unusual pattern is that the Sangha population (n = 5) is split into a group of two specimens with low values and a group of three specimens with high values. On Component 3, the *G. g. gorilla* populations have similar distributions, as well. The most notable distribution is that of the Ebolowa population, which is shifted slightly toward the higher PC values by a dense cluster of higher-value specimens.

Some interesting patterns present themselves in the relationships of the *G. beringei* populations. On Component 2, the very small samples of the more poorly-represented populations are disproportionately represented at the extremes of the *G.*

*beringei* distribution. Among the four specimens of this species with the lowest PC values on this component (plotted nearest to the *G. gorilla* distribution) are one of the two specimens from Kahuzi and two of the three specimens from Utu; two Utu specimens occupy a similar position on Component 2 of the analysis of all variables. Among the three specimens of this species with the highest PC values on this component are both of the two specimens from Tshiaberimu. On Component 3, the three Utu specimens have a distribution intermediate to the Mwenga-Fizi and Virungas distributions, similar to their distribution on Component 4 in the analysis of all variables. The two Kahuzi specimens clearly cluster with Mwenga-Fizi, but the two Tshiaberimu specimens have higher values than any other *G. b. graueri* specimens and cluster with the Virungas population.

Hindlimb

Population-level patterns in the analysis of hindlimb variables are explored on Component 2 (which best separates species) and Component 3 (which best separates subspecies of *G. beringei*) (Figure 3.25).

Four of the five populations of *G. g. gorilla* are tightly clustered on the two components. The fifth population, from the Sangha region, appears to be shifted toward higher values of the *G. gorilla* distribution on Component 3, making it more similar to *G. b. graueri* than to *G. b. beringei*, as also seen in the analysis of all variables. The small Sangha sample (n = 4) includes specimens with values near both extremes of the *G. gorilla* distribution on Component 2, as it also does in the analyses of all variables and forelimb variables.

The relationships of the populations of *G. beringei* on these components echo their relationships in the analysis of all variables. On Component 2, two of the four Utu

specimens have PC values that place them at the extreme low end of the *G. beringei* distribution, overlapping the *G. gorilla* distribution. On Component 3, the Utu, Kahuzi, and Tshiaberimu specimens are all located within the distribution of the Mwenga-Fizi sample. Three of the four Utu specimens are in or very near the zone of overlap between the Mwenga-Fizi and Virungas populations on this component. In addition, one of the two Tshiaberimu specimens is in this overlap zone and is near the boundary beyond which all *G. beringei* specimens are from the Virungas.

Long bones

Population-level patterns in the analysis of long bone variables are explored on Component 3 (which best separates species) and Component 2 (which best separates subspecies of *G. beringei*) (Figure 3.26).

The five populations of *G. g. gorilla* have similar distributions on Component 3, which separates the species. The Sangha sample does not have any extreme values on this component, unlike the pattern it displays in the preceding analyses. On Component 2, which separates the subspecies of *G. beringei*, the distributions of the five *G. g. gorilla* populations are also similar. On this component, two of the four Sangha specimens have high values and two have low values; the similarity of this population to *G. b. graueri* seen in the analyses of all variables and hindlimb variables is not seen here.

Among the populations of *G. beringei*, no clear patterns present themselves on Component 3; however, the most extreme positions are occupied by specimens from the smaller samples, with an Utu specimen placed nearest the center of the *G. gorilla* distribution and a Kahuzi specimen placed most distant from the *G. gorilla* distribution. On Component 2, the three Kahuzi specimens cluster neatly with Mwenga-Fizi, and the

four Utu specimens fall in or very near the overlap zone between Mwenga-Fizi and the Virungas, while the Tshiaberimu sample (n = 4), which straddles the overlap zone, appears slightly more like the Virungas sample than the Mwenga-Fizi sample. One Tshiaberimu specimen is located well within the Virungas distribution and far beyond the nearest Mwenga-Fizi specimen on Component 2.

Hand

Population-level patterns in the analysis of hand variables are explored on Component 2 (which best separates species) and Component 4 (which best separates subspecies of *G. beringei*) (Figure 3.27).

The five populations of *G. g. gorilla* have roughly similar distributions on these components, although the Coast population is more tightly clustered to the side farthest from *G. beringei* on Component 2. While the Sangha population has a wide range of values on both components, the extreme values for this population seen in some previous analyses are not apparent here.

The hand analysis shows great overlap between the species of *Gorilla* and between the subspecies of *G. beringei*; therefore, clustering patterns of the smallest *G. beringei* population samples are more ambiguous than in the preceding analyses. The *G. beringei* sample is mostly overlapped by the *G. gorilla* sample, and the Virungas sample is almost entirely overlapped by the Mwenga-Fizi sample. The four Utu specimens fall entirely within the Mwenga-Fizi distribution on both components, as would be predicted by their membership in *G. b. graueri*, but at the same time two of them fall well within the Virungas distribution and two of them fall well within the *G. gorilla* distribution. Of the two Kahuzi specimens, one lies in the overlap between the Mwenga-Fizi and

Virungas distributions but also well within the *G. g. gorilla* distribution on both components, while the other lies far beyond the *G. beringei* distribution and within the *G. gorilla* distribution on Component 2. One of the four Tshiaberimu specimens is located comfortably within the overlap between the two *G. beringei* subspecies (and the two *Gorilla* species), but the other three are more distinctively placed. One has the lowest PC score of the entire sample on Component 2, giving it an extreme value on the *G. beringei* end of the axis; another has a lower PC score than any other *G. beringei* specimen on Component 4, giving it an extreme value for *G. b. graueri*; and a third is placed very near the second specimen but in a less extreme position. The Tshiaberimu distribution as a whole gives the impression of being an exaggerated *G. b. graueri* sample on these components.

Foot

Population-level patterns in the analysis of foot variables are explored on Component 3 (which best separates species) and Component 2 (which best separates subspecies of *G. beringei*) (Figure 3.28). Although Component 3 best separates species, substantial separation of species is also visible on Component 2.

The five populations of *G. g. gorilla* overlap broadly, but the distributions of the four larger samples do not correspond as closely as they do in the other analyses, and the smaller Sangha sample is distinctive. Among the larger samples, the Coast population appears to have the most concentrated distribution on both components, bringing it the closest to the distribution of *G. beringei*. The smaller Sangha sample has generally high PC scores on Component 3, pulling it toward the *G. beringei* distribution, but its distribution on Component 2 is centered on lower PC scores, pushing it away from *G.*

*beringei* and especially from *G. b. beringei*, although five of its eight specimens overlap the *G. b. graueri* range. The Sangha sample also includes the second-to-lowest Component 2 PC score in the entire sample.

Despite the large overlap in the foot analysis between the species of *Gorilla* and the subspecies of *G. beringei*, the *G. beringei* populations with the smallest samples all cluster neatly with the Mwenga-Fizi population, as predicted by their membership in *G. b. graueri*. The four Utu specimens are in or very near the zone of overlap between the Mwenga-Fizi and Virungas populations on both components. One of the two Tshiaberimu specimens is in the overlap zone, but the other is beyond the Virungas distribution on both components. Of the two Kahuzi specimens, both are beyond the Virungas distribution on Component 2, and one is beyond the Virungas distribution on Component 3, as well. Due to the substantial overlap between species on both components, two Utu specimens, a Tshiaberimu specimen, and a Kahuzi specimen are in the overlap zone between Mwenga-Fizi and the populations of *G. g. gorilla*.

Summary

The exploration of population-level patterns in the principal components analyses demonstrates that the populations of *G. gorilla* and *G. beringei* cluster consistently by species. It also shows that, within the limits of small sample sizes for some populations, the populations of *G. beringei* usually cluster by currently-assigned subspecies. At the same time, there are indications that the distributions of some populations are different from others within the same subspecies.

Four of the five populations of *G. g. gorilla* tend to cluster together, sometimes tightly and sometimes more loosely. The fifth population, Sangha, tends to be distributed

quite differently from the others. The observed differences may be artifacts of sample size, as the Sangha samples range from four to eight specimens, but the observed patterns are seen in analyses including eight Sangha specimens as well as in analyses including only four. The Sangha sample tends to include extreme values for the *G. gorilla* distribution, sometimes in both directions, on the component that best separates species. Only the analysis of long bone variables shows neither extreme values nor a wide range of values for the Sangha sample on this component. In three analyses (all variables, hindlimb, and foot), the Sangha sample also varies more in the direction of *G. b. graueri* and less in the direction of *G. b. beringei* on the component that best separates the subspecies of *G. beringei*.

The five populations of *G. beringei* are all represented by smaller sample sizes than might be desired, but two of the sample sizes are consistently larger than the other three. The two populations with larger sample sizes are from the Virungas and Mwenga-Fizi. The Virungas population is the only *G. b. beringei* population included in this study; therefore, this population is equivalent to *G. b. beringei* for the purposes of these analyses. The Mwenga-Fizi population, on the other hand, is one of four *G. b. graueri* populations included in this study; however, the sample sizes for the other *G. b. graueri* populations are so small that, in every analysis except that for long bones, the Mwenga-Fizi sample is larger than the samples of the other three populations put together. Consequently, results pertaining to *G. b. graueri* are largely driven by characteristics of the Mwenga-Fizi sample, and graphs that show the relationship between the Mwenga-Fizi and Virungas samples mirror to a great extent graphs that show the relationship between *G. b. graueri* and *G. b. beringei*.

Given this backdrop, observations of population-level patterns within *G. beringei* focus on whether the three smaller samples representing populations of *G. b. graueri* tend to cluster with Mwenga-Fizi or with the Virungas. Individual tendencies of each smaller sample, including its position on the component that best separates species, are also noted.

The Utu population, with a sample size of three or four specimens for the various analyses, is consistently located in or near the zone of overlap between the Mwenga-Fizi and Virungas populations on the component that best separates the subspecies of *G. beringei*. On the component that best separates species, most analyses place one or two Utu specimens in extreme positions for *G. beringei* in the direction of the *G. gorilla* distribution; in the remaining analyses (hand and foot), two Utu specimens occupy positions that cannot be called extreme but that are very near the outer boundary of *G. beringei* on the side of *G. gorilla*.

The Kahuzi population, with a sample of two or three specimens, is always placed comfortably within the Mwenga-Fizi distribution on the component that best separates the subspecies of *G. beringei*, but it shows some extreme values on the species components. In the forelimb and hand analyses, one of two Kahuzi specimens has the most extreme value for *G. beringei* in the direction of the *G. gorilla* distribution. In contrast, one of three Kahuzi specimens in the long bone analysis has the most extreme value in the *G. beringei* direction.

The Tshiaberimu population, represented by either two or four specimens in the various analyses, does not consistently cluster with the Mwenga-Fizi population, but it is not consistently similar to the Virungas population, either. In two analyses, the

Tshiaberimu specimens cluster with the Virungas sample. In the analysis of forelimb variables, the two Tshiaberimu specimens both have PC scores within the Virungas range and beyond the value of any Mwenga-Fizi specimen. In the analysis of long bone variables, two of the four Tshiaberimu specimens have PC scores within the Virungas range and beyond the value of any Mwenga-Fizi specimen, while one is in the zone of overlap between Mwenga-Fizi and the Virungas and one is in the Mwenga-Fizi range and very slightly beyond the value of the most extreme Virungas specimen. On the other hand, the analyses of all variables and hand variables show extreme values for Tshiaberimu specimens toward the *G. b. graueri* end of the component that best separates subspecies of *G. beringei*. In addition, a Tshiaberimu specimen has the most extreme *G. beringei*-like value in the hand analysis, on the component that best separates species. In combination with its values on the subspecies component, this gives the Tshiaberimu population the appearance of being an exaggerated *G. b. graueri* in the hand analysis.

To sum up the relationships among the populations of *G. beringei*, the relationship between the Virungas and Mwenga-Fizi populations consistently mirrors the relationship between *G. b. beringei* and *G. b. graueri*, and the smaller populations of *G. b. graueri* usually cluster with Mwenga-Fizi on the component that best separates the subspecies of *G. beringei* but each have distinctive tendencies.

***Pan***

Tables 3.16 – 3.21 report eigenvalues, percent of total variance explained, and component loadings for the first five components of each of the six principal components analyses of *Pan* measurements.

In all six principal components analyses of the *Pan* sample, Component 1 separates specimens on the basis of both sex (although to a much lesser extent than in analyses of *Gorilla*) and species. The *P. paniscus* distributions are centered on lower PC scores than the *P. troglodytes* distributions, and the female distributions for each species are centered on lower PC values than the male distributions. As *P. paniscus* limb bone measurements are generally smaller than *P. troglodytes* limb bone measurements (see Table 3.5), and as female *Pan* limb bone measurements are generally smaller than male *Pan* limb bone measurements (see Table 4 of Appendix 4), this pattern on Component 1 appears likely to reflect size-based differences. In fact, in every one of the six principal components analyses, Pearson correlation analysis of Component 1 scores and geometric means results in a very high Pearson correlation coefficient (the lowest value is $r = 0.9784$) with a probability of $p < 0.0001$ (Table 3.22). On the basis of these results, Component 1 can be considered to account for size differences within the *Pan* sample in each principal components analysis, and shape differences can be assessed using the other components.

**Species and subspecies**

Variation at the levels of species and subspecies is discussed in this section, while variation at the population level is discussed in the next section.

A preliminary observation of patterns of variation reflected in scatterplots of PC scores showed that, based on these analyses, separation between species and between subspecies is generally more subtle in *Pan* than in *Gorilla* and that some degree of separation between taxa is seen in many components of each analysis. Whereas the *Gorilla* PCAs reflect strong differences between species and between subspecies in the

first few components, making it clear which components are most worth discussing in the Results, differences between *Pan* taxa are present but not dramatic in the first few components and are sometimes equally or even more apparent in later components. These later components explain less of the total variance, and their variables frequently have lower loadings, yet they may separate taxa as well as earlier components. Further, as the *Pan* analyses include four subspecies within a single species and the *Gorilla* analyses only include two, there are far more potential patterns of variation between subspecies (i.e., different ways the subspecies could sort with regard to similarities and differences between each pair) that could be sought in the components of a *Pan* analysis and described in the Results.

This situation presents a challenge in how to approach the PCA results for *Pan* in a manner that will be focused and meaningful without being entirely arbitrary and subjective. The usual solution to this problem is to limit discussion to components with eigenvalues of less than 1; however, the first component of each analysis, interpreted here as representing size and not shape, explains such a large proportion of the total variance that eigenvalues of subsequent components, representing the shape factors of interest, quickly drop below 1. Taking into consideration the results of previous studies and the predictions of the current study, an approach was chosen in which four specific questions are addressed and only the first four shape components (Components 2-5) in each analysis are inspected. The four questions are :

(1) Does *P. paniscus* separate from *P. troglodytes*?

(2) Does *P. t. verus* separate from *P. t. schweinfurthii* and *P. t. troglodytes*?

(3) Does *P. t. vellerosus* separate from other subspecies?

(4) Do *P. t. schweinfurthii* and *P. t. troglodytes* separate from one another?

If these four taxonomic distinctions are evident in the data, and if taxonomic distinctions explain most of the variance after size, these four questions are likely to be answered in Components 2-5. Further components may contribute to an understanding of shape differences between taxa, but the first four components should convey where the greatest taxonomic differences (and similarities) lie and which variables contribute the most to shape differences (and similarities) between these taxa.

All variables

Table 3.16 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of all variables.

Component 1 explains 54.56% of the total variance. The specimens of *P. paniscus* are clustered at the lower end of the PC score distribution for *P. troglodytes*; this side of the *P. troglodytes* cluster is mostly occupied by female *P. troglodytes* specimens (Figure 3.29). In addition, female *P. paniscus* specimens have a slightly lower PC score distribution than male *P. paniscus* specimens. As discussed above, lower PC scores correspond to smaller measurements on this component. The pattern of differences between species and differences between sexes seen on Component 1 of this analysis is similar to the pattern seen on Component 1 of the other five analyses

When further components, which can be considered shape components, are inspected, differences in the distributions of the two species of *Pan* are seen on Component 2 (Figure 3.30), which explains 7.86% of the total variance. On this component, *P. paniscus* specimens are clustered on one side of the *P. troglodytes* distribution but are entirely contained within it, and *P. paniscus* is particularly

differentiated from *P. t. verus*. The six variables that contribute most to this component are all bone lengths or partial bone lengths. Femoral and tibial lengths have substantially higher loadings than the other variables, and they are followed by the lengths of the calcaneal tuberosity, humerus, third metacarpal, and radius.

The distribution of *P. paniscus* on Component 3, which explains 4.44% of the total variance, is somewhat discontinuous, with one cluster having PC scores of near zero and below, while another cluster has PC scores in the upper range of positive values (Figure 3.30). This distribution particularly differentiates the upper cluster of *P. paniscus* from the sample of *P. t. verus*, which clusters near and below zero. Component 3 is dominated by the antero-posterior midshaft diameter of the tibia. Two other variables, medio-lateral midshaft diameters of the tibia and radius, also have loadings considerably greater than other variables.

The two species also differ in their distributions on Components 4 and 5, which explain 4.05% and 2.78% of the total variance, respectively. On Component 4, *P. paniscus* and *P. t. verus* both tend to one side of the *P. troglodytes* distribution. The first four variables in order of loading on this component are all measurements of articular surfaces: cuboid facet depth of the calcaneus, bicondylar width of the femur, distal width of the radius, and width of the tibial plateau. On Component 5, *P. paniscus* clusters on one side and goes slightly beyond the distribution of *P. troglodytes*. Calcaneal tuberosity length and calcaneus length contribute far more than other variables to this component.

Differences between *P. t. verus* and the subspecies *P. t. schweinfurthii* and *P. t. troglodytes* on Components 2-5 are slight. On Component 2, *P. t. verus* clusters on one side of the *P. t. schweinfurthii* distribution, and two of the eight *P. t. verus* specimens in

the analysis of all variables have extremely low values on Component 4 (Figure 3.31). As described above, Component 2 is driven by bone lengths and partial lengths, particularly those of the hindlimb, and Component 4 primarily reflects the contributions of articular surface measurements.

The very small sample of *P. t. vellerosus* included in the analysis of all variables (n = 3) is not differentiated from other subspecies on Components 2-5. These components also do not show differentiation of *P. schweinfurthii* and *P. t. troglodytes*.

Forelimb

Table 3.17 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of forelimb variables.

Component 1 explains 59.42% of the total variance. The pattern of differences between sexes and differences between species is similar to the pattern seen in the analysis of all variables (Figure 3.32).

On Component 2, the first shape component, the specimens of *P. paniscus* are tightly clustered on one side of, but entirely contained within, the *P. troglodytes* distribution on Component 2 (Figure 3.33), which explains 8.31% of the total variance. *Pan paniscus* and *P. t. verus* have very little overlap on this component. Component 2 is driven by the lengths of the forelimb elements included in the analysis: humerus, third metacarpal, radius, and third proximal hand phalanx.

The *P. paniscus* sample is poorly differentiated from *P. troglodytes* on Component 3, and the two species are generally not well-differentiated on Component 4; however, two specimens of the *P. paniscus* sample have values below the *P. troglodytes* range on Component 4, and four specimens (including those two) have extremely low

values on this component (Figure 3.33). Component 4 (explaining 4.51% of the total variance) is dominated by articular measurements of the humerus and radius, although length of the third proximal hand phalanx also has a heavy loading. The variables with the greatest loadings on this component are, in order, distal articular width of the humerus, medio-lateral head width of the radius, length of the third proximal hand phalanx, distal width of the radius, supero-inferior head diameter of the humerus, and biepicondylar width of the humerus.

*Pan paniscus* is most strongly differentiated from *P. troglodytes* on Component 5 (Figure 3.34), which explains 2.88% of the total variance, although it does not exceed the *P. troglodytes* range on this component. The three variables that drive Component 5 are third metacarpal length, humerus length, and distal width of the radius.

Differences between *P. t. verus* and the subspecies *P. t. schweinfurthii* and *P. t. troglodytes* are slight on Components 2-4 and not apparent on Component 5. Figure 3.33 plots Components 2 and 4 by subspecies. On Component 2, which is driven by bone lengths, *P. t. verus* clusters toward one side of the distributions of the other subspecies. On both Components 3 and 4, the *P. t. verus* sample is most different from the *P. t. schweinfurthii* sample. Variables with the greatest loadings on Component 3 (which explains 4.83% of the total variance), on which *P. t. verus* clusters slightly on one side of the distribution of other subspecies, but more to one side of the *P. t. schweinfurthii* distribution, are medio-lateral midshaft diameter of the radius, antero-posterior midshaft diameter of the radius, head width of the third metacarpal, antero-posterior midshaft diameter of the humerus, and biepicondylar width of the third metacarpal. This group of five variables can be broken down into two groups, midshaft diameters of forelimb long

bones and widths of the distal articular region of the third metacarpal. On Component 4, the ranges of *P. t. verus* and *P. t. schweinfurthii* are actually slightly offset from one another, and *P. t. verus* clusters on one side of the *P. t. troglodytes* distribution. As described above, Component 4 is dominated mostly by articular measurements of the humerus and radius.

The small sample of six *P. t. vellerosus* specimens included in the forelimb analysis is not differentiated from the other subspecies of *P. troglodytes* on Components 2-5. A slight difference in distributions of *P. t. schweinfurthii* and *P. t. troglodytes* is evident on Component 4 (Figure 3.33), on which the *P. t. schweinfurthii* cluster is pushed slightly to one side of the *P. t. troglodytes* distribution.

Hindlimb

Table 3.18 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of hindlimb variables.

Component 1 explains 50.93% of the total variance. The pattern of differences between sexes and differences between species is similar to the pattern seen in the analysis of all variables (Figure 3.35). Interestingly, one male *P. paniscus* has a PC score that places it among the largest *P. troglodytes* specimens, and another is placed near the center of the male *P. troglodytes* distribution.

When the shape components are inspected, the two species of *Pan* are differentiated on Component 2 (Figure 3.36), which explains 9.18% of the total variance. The distribution of *P. paniscus* specimens is entirely contained within, but clusters on one side of, the distribution of *P. troglodytes* specimens. The variables with the greatest loadings on Component 2 are the lengths of the femur, calcaneal tuberosity, and tibia,

followed by several width measurements of the foot ray bones (biepicondylar width of the third metatarsal, maximum shaft width of the third proximal foot phalanx, minimum shaft width of the third proximal foot phalanx, and medio-lateral head width of the third metatarsal).

Differences between the two species are not apparent on Component 3 and weak on Component 4, but they are clearly apparent on Component 5, which explains 4.28% of the total variance. Component 5 is strongly driven by length of the calcaneal tuberosity, which also has the second greatest loading on Component 2.

*Pan troglodytes verus* is differentiated from other subspecies on Components 3 and 5, but differences are weak on Components 2 and 4. On Component 3, which explains 6.25% of the total variance, the *P. t. verus* sample occupies only one side of the *P. t. troglodytes* distribution (Figure 3.37). This component is dominated by the depth of the cuboid facet of the calcaneus, followed by the midshaft diameters of the tibia, and further followed by the midshaft diameters of the femur. On Component 5, which is driven by the length of the calcaneal tuberosity (described above), the *P. t. verus* sample is contained within the ranges of *P. t. schweinfurthii* and *P. t. troglodytes* but does not extend to the lower part of their ranges.

The small sample of three *P. t. vellerosus* specimens is not distinguished from the other subspecies on Components 2-5. Only Component 3 (described above) displays a difference worth noting between *P. t. schweinfurthii* and *P. t. troglodytes*; the distribution of *P. t. troglodytes* extends considerably below most of the *P. t. schweinfurthii* specimens (Figure 3.37).

Long bones

Table 3.19 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of long bone variables (including humerus, radius, femur, and tibia but not including bones of the hands and feet).

Component 1 explains 61.08% of the total variance. The pattern of differences between sexes and differences between species is similar to the pattern seen in the analysis of all variables (Figure 3.38).

The *P. paniscus* sample clusters tightly within the *P. troglodytes* distribution on Component 2, the first shape component, with most *P. paniscus* specimens occupying one side of the *P. troglodytes* distribution. Component 2 explains 8.92% of the total variance, and the variables with the greatest loadings on it are the lengths of the femur, tibia, humerus, and radius, closely followed by the medio-lateral midshaft diameters of the tibia and radius.

Component 3 does not differentiate the two species, but Components 4 and 5 both clearly do (Figure 3.39). On Component 4, which explains 3.80% of the total variance, the *P. paniscus* distribution is greatly shifted toward the upper values of the *P. troglodytes* range, and there is no overlap at all between the ranges of *P. paniscus* and *P. t. verus*. The variables with the greatest loadings on this component are antero-posterior midshaft diameters of the radius, femur, and tibia. On Component 5, which explains 2.88% of the total variance, the *P. paniscus* sample is also shifted toward the upper values of the *P. troglodytes* sample, although it is not shifted quite as far as on Component 4, and there is no overlap between the ranges of *P. paniscus* and *P. t. vellerosus*. Antero-posterior midshaft diameters of the humerus, tibia, and femur top the

list of loadings on Component 5, followed by medio-lateral midshaft diameters of the femur and tibia (and further variables with loadings of slightly smaller absolute values).

The *P. t. verus* sample is not distinguished from the samples of *P. t. schweinfurthii* and *P. t. troglodytes* on Components 2 and 5, but it is pushed toward the lower end of their ranges on Component 3 and tightly clustered in the low values of Component 4 (Figure 3.40). The variables with the greatest loadings on Component 3, which explains 6.36% of the total variance, are the two measurements of the articular surfaces of the knee joint: bicondylar width of the femur and width of the tibial plateau. Component 4 is dominated by antero-posterior midshaft diameters, as described above.

The analysis of long bone variables seems to pick up a signal from the small *P. t. vellerosus* sample (n = 3) on Components 4 and 5 (Figure 3.41). On Component 4, dominated by antero-posterior midshaft diameters and described above, the three *P. t. vellerosus* specimens are very tightly clustered. They fall in the middle of the distributions of *P. t. schweinfurthii* and *P. t. troglodytes* and at the intersection of the non-overlapping *P. paniscus* and *P. t. verus* samples. On Component 5, dominated by a slightly different set of midshaft diameters and described above, the *P. t. vellerosus* sample is clustered at the low ends of the distributions of the other subspecies and has no overlap with *P. paniscus*.

Only weak differences between *P. t. schweinfurthii* and *P. t. troglodytes* are apparent on Components 2-5.

Hand

Table 3.20 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of hand variables.

Component 1 explains 65.33% of the total variance. Although the pattern of differences between sexes and differences between species is roughly similar to the pattern seen in the analysis of all variables, the sexes of each species differ less from one another in the analysis of hand variables (Figure 3.42). Component 1 of the hand analysis shows greater overlap between the distributions of male and female *P. troglodytes* than seen in Component 1 of the analysis of all variables, and the distribution of *P. paniscus* males is entirely contained within the distribution of *P. paniscus* females on this component (as it is also on Component 1 of the forelimb analysis). While sex differences in hand bone size appear to be smaller than sex differences in the size of other elements, differences between the species in hand bone size are of a similar magnitude as species differences observed for other sets of variables.

When shape components are explored, differences between the two species of *Pan* are seen on Component 2 of the analysis of hand variables, with *P. paniscus* specimens clustering toward one side of the *P. troglodytes* distribution, but Component 2 of this analysis shows less differentiation between species than the second components of the other analyses discussed above. Differences between *P. paniscus* and *P. t. verus* are more marked than differences between *P. paniscus* and the other subspecies, but the samples of these two taxa greatly overlap. The variables with the greatest loadings on Component 2, which explains 10.60% of the total variance, are the lengths of the third metacarpal and third proximal hand phalanx, distantly followed by the minimum and maximum shaft widths of the third proximal hand phalanx.

Components 3 and 4, but not Component 5, also reflect differences between the samples of *P. paniscus* and *P. troglodytes* (Figures 3.43 and 3.44); Component 4

distinguishes the two species better than Components 2 or 3. Component 3, which explains 5.65% of the total variance, echoes Component 2 in its pattern of relationships between taxa. The *P. paniscus* sample clusters somewhat toward one side of the *P. troglodytes* distribution, and it is particularly differentiated from the *P. t. verus* sample. The variables that load the most heavily on this component are dorso-palmar midshaft diameter of the third metacarpal and trochlear width of the third proximal hand phalanx, followed more distantly by head width of the third metacarpal, minimum shaft width of the third proximal hand phalanx, biepicondylar width of the third metacarpal, and radio-ulnar midshaft diameter of the third metacarpal. Three of these last four measurements are widths of the third metacarpal. Component 4, which explains 4.51% of the total variance, also shows *P. paniscus* clustered on one side of the *P. troglodytes* distribution, but the *P. paniscus* range is similar to that of *P. t. verus* on this component. The set of variables loading most greatly on this component is trochlear width of the third proximal hand phalanx, maximum shaft width of the third proximal hand phalanx, and the three third metacarpal widths (radio-ulnar midshaft diameter, head width, and biepicondylar width).

As suggested above in the descriptions of the relationships between *P. paniscus* and *P. t. verus*, Components 2-4 reflect differences between the *P. t. verus* distribution and the distributions of *P. t. schweinfurthii* and *P. t. troglodytes*. On each of these components, and particularly on Component 3, the *P. t. verus* specimens are pushed toward one side of the distributions of the other two subspecies (Figure 3.44). Details of these components are given in the paragraphs above.

The six specimens of *P. t. vellerosus* in this analysis are not distinguished from the other subspecies samples on Components 2-5. While this subspecies includes a single very low value on Component 4 and a single extremely low value on Component 5, the range of this small sample is too great on every component to characterize it as different from the other samples. The samples of *P. t. schweinfurthii* and *P. t. troglodytes* have very similar distributions on Components 2-5.

Foot

Table 3.21 reports eigenvalues, percent of total variance explained, and component loadings for the first five components of the analysis of foot variables.

Component 1 explains 49.07% of the total variance. The pattern of differences between sexes and differences between species is similar to the pattern seen in the analysis of all variables (Figure 3.45). As in the hindlimb analysis, the PC score of one male *P. paniscus* places it among the largest *P. troglodytes* specimens. Another *P. paniscus* specimen is near the center of the male *P. troglodytes* distribution, and several others also are plotted within the distribution of male *P. troglodytes*.

Component 2 reflects shape differences between the two species of *Pan*, pushing the *P. paniscus* specimens toward one side of the *P. troglodytes* distribution (Figure 3.46). This component, which explains 11.75% of the total variance, is driven by calcaneal tuberosity length, distantly followed by maximum and minimum shaft widths of the third proximal foot phalanx.

On Components 3 and 5, the *P. paniscus* sample is pushed to the side to a similar extent as on Component 2 (Figure 3.46), but it is not distinguished from the *P. troglodytes* sample on Component 4. Component 3, which explains 8.56% of the total

variance, is dominated by cuboid facet depth of the calcaneus, followed by length of the third proximal foot phalanx, tendon facet width of the calcaneus, and three other length measurements (lengths of the first metatarsal, third metatarsal, and calcaneal tuberosity length). Component 5, which explains 4.64% of the total variance, is driven by the biepicondylar width of the third metatarsal.

Slight differences can be seen between the *P. t. verus* sample and the samples of *P. t. schweinfurthii* and *P. t. troglodytes*. On Component 3, described above, the distributions of both *P. t. verus* and *P. t. schweinfurthii* are shifted slightly toward the low end of the *P. t. troglodytes* range. On Component 4, the *P. t. verus* sample does not extend to the lower parts of the *P. t. schweinfurthii* and *P. t. troglodytes* ranges. Figure 3.47 plots Components 3 and 4 against one another by subspecies. Component 4, which explains 6.60% of the total variance, is strongly driven by the depth of the cuboid facet of the calcaneus.

The six specimens of *P. t. vellerosus* in this analysis are differentiated from other subspecies on Components 2, 4, and 5. On Component 2, they occupy only one side of the distributions of the other subspecies; their distribution is similar to, but more clustered than, the *P. paniscus* distribution. On Component 4, the *P. t. vellerosus* sample occupies only the lower parts of the ranges of the other subspecies, and its distribution is particularly different from that of *P. t. verus*. Figure 3.48 plots Components 2 and 4 against one another by subspecies. On Component 5, it is tightly clustered in the lower parts of the ranges of the other subspecies, varying in the same direction as the *P. paniscus* sample. These components are described in more detail above.

Differences between the *P. t. schweinfurthii* and *P. t. troglodytes* samples are only apparent on Component 3 (Figure 3.47), and these differences are slight. As described above, the *P. t. schweinfurthii* sample, along with the *P. t. verus* sample, is shifted slightly toward the low end of the *P. t. troglodytes* range on Component 3.

Summary

In principal components analyses of *Pan* variables, Component 1, which is strongly correlated with size (as measured by the geometric mean), explains between 49% and 65% (approximately) of the total variance in the six sets of analyzed variables. The analyses of foot and hindlimb variables account for the smallest percentages of the total variance on Component 1, followed by the analysis of all variables. The analyses of forelimb, long bone, and hand variables account for greater percentages of the total variance on Component 1, with the largest percentage found in the hand analysis. Male and female *P. troglodytes* individuals have different, yet greatly overlapping, distributions on Component 1 of every analysis, with notably less overlap in the hand analysis. Sex differences in *P. paniscus* are also present, despite a great overlap, on Component 1 of every analysis, with notably smaller differences in the forelimb and hand analyses. In every analysis, it is clear that *P. paniscus* has smaller measurements, overall, than *P. troglodytes*, despite substantial overlap in the Component 1 plots. All the same, two *P. paniscus* specimens have relatively high PC scores, corresponding to relatively large measurements, on Component 1 of the forelimb and foot analyses.

After size differences are accounted for on Component 1 of each principal components analysis, differences between species and subspecies of *Pan* are clearly apparent on further components. At the same time, species and subspecies differences

explain far less of the non-size-related variance than they explain in *Gorilla*, judging by the generally greater amount of overlap between groups in PC score plots for *Pan*.

When results from PCAs of all six sets of variables are compared, differences between *P. paniscus* and *P. troglodytes* account for more of the non-size-related variance than any of the subspecies-level differences. In the analyses of all six sets of variables, the two species have different distributions on Component 2; the *P. paniscus* distribution is always clustered on one side of the *P. troglodytes* distribution, despite being entirely or almost entirely contained within it. Notable differences between the two species are also seen on at least one further component (Component 3, 4, and/or 5) in every analysis.

The three sets of variables that best distinguish the two species on Component 2 are the sets of all variables, hindlimb variables, and foot variables. A clear pattern emerges from the variables with the greatest loadings on Component 2 in these analyses. In the analyses of all variables and hindlimb bones, the three measurements with the greatest loadings are lengths of the femur, tibia, and calcaneal tuberosity. In the analysis of foot bones, which does not include femur and tibia lengths, Component 2 is strongly driven by calcaneal tuberosity length. None of these three variables are significantly different between the species, in either sex, in the comparisons of means.

Analyses of variables from the forelimb, long bones, and hand also distinguish the two species on Component 2, although not as well. The variables that have the greatest loadings on Component 2 in these analyses also fit a pattern and also are dominated by length measurements. In the analysis of long bones (which does not include bones of the hands and feet), lengths of the femur, tibia, humerus, and radius dominate Component 2. As described in the previous paragraph, femur and tibia lengths are among the highest-

loading variables on Component 2 of the analyses of all variables and hindlimbs. In the forelimb analysis, Component 2 is driven by lengths of all the included forelimb elements (including those of the hand), and Component 2 of the hand analysis is driven by lengths of the two hand elements. Humerus and radius lengths are among the most heavily loaded variables on Component 2 of both the long bone and forelimb analyses, and third metacarpal and third proximal hand phalanx lengths are among the most heavily loaded variables on Component 2 of both the forelimb and hand analyses. Although femur and tibia lengths are not significantly different between species, some significant differences are found in the length measurements of the forelimb. Humerus and radius lengths are significantly greater in *P. troglodytes* males than in *P. paniscus* males, and third proximal hand phalanx length is significantly greater in both sexes of *P. troglodytes*. Third metacarpal length is not significantly different between species in either sex, and humerus and radius lengths are not significantly different in females.

In two of the latter three analyses, those of the forelimbs and long bones, Component 2 does not differentiate the two species as well as one of the other components inspected. The analysis of forelimb variables shows the best differentiation between the two species on Component 5, which is driven by third metacarpal length, humerus length, and distal width of the radius. This list duplicates two of the variables that drive Component 2 of the forelimb analysis. Of these three variables, a significant difference between species in comparisons of means is only found in humerus length, and only among males. The analysis of long bones best differentiates the species on Component 4, which is dominated by antero-posterior midshaft diameters of the radius, femur, and tibia. Antero-posterior midshaft diameter of the radius is significantly greater

in both sexes of *P. troglodytes*, but the other two variables are not significantly different between species in either sex. This is the only analysis in which the component that clearly achieves the best differentiation of species is not dominated by length measurements, although Component 2 is dominated by length measurements and does clearly differentiate the species. This is also the only analysis that does not include hands and/or feet. Interestingly, although hand bone lengths appear to play a large role in differentiating species in the analysis of forelimb variables, the analysis of hand variables alone shows the weakest differentiation between species of all the analyses.

Differences between *P. t. verus* and the subspecies *P. t. schweinfurthii* and *P. t. troglodytes* are apparent in every analysis, and they can always be identified on more than one of the inspected components, but these differences are always weak or absent on Component 2. The analyses of all variables and of foot bones show only weak differentiation of *P. t. verus*, but analyses of the other four sets of variables each include one component (Component 3 or 4) that shows *P. t. verus* clearly clustered on one side of the distribution of *P. t. troglodytes* and/or *P. t. schweinfurthii*. When these components are examined, the forelimb analysis differentiates *P. t. verus* from *P. t. schweinfurthii* (Component 4), the hindlimb analysis differentiates *P. t. verus* from *P. t. troglodytes* (Component 3), and the analyses of long bones (Component 4) and hands (Component 3) each differentiate *P. t. verus* from both of the other subspecies. The variables with the greatest loadings on these components are dominated almost entirely by measurements of articular surfaces and shaft widths, but further patterns are difficult to discern. Midshaft diameters of the femur and tibia contribute prominently to both Component 3 of the hindlimb analysis and Component 4 of the long bone analysis, but there is no overlap

between variables that load heavily on the components that best differentiate *P. t. verus* in the long bone, forelimb, and hand analyses, although there is overlap in the variables included in these analyses.

Only one variable is significantly different between *P. t. verus* and *P. t. schweinfurthii* in the comparisons of means. In males only, medio-lateral midshaft diameter of the humerus has a significantly greater mean in *P. t. schweinfurthii* than in *P. t. verus*. This variable is included in two of the three principal components analyses that clearly differentiate *P. t. verus* from *P. t. schweinfurthii*, the forelimb and long bone analyses, but it is not among the variables with the greatest loadings on the components that differentiate these two subspecies.

Ten variables are significantly different, in one or both sexes, between *P. t. verus* and *P. t. troglodytes*, but the principal components analyses that best differentiate these two subspecies do not always emphasize these ten variables among the variables with the greatest loadings on the differentiating components. All of these significantly different variables have greater means in *P. t. troglodytes*. Component 3 of the hindlimb analysis is dominated by the cuboid facet depth of the calcaneus, which is not significantly different between the subspecies. The other variables with heavy loadings on this component are midshaft diameters of the tibia and femur, but only the antero-posterior midshaft diameters are significantly different. The heaviest loadings on Component 4 of the long bone analysis are antero-posterior midshaft diameters of the radius, femur, and tibia, but the radius measurement, which has the greatest loading, is not significantly different between these subspecies. Loadings on Component 3 of the hand analysis are led by the dorso-palmar midshaft diameter of the third metacarpal and the trochlear width

of the third proximal hand phalanx, as well as several other measurements, none of which is among the hand variables that are significantly different between *P. t. verus* and *P. t. troglodytes*.

The distribution of *P. t. vellerosus* is not well-distinguished from the distributions of the other *P. troglodytes* subspecies in most analyses, but it clearly differs from the others in the analyses of long bones and foot bones. The analysis of long bone variables distinguishes *P. t. vellerosus* from the other subspecies, especially *P. t. verus*, based on midshaft diameters of both forelimb and hindlimb elements (Components 4 and 5), and these variables separate it from *P. paniscus*, as well. Although the *P. t. vellerosus* sample size is very small in this analysis (n = 3), the signal appears strong. In the foot analysis, differences between the distributions of *P. t. vellerosus* and the other subspecies appear on Components 2, 4, and 5. No pattern is apparent in the variables with the greatest loadings on these components, as they include lengths, shaft widths, and articular regions, and they include all three foot elements in the study. As there is no overlap between variables included in the foot analysis and variables included in the long bone analysis, there can be no overlap in the variables that contribute most to distinguishing the *P. t. vellerosus* distribution in the two analyses; there is also no obvious correspondence between the types of variables (e.g., lengths, midshaft diameters) that make the greatest contributions. The *P. t. vellerosus* sample in the foot analysis is slightly larger (n = 6) than in the long bone analysis.

Due to the small sample size of *P. t. vellerosus* and its representation of females only, no statistical comparisons of means are made between this subspecies and the others, but the *P. t. vellerosus* mean for cuboid facet depth of the calcaneus is notable for

being greater than the means for this measurement in all three of the other subspecies and especially greater than the *P. t. verus* mean. As one might predict, this variable, cuboid facet depth of the calcaneus, strongly drives a component of the foot analysis that distinguishes *P. t. vellerosus* from the rest of the *P. troglodytes* subspecies but particularly separates the *P. t. vellerosus* sample from the *P. t. verus* sample.

Differences between the distributions of *P. t. troglodytes* and *P. t. schweinfurthii* are very weak. Three of the six analyses show no clear difference between these two subspecies. The other three analyses, those of the forelimb, hindlimb, and foot, show only weak differences between the subspecies, and these differences are only seen in one component of each analysis. Each of these components also distinguishes *P. t. verus* from either *P. t. troglodytes* or *P. t. schweinfurthii*, although this signal is weak in the foot analysis. No differences between *P. t. troglodytes* and *P. t. schweinfurthii* appear in Component 2 of any analysis.

**Populations**

Variation at the population level, based on principal components analyses, is discussed in this section. The most important aspect of population-level variation to be described is the extent to which the included populations of *P. troglodytes* cluster into their assigned species and subspecies. For this reason, only two components of each analysis are inspected, using a scatterplot, for the discussion of population-level variation: the component that best separates the species of *Pan* (which is plotted on the x-axis) and, because *P. t. verus* is the most distinctive subspecies and is differentiated in every analysis, the component that best separates *P. t. verus* from *P. t. schweinfurthii* and/or *P. t. troglodytes* (which is plotted on the y-axis). These two components are

identified based on the preceding evaluation of variation at the species and subspecies levels. Plots of PC scores on these two components of each analysis, grouped by population, are presented in Figures 3.49 – 3.54.

Ten "populations" are included in this population-level exploration of *Pan* variation, but only seven are actually geographic subgroups of a subspecies, while the remaining three each represent an entire subspecies or species. The geographic subgroups (below the subspecies level) include two populations of *P. t. schweinfurthii* and five populations of *P. t. troglodytes*. The other three groups represent *P. t. verus*, *P. t. vellerosus*, and *P. paniscus*. These taxa are not divided into geographic subgroups due to small sample sizes. These three taxon-level groups are nevertheless important to include in the exploration of population-level variation because they permit evaluation of whether the seven populations of *P. t. schweinfurthii* and *P. t. troglodytes* cluster according to their assigned species and subspecies. The ten groups included in this evaluation of population-level variation are listed in Table 2.3.

Because the overlaps between species and between subspecies are much greater in *Pan* than in *Gorilla*, clustering patterns of *P. troglodytes* populations are more ambiguous than clustering patterns of *Gorilla* populations.

All variables

Population-level patterns in the analysis of all variables are explored on Components 2 and 4 (Figure 3.49). Component 2 best differentiates the species of *Pan*. Components 2 and 4 both differentiate *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, but this differentiation is weak. Component 4 also differentiates the two species, but it does not do this as well as Component 2.

All the populations of *P. t. schweinfurthii* and *P. t. troglodytes* greatly overlap on these two components, and the two populations of *P. t. schweinfurthii* do not appear more similar to one another than they are to the populations of *P. t. troglodytes*. In fact, the Northwest population of *P. t. schweinfurthii* ("NW eastern" on the scatterplots) has the most distinctive distribution of any population of *P. t. schweinfurthii* or *P. t. troglodytes*, and it is well-differentiated from the Southeast population of *P. t. schweinfurthii* ("SE eastern" on the scatterplots) on Component 2. The distribution of the Southeast population of *P. t. schweinfurthii* on both components is most similar to that of the Ebolowa population of *P. t. troglodytes*. Minor differences between the populations of *P. t. troglodytes* are apparent on both components. In particular, the distributions of the Batouri and Coast populations are offset from one another on Component 4.

No population of *P. t. schweinfurthii* or *P. t. troglodytes* has a distribution on these two components that is particularly similar to the distributions of either *P. paniscus* or *P. t. verus*, although the Coast population of *P. t. troglodytes* is similar to both *P. paniscus* and *P. t. verus* in including a number of low PC scores on Component 4. The *P. t. vellerosus* sample is not differentiated from *P. t. troglodytes* and *P. t. schweinfurthii* in this analysis.

Forelimb

Population-level patterns in the analysis of forelimb variables are explored on Components 5 and 4 (Figure 3.50). Component 5 best differentiates the species of *Pan*. The species also are distinguished to some extent on Component 4. Component 4 best differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, particularly *P. t.*

*schweinfurthii*. It also weakly distinguishes *P. t. schweinfurthii* and *P. t. troglodytes* from one another.

The populations of *P. t. schweinfurthii* and *P. t. troglodytes* greatly overlap on the two components, but the populations of *P. t. troglodytes* cluster tightly with one another, while the populations of *P. t. schweinfurthii* take on a slightly different distribution. The two *P. t. schweinfurthii* populations appear very similar, given their relatively small sample sizes, except the Southeast population has a greater range in both directions on both components.

The distribution of *P. paniscus* is distinguished on both components from the distributions of all populations of *P. t. schweinfurthii* and *P. t. troglodytes*, despite great overlap. The distribution of *P. t. verus* is quite similar to the distributions of other *P. troglodytes* groups on Component 5, but no population of *P. t. schweinfurthii* or *P. t. troglodytes* is particularly similar to *P. t. verus* on Component 4. The *P. t. vellerosus* sample is not well-distinguished from *P. t. schweinfurthii* and *P. t. troglodytes* in this analysis.

Hindlimb

Population-level patterns in the analysis of hindlimb variables are explored on Components 2 and 3 (Figure 3.51). Component 2 best differentiates the species of *Pan*. Component 3 best differentiates *P. t. verus* from *P. t. troglodytes*. *Pan troglodytes schweinfurthii* and *P. t. troglodytes* are also weakly distinguished from one another on Component 3.

The populations of *P. t. schweinfurthii* and *P. t. troglodytes* overlap to a large extent. The *P. t. troglodytes* populations cluster together loosely on Component 2, while

some of their ranges are slightly offset from one another on Component 3. In particular, the distributions of the Batouri and Coast populations are offset from one another on Component 3, as also seen on Component 4 of the analysis of all variables. The two populations of *P. t. schweinfurthii* have clearly different distributions on Component 2, as in the analysis of all variables, and roughly similar distributions, given their small sample sizes, on Component 3. The populations of *P. t. troglodytes* appear more similar to one another than to either of the populations of *P. t. schweinfurthii* on these two components, but the populations of *P. t. schweinfurthii* each appear more similar to the *P. t. troglodytes* populations than to one another.

Not only do the two populations of *P. t. schweinfurthii* fail to cluster according to their assigned subspecies, but one of them also does not clearly cluster with its species. On Component 2, which best separates the species of *Pan*, the distribution of the Northwest population of *P. t. schweinfurthii* is possibly more similar to that of *P. paniscus* than it is to that of any other *P. troglodytes* group. In addition, the distribution of the Coast population of *P. t. troglodytes* is possibly more similar to that of *P. t. verus* than to the distributions of the other *P. t. troglodytes* populations. The *P. t. vellerosus* sample is not differentiated from *P. t. schweinfurthii* and *P. t. troglodytes* in this analysis.

Long bones

Population-level patterns in the analysis of long bone variables are explored on Components 4 and 3 (Figure 3.52). Component 4 best differentiates the species of *Pan* and best differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*. Component 3 also differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, but it does so less well than Component 4.

The populations of *P. t. schweinfurthii* and *P. t. troglodytes* overlap each other greatly, excepting two populations with more restricted ranges within the larger cluster: the Sangha population of *P. t. troglodytes* and the Northwest population of *P. t. schweinfurthii*. The populations of *P. t. troglodytes* are quite similar on Component 4, except for the small Sangha sample (n = 4). On Component 3, the Batouri and Coast populations are offset from one another, as in the analyses of all variables and hindlimb variables. The populations of *P. t. schweinfurthii* are more similar to one another on Component 3 and less similar on Component 4, where the distribution of the Northwest population is clustered on one side of the Southeast population's distribution. The Southeast population of *P. t. schweinfurthii* has almost exactly the same distribution on these two components as the Ebolowa population of *P. t. troglodytes*, and the Northwest population of *P. t. schweinfurthii* appears similar to the small Sangha sample of *P. t. troglodytes*.

On Component 4, which best differentiates the two species of *Pan*, the *P. paniscus* distribution is entirely unlike that of any *P. troglodytes* group. *Pan troglodytes verus* is relatively well-differentiated from *P. t. schweinfurthii* and *P. t. troglodytes* on Component 4, as well, but its position on this component is very near the positions of the Sangha population of *P. t. troglodytes* and the Northwest population of *P. t. schweinfurthii*. Component 3 differentiates *P. t. verus* less strongly, and the Coast and Abong Mbang populations of *P. t. troglodytes* appear to vary in the direction of *P. t. verus* on this component, although the effect is not strong. The three specimens of *P. t. vellerosus* are tightly clustered on Components 4 and 3, but they are positioned near the

middle of the larger cluster of *P. t. schweinfurthii* and *P. t. troglodytes*, which fails to differentiate them well from the populations of these other subspecies.

Hand

Population-level patterns in the analysis of hand variables are explored on Components 4 and 3 (Figure 3.53). Component 4 best differentiates the species of *Pan*, although no component in the hand analysis strongly differentiates the species. Component 3 best differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*. Component 4 also differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, but differences are not as strong as on Component 3.

No distinctions between *P. t. schweinfurthii* and *P. t. troglodytes* are seen at the population level. While the populations are not tightly clustered, differences between them are weak on both components. The Northwest population of *P. t. schweinfurthii* is especially similar to the Abong Mbang and Sangha populations of *P. t. troglodytes* in exhibiting a negative correlation between the components, but their distributions on each component separately are not different from those of the other *P. t. schweinfurthii* and *P. t. troglodytes* populations.

On Component 4, both *P. paniscus* and *P. t. verus* are clustered on the same side of the *P. t. troglodytes* distribution, and no other groups have a similar distribution. On Component 3, which best differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, no other group has a distribution similar to that of *P. t. verus*. *Pan troglodytes vellerosus* is poorly distinguished from the other groups on these two components.

Foot

Population-level patterns in the analysis of foot variables are explored on Components 2 and 4 (Figure 3.54). Component 2 best differentiates the species of *Pan*. Component 4 best differentiates *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, although no component in the foot analysis strongly differentiates *P. t. verus*.

Most of the populations of *P. t. schweinfurthii* and *P. t. troglodytes* are loosely clustered together on both components, with minor differences in distribution. The two exceptions are the Sangha population of *P. t. troglodytes*, the distribution of which is extended substantially beyond the others on one side of Component 2, and the Southeast population of *P. t. schweinfurthii*, the distribution of which is shifted to the other side of Component 2. The two populations of *P. t. schweinfurthii* do not cluster together, and one of them clusters with populations of *P. t. troglodytes*; the distribution of the Northwest population of *P. t. schweinfurthii* is similar to the distributions of the Abong Mbang and Coast populations of *P. t. troglodytes*.

In the foot analysis, *P. t. schweinfurthii* and *P. t. troglodytes* are weakly differentiated on Component 3. In order to examine whether the populations of these two subspecies cluster more clearly by subspecies when plotted on the component that best separates the subspecies, an additional scatterplot was examined using Component 3 in place of Component 4. Once again, the populations of *P. t. schweinfurthii* and *P. t. troglodytes* do not cluster into their assigned subspecies.

No particular similarities are seen between *P. paniscus* and any other group on Component 2, which best differentiates species, although *P. paniscus* is not dissimilar to some of the other groups, either. On Component 4, which best differentiates *P. t. verus*

from *P. t. schweinfurthii* and *P. t. troglodytes*, no other group is particularly similar to *P. t. verus*, although the distributions of several populations are not unlike its distribution. The *P. t. vellerosus* sample is differentiated from the other subspecies on both Components 2 and 4, and no other group's distribution is similar to its distribution on these components.

Summary

The primary question asked in this section is whether the populations of *P. t. schweinfurthii* and *P. t. troglodytes* cluster according to their assigned species and subspecies. The secondary question asked is whether the individual populations in each of these subspecies vary from one another.

Due to the great overlaps already observed between species and between subspecies within *Pan*, even strong clustering patterns of populations into species and subspecies might be somewhat ambiguous. In addition, the populations of *P. t. schweinfurthii* and *P. t. troglodytes* always greatly overlap one another. As a result, it is impossible to address clustering patterns based on well-separated distributions, and results must rely on more subtle patterns of similarity and difference.

In five of the six analyses, no subspecies-level clustering is seen among the populations of *P. t. schweinfurthii* and *P. t. troglodytes*, and the subspecies-level clustering seen in the forelimb analysis is only slight. Frequently, greater similarities are seen between a population of *P. t. schweinfurthii* and a population of *P. t. troglodytes* than between the two populations of *P. t. schweinfurthii*.

Although the component on the y-axis of the scatterplots is the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes*, the

components that distinguish *P. t. schweinfurthii* and *P. t. troglodytes* from one another are also included in the examination of population clustering patterns. In the subspecies-level results, only three analyses (forelimb, hindlimb, and foot) are found to distinguish *P. t. schweinfurthii* and *P. t. troglodytes*. In each of these three analyses, only one component distinguishes these two subspecies, and it does so only weakly. In the forelimb and hindlimb analyses, this component is the same component that best distinguishes *P. t. verus*; therefore, it is one of the components included in the scatterplot on which population-level results are based. In the foot analysis, this component is not the same as the component that best distinguishes *P. t. verus*. This component was examined in an additional scatterplot for this analysis, but results were no different.

When distributions for *P. t. verus* are compared to distributions for the populations of *P. t. schweinfurthii* and *P. t. troglodytes*, four of six analyses show no particular similarities. In the other two analyses, those of hindlimb and long bone variables, the distributions of one or more populations of *P. t. schweinfurthii* and/or *P. t. troglodytes* have strong similarities to the distribution of *P. t. verus*, but they do not clearly cluster with *P. t. verus*. The small sample of *P. t. vellerosus* is differentiated from *P. t. schweinfurthii* and *P. t. troglodytes* in the foot analysis only, and no population has a similar distribution to that of *P. t. vellerosus* in this analysis.

Despite the overlap between *P. paniscus* and *P. troglodytes* distributions in these analyses, only one case is found where a *P. troglodytes* population appears possibly more similar to *P. paniscus* than to any other population of *P. troglodytes*. In the hindlimb analysis, the Northwest population of *P. t. schweinfurthii* is possibly most similar to *P. paniscus* on the component that best separates species.

Differences between populations of *P. t. troglodytes* are present but small. The Sangha population appears to have a notably different distribution on the x-axes of two analyses, those for long bone and foot variables. At the same time, no pattern is apparent between its distributions in these two analyses, and these results may be artifacts of its small sample sizes. A clearer pattern is seen in the differences between the Batouri and Coast distributions, which are evident on the y-axes of the scatterplots for all variables, hindlimbs, and long bones. On each of these plotted components, there is a small offset between the distributions for these two populations. This offset seems to relate to the distribution of *P. t. verus*, which is distinguished from *P. t. schweinfurthii* and *P. t. troglodytes* on the y-axis component of each analysis. In each case, the Coast distribution is more similar, and the Batouri distribution is less similar, to that of *P. t. verus*.

Within *P. t. schweinfurthii*, the distributions of the two populations clearly differ in four of the six analyses. These differences are always on the x-axis component, and one population always has a smaller distribution. The Southeast population has the smaller distribution in the analyses of all variables, hindlimb variables, and foot variables, and the Northwest population has the smaller distribution in the analysis of long bone variables. The two *P. t. schweinfurthii* populations do not clearly differ in the forelimb and hand analyses.

When attention is focused on cases where there is a particular similarity between a *P. t. schweinfurthii* population and a *P. t. troglodytes* population, three such relationships appear in more than one analysis. The Southeast population of *P. t. schweinfurthii* and the Ebolowa population of *P. t. troglodytes* are particularly similar in analyses of all variables and long bones; the Northwest population of *P. t. schweinfurthii*

and the Sangha population of *P. t. troglodytes* are particularly similar in the analyses of long bones and the hand; and the Northwest population and the Abong Mbang population of *P. t. troglodytes* are particularly similar in the analyses of the hand and foot. As each of these relationships is only present in two analyses, and overlap is great between all the populations of *P. t. schweinfurthii* and *P. t. troglodytes*, these relationships appear to be based on rather limited correspondences.

In brief, the populations of *P. t. schweinfurthii* and *P. t. troglodytes* cluster according to species but not according to subspecies. Small differences can be detected among the populations of *P. t. troglodytes*, and greater differences are apparent between the two populations of *P. t. schweinfurthii*.

## Summary of raw measurement analyses: *Gorilla* and *Pan* compared

### Comparisons of means

Although comparisons of raw measurement means show clear interspecific differences within both *Gorilla* and *Pan*, the patterns of variation between species are different in the two genera. In *Gorilla*, the two species differ primarily in hand and foot bone measurements. In *Pan*, the species differ strongly in some of their hand and foot bones but also in other limb bones; however, interspecific differences are much greater in the forelimb than in the hindlimb. In *Gorilla*, hand and foot ray bone lengths differentiate the species particularly well. In *Pan*, lengths of the third proximal hand and foot phalanges and the first metatarsal are significantly different between species, but lengths of the third metacarpal and third metatarsal are not.

Significant differences between subspecies in raw measurement means are found within both *G. beringei* and *P. troglodytes*, but, when patterns are sought in which

anatomical regions or types of measurements differ the most, no patterns of variation are evident within *G. beringei*. On the other hand, patterns can be detected in which limb elements and measurement types distinguish *P. t. troglodytes* from both *P. t. verus* and *P. t. schweinfurthii*. While most measurements that differ significantly between *P. t. troglodytes* and *P. t. verus* are not the same as the measurements that differ significantly between *P. t. troglodytes* and *P. t. schweinfurthii*, several measurements of the third proximal phalanges are significantly greater in *P. t. troglodytes* than in either *P. t. verus* or *P. t. schweinfurthii*, including phalangeal length in both the hand and the foot. Lengths of hand and foot phalanges also differentiate the two species of *Pan* and the two species of *Gorilla*, but the two subspecies of *G. beringei* have no significant differences in hand or foot phalanx lengths in either sex.

**Principal components analyses**

The first component of every principal components analysis is strongly and significantly correlated with size, as represented by the geometric mean, in both *Gorilla* and *Pan*. Component 1 explains a substantially greater percentage of the total variance in the analyses of *Gorilla* measurements than it does in the analyses of *Pan* measurements, but analyses of foot and hindlimb variables explain the smallest percentage of the total variance in both genera. On the first component of each *Gorilla* analysis, the major separation of groups is between males and females, with the two species separated within each sex cluster in every analysis except that of long bone variables. As hand and foot bones are not included in the analysis of long bone variables, this result is consistent with results from the comparisons of means that show that size differences between the two species of *Gorilla* are concentrated in the hands and feet. The analysis of foot variables

achieves the best separation of species on Component 1. In contrast to the *Gorilla* analyses, the first component of each *Pan* analysis primarily separates the two species, while the sexes are separated within each species cluster. The separation of sexes on the first components of the *Gorilla* analyses is much stronger than the separation of either species or sexes on the first components of the *Pan* analyses. The *Pan* analyses do not differ greatly in the extent of species-level separation on Component 1, but both *P. troglodytes* and *P. paniscus* show notably smaller differences between the sexes in the analysis of hand variables.

Because the first component of each principal components analysis accounts for size-related differences, subsequent components can be considered to reflect differences in shape. In both *Gorilla* and *Pan*, principal components analyses demonstrate a taxonomic hierarchy in the extents of group separation on low-numbered shape components. Separation of species is stronger than separation of subspecies within a species, and separation of subspecies is generally stronger than separation of populations within a subspecies. At all three levels, those of species, subspecies, and populations, separation between groups is greater and more consistent in *Gorilla* than in *Pan*. Patterns of group clustering also reflect the taxonomic hierarchy in *Gorilla*, but group clustering patterns are weaker in *Pan*. In *Gorilla*, the subspecies consistently cluster according to species on the components that best separate species, and the populations usually cluster according to subspecies on the components that best separate subspecies. In *Pan*, detection of clustering patterns is made more difficult by the lesser extent of separation between species and subspecies. When this situation is considered, the subspecies of *P. troglodytes* usually, but not always, appear to cluster with one another to the exclusion of

*P. paniscus*. Taxonomic structuring is even weaker when population-level clustering is examined in populations of *P. t. troglodytes* and *P. t. schweinfurthii*. These populations cluster according to species but not according to subspecies.

Some similarities are seen between principal components analyses of *Gorilla* and *Pan* in the elements and the variables that contribute most to distinguishing species. In both genera, the best separation of species is seen in components that emphasize measurements of hindlimb elements. In *Gorilla*, components that best separate species are found in analyses of all variables and hindlimb variables. In *Pan*, these components are found in analyses of all variables, hindlimb variables, and foot variables. High-loading variables on the component that best separates species in each of these analyses include one or more measurements of foot bones. More specific similarities between the genera are seen in the analyses of hindlimb elements, in which the components that best separate species have in common several high-loading variables: biepicondylar width of the third metatarsal and minimum and maximum shaft width of the third proximal foot phalanx. Curiously, despite the high loading of foot variables on the component that best separates the species of *Gorilla* in the hindlimb analysis, the set of variables that includes only foot bones is among the two sets of variables that separate the species of *Gorilla* least well.

Important differences between *Gorilla* and *Pan* are also apparent in the elements and variables that contribute most to separating species in the principal components analyses. Although the two genera have several measurements in common among the variables with the highest loadings on the components that best separate species, the two genera do not share the stronger pattern seen in *Pan* among high-loading variables on

these components. The components that best separate species of *Pan* (which arise from analyses of all variables, hindlimb variables, and foot variables) are dominated by length measurements, while the components that best separate species of *Gorilla* (which arise from analyses of all variables and hindlimb variables) do not include any length measurements among their high-loading variables. In both genera, however, length measurements are among high-loading variables on the components that best separate species in the analyses of hand and forelimb variables; analyses of other sets of variables better separate the species of each genus, but these analyses do show some species-level separation.

Similarities between *Gorilla* and *Pan* are present but not strong in the elements and variables that contribute most to distinguishing subspecies using principal components analysis. The two components that best separate the two subspecies of *G. beringei* (one from the analysis of all variables and one from the analysis of hindlimb variables) are both driven by the cuboid facet depth of the calcaneus. Interestingly, this is also the highest-loading variable in the component of the hindlimb analysis that best separates *Gorilla* species, and it is the second-highest-loading variable in the component of the analysis of all variables that best separates *Gorilla* species. While this variable does not seem to play a major role in separating the species of *Pan*, it figures prominently in several components that separate subspecies of *P. troglodytes*. It drives a component of the foot analysis that separates *P. t. vellerosus* from *P. t. verus*, and it has the greatest loading on components of the analyses of all variables and hindlimb variables that distinguish *P. t. verus* from other subspecies. At the same time, the more general pattern seen in *P. troglodytes* is that variables that contribute most to distinguishing subspecies

(focusing on components that distinguish *P. t. verus* from *P. t. troglodytes* and/or *P. t. schweinfurthii*, because comparisons of other subspecies show them to be weakly or inconsistently distinguished) tend to be shaft widths and articular surfaces of both forelimb and hindlimb elements. Aside from the strong contribution of the cuboid facet depth of the calcaneus, which is an articular surface, variables of the forelimb and hindlimb that contribute most to separation of *G. beringei* subspecies tend to be shaft widths and bone lengths.

TABLE 3.1. *Gorilla* species (*G. gorilla* vs. *G. beringei*): Results of comparisons of means and two-sample t-tests[1,2] for raw measurements

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value[3]** | **greater mean** | **uncorrected p-value** | **corrected p-value[3]** |
| ***Forelimb*** | | | | | | |
| *Humerus* | | | | | | |
| HUM_LENGTH | gorilla | 0.0235 | 1.0000 | gorilla | 0.1377 | 1.0000 |
| HUM_ML_MID | gorilla | 0.0171 | 0.7368 | gorilla | 0.0573 | 1.0000 |
| HUM_AP_MID | gorilla | 0.5467 | 1.0000 | gorilla | 0.6116 | 1.0000 |
| HUM_SI_HEAD | beringei | 0.3203 | 1.0000 | beringei | 0.0106 | 0.4550 |
| HUM_DISTARTWD | gorilla | 0.1798 | 1.0000 | gorilla | 0.1398 | 1.0000 |
| HUM_BIEPI | gorilla | 0.7577 | 1.0000 | beringei | 0.1708 | 1.0000 |
| *Radius* | | | | | | |
| RAD_LENGTH | gorilla | 0.1632 | 1.0000 | gorilla | 0.0288 | 1.0000 |
| RAD_ML_MID | beringei | 0.6727 | 1.0000 | beringei | 0.0548 | 1.0000 |
| RAD_AP_MID | gorilla | 0.0054 | 0.2311 | gorilla | 0.0000 | **0.0014** |
| RAD_ML_HEAD | beringei | 0.1023 | 1.0000 | beringei | 0.0594 | 1.0000 |
| RAD_DISTALWD | gorilla | 0.0297 | 1.0000 | gorilla | 0.0160 | 0.6865 |
| *Metacarpal 3* | | | | | | |
| MC_LENGTH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| MC_RU_MID | gorilla | 0.5521 | 1.0000 | beringei | 0.8645 | 1.0000 |
| MC_DP_MID | gorilla | 0.0492 | 1.0000 | gorilla | 0.9713 | 1.0000 |
| MC_RU_HEAD | gorilla | 0.0032 | 0.1370 | gorilla | 0.0269 | 1.0000 |
| MC_BIEPI | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
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| Variables | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | greater mean | uncorrected p-value | corrected p-value[3] | greater mean | uncorrected p-value | corrected p-value[3] |
| *Proximal hand phalanx 3* | | | | | | |
| HP_LENGTH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0002** |
| HP_RU_MAX | gorilla | 0.7638 | 1.0000 | gorilla | 0.0458 | 1.0000 |
| HP_RU_MIN | gorilla | 0.0003 | **0.0109** | gorilla | 0.0001 | **0.0031** |
| HP_RU_BASE | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| HP_RU_TROCH | gorilla | 0.0005 | **0.0227** | gorilla | 0.0000 | **0.0019** |
| ***Hindlimb*** | | | | | | |
| *Femur* | | | | | | |
| FEM_LENGTH | beringei | 0.9917 | 1.0000 | beringei | 0.9230 | 1.0000 |
| FEM_ML_MID | gorilla | 0.2780 | 1.0000 | gorilla | 0.1238 | 1.0000 |
| FEM_AP_MID | beringei | 0.0000 | **0.0000** | beringei | 0.0038 | 0.1614 |
| FEM_HEAD_HT | beringei | 0.0546 | 1.0000 | beringei | 0.6066 | 1.0000 |
| FEM_BICON_WD | beringei | 0.1419 | 1.0000 | beringei | 0.9781 | 1.0000 |
| *Tibia* | | | | | | |
| TIB_LENGTH | gorilla | 0.0000 | **0.0008** | gorilla | 0.0001 | **0.0049** |
| TIB_ML_MID | gorilla | 0.1729 | 1.0000 | gorilla | 0.0423 | 1.0000 |
| TIB_AP_MID | gorilla | 0.2623 | 1.0000 | beringei | 0.2539 | 1.0000 |
| TIB_PLATEAU | beringei | 0.4744 | 1.0000 | gorilla | 0.6403 | 1.0000 |
| *Calcaneus* | | | | | | |
| C_LENGTH | gorilla | 0.0078 | 0.3372 | gorilla | 0.0080 | 0.3421 |
| C_TUB_LENGTH | beringei | 0.3590 | 1.0000 | beringei | 0.9772 | 1.0000 |
| C_TUB_HTADJ | gorilla | 0.0713 | 1.0000 | gorilla | 0.0449 | 1.0000 |
| C_TENDON_WD | gorilla | 0.0002 | **0.0076** | gorilla | 0.0000 | **0.0002** |
| C_CUB_WD | gorilla | 0.0000 | **0.0000** | gorilla | 0.0035 | 0.1525 |
| C_CUB_DPADJ | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0015** |
| | | | | | | |
| | | | | | | |

| Variables | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | greater mean | uncorrected p-value | corrected p-value[3] | greater mean | uncorrected p-value | corrected p-value[3] |
| *Metatarsal 1* | | | | | | |
| MT1_LENGTH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0002** |
| *Metatarsal 3* | | | | | | |
| MT3_LENGTH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| MT3_ML_HEAD | gorilla | 0.0000 | **0.0021** | gorilla | 0.0012 | **0.0528** |
| MT3_BIEPI | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| *Proximal foot phalanx 3* | | | | | | |
| FP_LENGTH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| FP_MAXSHAFT | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| FP_MINSHAFT | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 3.2. *G. g. gorilla* vs. *G. b. beringei*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | gorilla | **0.0100** | gorilla | 0.3514 |
| HUM_ML_MID | gorilla | **0.0201** | gorilla | 1.0000 |
| HUM_AP_MID | gorilla | 1.0000 | beringei | 1.0000 |
| HUM_SI_HEAD | beringei | 0.9435 | beringei | 0.0563 |
| HUM_DISTARTWD | gorilla | **0.0012** | gorilla | 0.1950 |
| HUM_BIEPI | gorilla | 0.4558 | beringei | 1.0000 |
| *Radius* | | | | |
| RAD_LENGTH | gorilla | 1.0000 | gorilla | 1.0000 |
| RAD_ML_MID | beringei | 1.0000 | beringei | 0.1050 |
| RAD_AP_MID | gorilla | 0.0921 | gorilla | 0.0652 |
| RAD_ML_HEAD | beringei | 0.5240 | beringei | 0.6468 |
| RAD_DISTALWD | gorilla | 0.1839 | gorilla | **0.0057** |
| *Metacarpal 3* | | | | |
| MC_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| MC_RU_MID | beringei | 1.0000 | beringei | 0.1946 |
| MC_DP_MID | gorilla | 1.0000 | beringei | 1.0000 |
| MC_RU_HEAD | gorilla | 1.0000 | gorilla | 1.0000 |
| MC_BIEPI | gorilla | **0.0000** | gorilla | **0.0014** |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | gorilla | **0.0002** | gorilla | **0.0025** |
| HP_RU_MAX | gorilla | 0.8910 | gorilla | 0.5025 |
| HP_RU_MIN | gorilla | **0.0008** | gorilla | 0.0842 |
| HP_RU_BASE | gorilla | **0.0000** | gorilla | **0.0004** |
| HP_RU_TROCH | gorilla | **0.0447** | gorilla | **0.0286** |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | gorilla | 1.0000 | beringei | 1.0000 |
| FEM_ML_MID | gorilla | 0.2695 | gorilla | 1.0000 |
| FEM_AP_MID | beringei | **0.0000** | beringei | **0.0003** |
| FEM_HEAD_HT | gorilla | 1.0000 | beringei | 1.0000 |
| FEM_BICON_WD | gorilla | 1.0000 | gorilla | 1.0000 |
| *Tibia* | | | | |
| TIB_LENGTH | gorilla | **0.0005** | gorilla | **0.0263** |
| TIB_ML_MID | gorilla | 0.7986 | gorilla | 1.0000 |
| TIB_AP_MID | gorilla | 1.0000 | beringei | 0.6314 |
| TIB_PLATEAU | gorilla | 1.0000 | gorilla | 0.4700 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | gorilla | 0.2831 | gorilla | 0.1192 |
| C_TUB_LENGTH | beringei | 1.0000 | gorilla | 1.0000 |
| C_TUB_HTADJ | beringei | 0.9958 | gorilla | 1.0000 |
| C_TENDON_WD | gorilla | **0.0047** | gorilla | **0.0000** |
| C_CUB_WD | gorilla | **0.0066** | gorilla | 0.0678 |
| C_CUB_DPADJ | gorilla | **0.0000** | gorilla | **0.0005** |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | gorilla | **0.0021** | gorilla | **0.0060** |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| MT3_ML_HEAD | gorilla | 0.3053 | gorilla | 0.7297 |
| MT3_BIEPI | gorilla | **0.0000** | gorilla | **0.0001** |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | gorilla | **0.0011** | gorilla | **0.0000** |
| FP_MAXSHAFT | gorilla | **0.0002** | gorilla | **0.0000** |
| FP_MINSHAFT | gorilla | **0.0000** | gorilla | **0.0000** |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 3.3. *G. g. gorilla* vs. *G. b. graueri*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | gorilla | 1.0000 | gorilla | 1.0000 |
| HUM_ML_MID | gorilla | 1.0000 | gorilla | 0.2068 |
| HUM_AP_MID | gorilla | 1.0000 | gorilla | 1.0000 |
| HUM_SI_HEAD | graueri | 1.0000 | graueri | 0.2918 |
| HUM_DISTARTWD | graueri | 0.7503 | gorilla | 1.0000 |
| HUM_BIEPI | graueri | 1.0000 | graueri | 0.8921 |
| *Radius* | | | | |
| RAD_LENGTH | gorilla | 0.4602 | gorilla | **0.0341** |
| RAD_ML_MID | graueri | 1.0000 | graueri | 1.0000 |
| RAD_AP_MID | gorilla | 0.1861 | gorilla | **0.0012** |
| RAD_ML_HEAD | graueri | 0.9153 | graueri | 0.1998 |
| RAD_DISTALWD | gorilla | 0.3782 | gorilla | 1.0000 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| MC_RU_MID | gorilla | 0.6768 | gorilla | 0.2627 |
| MC_DP_MID | gorilla | **0.0471** | gorilla | 1.0000 |
| MC_RU_HEAD | gorilla | **0.0001** | gorilla | **0.0072** |
| MC_BIEPI | gorilla | **0.0000** | gorilla | **0.0001** |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | gorilla | **0.0002** | gorilla | **0.0009** |
| HP_RU_MAX | graueri | 1.0000 | gorilla | 0.5157 |
| HP_RU_MIN | gorilla | **0.0073** | gorilla | **0.0021** |
| HP_RU_BASE | gorilla | **0.0000** | gorilla | **0.0000** |
| HP_RU_TROCH | gorilla | **0.0008** | gorilla | **0.0043** |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | graueri | 1.0000 | graueri | 1.0000 |
| FEM_ML_MID | gorilla | 1.0000 | gorilla | 0.1866 |
| FEM_AP_MID | graueri | **0.0008** | graueri | 1.0000 |
| FEM_HEAD_HT | graueri | **0.0009** | graueri | 1.0000 |
| FEM_BICON_WD | graueri | **0.0347** | graueri | 0.8516 |
| *Tibia* | | | | |
| TIB_LENGTH | gorilla | 0.2475 | gorilla | **0.0099** |
| TIB_ML_MID | gorilla | 1.0000 | gorilla | **0.0034** |
| TIB_AP_MID | gorilla | 0.7538 | gorilla | 1.0000 |
| TIB_PLATEAU | graueri | 0.2372 | graueri | 1.0000 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | gorilla | **0.0128** | gorilla | 0.1307 |
| C_TUB_LENGTH | graueri | 0.6550 | graueri | 1.0000 |
| C_TUB_HTADJ | gorilla | **0.0044** | gorilla | **0.0029** |
| C_TENDON_WD | gorilla | **0.0021** | gorilla | **0.0173** |
| C_CUB_WD | gorilla | **0.0000** | gorilla | 0.6455 |
| C_CUB_DPADJ | gorilla | **0.0009** | gorilla | 0.5072 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| MT3_ML_HEAD | gorilla | **0.0000** | gorilla | **0.0001** |
| MT3_BIEPI | gorilla | **0.0000** | gorilla | **0.0001** |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | gorilla | **0.0000** | gorilla | **0.0000** |
| FP_MAXSHAFT | gorilla | **0.0000** | gorilla | **0.0007** |
| FP_MINSHAFT | gorilla | **0.0000** | gorilla | **0.0000** |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 3.4. *G. b. beringei* vs. *G. b. graueri*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | graueri | 0.1408 | graueri | 1.0000 |
| HUM_ML_MID | graueri | 0.3935 | beringei | 0.8894 |
| HUM_AP_MID | graueri | 1.0000 | beringei | 1.0000 |
| HUM_SI_HEAD | beringei | 1.0000 | beringei | 1.0000 |
| HUM_DISTARTWD | graueri | **0.0012** | graueri | 0.7014 |
| HUM_BIEPI | graueri | 0.2018 | graueri | 1.0000 |
| *Radius* | | | | |
| RAD_LENGTH | beringei | 1.0000 | beringei | 0.3997 |
| RAD_ML_MID | graueri | 1.0000 | beringei | 0.5720 |
| RAD_AP_MID | graueri | 1.0000 | beringei | 0.5202 |
| RAD_ML_HEAD | beringei | 1.0000 | graueri | 1.0000 |
| RAD_DISTALWD | graueri | 1.0000 | graueri | 0.1484 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | beringei | 0.9756 | beringei | 0.0772 |
| MC_RU_MID | beringei | 0.8318 | beringei | **0.0281** |
| MC_DP_MID | beringei | 0.6928 | beringei | 0.5983 |
| MC_RU_HEAD | beringei | 0.0663 | beringei | 0.3074 |
| MC_BIEPI | graueri | 1.0000 | beringei | 1.0000 |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | graueri | 1.0000 | beringei | 1.0000 |
| HP_RU_MAX | graueri | 0.9111 | graueri | 1.0000 |
| HP_RU_MIN | graueri | 1.0000 | beringei | 1.0000 |
| HP_RU_BASE | graueri | 1.0000 | beringei | 1.0000 |
| HP_RU_TROCH | beringei | 1.0000 | beringei | 1.0000 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | graueri | 1.0000 | graueri | 1.0000 |
| FEM_ML_MID | graueri | 0.6363 | beringei | 0.5383 |
| FEM_AP_MID | beringei | 0.4034 | beringei | 0.0606 |
| FEM_HEAD_HT | graueri | **0.0097** | graueri | 1.0000 |
| FEM_BICON_WD | graueri | 0.0696 | graueri | 0.4463 |
| *Tibia* | | | | |
| TIB_LENGTH | graueri | 0.3459 | beringei | 1.0000 |
| TIB_ML_MID | graueri | 1.0000 | beringei | **0.0365** |
| TIB_AP_MID | beringei | 1.0000 | beringei | 1.0000 |
| TIB_PLATEAU | graueri | 0.1656 | graueri | 0.2433 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | beringei | 1.0000 | graueri | 1.0000 |
| C_TUB_LENGTH | graueri | 1.0000 | graueri | 1.0000 |
| C_TUB_HTADJ | beringei | **0.0188** | beringei | **0.0365** |
| C_TENDON_WD | graueri | 1.0000 | graueri | 0.7079 |
| C_CUB_WD | beringei | 1.0000 | graueri | 1.0000 |
| C_CUB_DPADJ | graueri | 0.2971 | graueri | 0.2521 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | beringei | 1.0000 | beringei | 0.7844 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | graueri | 1.0000 | graueri | 1.0000 |
| MT3_ML_HEAD | beringei | **0.0442** | beringei | 0.0739 |
| MT3_BIEPI | beringei | 1.0000 | graueri | 1.0000 |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | beringei | 1.0000 | graueri | 1.0000 |
| FP_MAXSHAFT | graueri | 1.0000 | graueri | 1.0000 |
| FP_MINSHAFT | beringei | 0.9483 | beringei | 0.5534 |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

TABLE 3.5. *Pan* species (*P. troglodytes* vs. *P. paniscus*): Results of comparisons of means and two-sample t-tests[1,2] for raw measurements

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value[3]** | **greater mean** | **uncorrected p-value** | **corrected p-value[3]** |
| ***Forelimb*** | | | | | | |
| *Humerus* | | | | | | |
| HUM_LENGTH | trog. | 0.0001 | **0.0054** | trog. | 0.0334 | 1.0000 |
| HUM_ML_MID | trog. | 0.0000 | **0.0009** | trog. | 0.0000 | **0.0000** |
| HUM_AP_MID | trog. | 0.0000 | **0.0000** | trog. | 0.0010 | **0.0433** |
| HUM_SI_HEAD | trog. | 0.0001 | **0.0026** | trog. | 0.0002 | **0.0073** |
| HUM_DISTARTWD | trog. | 0.0000 | **0.0001** | trog. | 0.0004 | **0.0173** |
| HUM_BIEPI | trog. | 0.0008 | **0.0331** | trog. | 0.0030 | 0.1306 |
| *Radius* | | | | | | |
| RAD_LENGTH | trog. | 0.0002 | **0.0100** | trog. | 0.0592 | 1.0000 |
| RAD_ML_MID | trog. | 0.0000 | **0.0002** | trog. | 0.0000 | **0.0011** |
| RAD_AP_MID | trog. | 0.0000 | **0.0000** | trog. | 0.0000 | **0.0014** |
| RAD_ML_HEAD | trog. | 0.0000 | **0.0000** | trog. | 0.0008 | **0.0324** |
| RAD_DISTALWD | trog. | 0.0043 | 0.1863 | trog. | 0.4953 | 1.0000 |
| *Metacarpal 3* | | | | | | |
| MC_LENGTH | trog. | 0.3055 | 1.0000 | trog. | 0.0771 | 1.0000 |
| MC_RU_MID | trog. | 0.0000 | **0.0012** | trog. | 0.0031 | 0.1323 |
| MC_DP_MID | trog. | 0.0000 | **0.0006** | trog. | 0.0013 | 0.0568 |
| MC_RU_HEAD | trog. | 0.0020 | 0.0881 | trog. | 0.0007 | **0.0304** |
| MC_BIEPI | trog. | 0.0000 | **0.0013** | trog. | 0.0006 | **0.0250** |
| | | | | | | |
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| | | | | | | |
| | | | | | | |

| Variables | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | greater mean | uncorrected p-value | corrected p-value[3] | greater mean | uncorrected p-value | corrected p-value[3] |
| *Proximal hand phalanx 3* | | | | | | |
| HP_LENGTH | trog. | 0.0003 | **0.0146** | trog. | 0.0000 | **0.0004** |
| HP_RU_MAX | trog. | 0.0000 | **0.0000** | trog. | 0.0000 | **0.0000** |
| HP_RU_MIN | trog. | 0.0000 | **0.0000** | trog. | 0.0001 | **0.0056** |
| HP_RU_BASE | trog. | 0.0002 | **0.0080** | trog. | 0.0000 | **0.0001** |
| HP_RU_TROCH | trog. | 0.0000 | **0.0006** | trog. | 0.0002 | **0.0077** |
| ***Hindlimb*** | | | | | | |
| *Femur* | | | | | | |
| FEM_LENGTH | trog. | 0.1314 | 1.0000 | trog. | 0.6397 | 1.0000 |
| FEM_ML_MID | trog. | 0.0002 | **0.0085** | trog. | 0.0000 | **0.0001** |
| FEM_AP_MID | trog. | 0.1270 | 1.0000 | trog. | 0.0046 | 0.1997 |
| FEM_HEAD_HT | trog. | 0.0007 | **0.0307** | trog. | 0.0074 | 0.3195 |
| FEM_BICON_WD | trog. | 0.0339 | 1.0000 | trog. | 0.0050 | 0.2168 |
| *Tibia* | | | | | | |
| TIB_LENGTH | trog. | 0.1883 | 1.0000 | trog. | 0.0615 | 1.0000 |
| TIB_ML_MID | trog. | 0.1164 | 1.0000 | trog. | 0.0889 | 1.0000 |
| TIB_AP_MID | paniscus | 0.9209 | 1.0000 | trog. | 0.0711 | 1.0000 |
| TIB_PLATEAU | trog. | 0.0298 | 1.0000 | trog. | 0.0041 | 0.1769 |
| *Calcaneus* | | | | | | |
| C_LENGTH | paniscus | 0.9939 | 1.0000 | trog. | 0.2071 | 1.0000 |
| C_TUB_LENGTH | paniscus | 0.0678 | 1.0000 | paniscus | 0.4800 | 1.0000 |
| C_TUB_HTADJ | trog. | 0.0362 | 1.0000 | trog. | 0.0000 | **0.0007** |
| C_TENDON_WD | trog. | 0.0494 | 1.0000 | trog. | 0.0297 | 1.0000 |
| C_CUB_WD | trog. | 0.0807 | 1.0000 | trog. | 0.0210 | 0.9028 |
| C_CUB_DPADJ | trog. | 0.8101 | 1.0000 | paniscus | 0.3711 | 1.0000 |
| | | | | | | |
| | | | | | | |

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Metatarsal 1* | | | | | | |
| MT1_LENGTH | trog. | 0.0003 | **0.0108** | trog. | 0.0000 | **0.0000** |
| *Metatarsal 3* | | | | | | |
| MT3_LENGTH | trog. | 0.1325 | 1.0000 | trog. | 0.0044 | 0.1908 |
| MT3_ML_HEAD | trog. | 0.0353 | 1.0000 | trog. | 0.0029 | 0.1267 |
| MT3_BIEPI | trog. | 0.0836 | 1.0000 | trog. | 0.0079 | 0.3416 |
| *Proximal foot phalanx 3* | | | | | | |
| FP_LENGTH | trog. | 0.0010 | **0.0441** | trog. | 0.0000 | **0.0006** |
| FP_MAXSHAFT | trog. | 0.0017 | 0.0729 | trog. | 0.0000 | **0.0002** |
| FP_MINSHAFT | trog. | 0.0004 | **0.0177** | trog. | 0.0004 | **0.0151** |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 3.6. *P. t. verus* vs. *P. t. schweinfurthii*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HUM_ML_MID | schweinfurthii | **0.0027** | schweinfurthii | 0.1155 |
| HUM_AP_MID | verus | 1.0000 | verus | 1.0000 |
| HUM_SI_HEAD | verus | 1.0000 | schweinfurthii | 0.8754 |
| HUM_DISTARTWD | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HUM_BIEPI | verus | 0.2878 | verus | 0.3593 |
| *Radius* | | | | |
| RAD_LENGTH | schweinfurthii | 1.0000 | verus | 1.0000 |
| RAD_ML_MID | schweinfurthii | 0.0915 | schweinfurthii | 1.0000 |
| RAD_AP_MID | schweinfurthii | 1.0000 | verus | 0.5337 |
| RAD_ML_HEAD | verus | 0.3284 | verus | 0.2747 |
| RAD_DISTALWD | verus | 1.0000 | verus | 0.2158 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | verus | 1.0000 | schweinfurthii | 0.7777 |
| MC_RU_MID | verus | 1.0000 | verus | 1.0000 |
| MC_DP_MID | schweinfurthii | 0.6308 | schweinfurthii | 1.0000 |
| MC_RU_HEAD | verus | 1.0000 | verus | 0.3785 |
| MC_BIEPI | verus | 1.0000 | verus | 0.1662 |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | verus | 1.0000 | schweinfurthii | 0.2489 |
| HP_RU_MAX | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HP_RU_MIN | schweinfurthii | 1.0000 | verus | 1.0000 |
| HP_RU_BASE | verus | 1.0000 | verus | 1.0000 |
| HP_RU_TROCH | verus | 0.9337 | verus | 0.4946 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | schweinfurthii | 1.0000 | schweinfurthii | 0.6801 |
| FEM_ML_MID | verus | 0.1715 | verus | 0.5247 |
| FEM_AP_MID | schweinfurthii | 0.0590 | schweinfurthii | 0.0843 |
| FEM_HEAD_HT | schweinfurthii | 0.0681 | schweinfurthii | 0.2792 |
| FEM_BICON_WD | verus | 0.5604 | verus | 1.0000 |
| *Tibia* | | | | |
| TIB_LENGTH | schweinfurthii | 0.2438 | schweinfurthii | 0.7564 |
| TIB_ML_MID | verus | 1.0000 | schweinfurthii | 1.0000 |
| TIB_AP_MID | schweinfurthii | 1.0000 | schweinfurthii | 0.8585 |
| TIB_PLATEAU | verus | 0.8017 | schweinfurthii | 1.0000 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | schweinfurthii | 1.0000 | schweinfurthii | 0.5170 |
| C_TUB_LENGTH | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| C_TUB_HTADJ | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| C_TENDON_WD | verus | 0.4960 | verus | 0.3306 |
| C_CUB_WD | schweinfurthii | 1.0000 | verus | 1.0000 |
| C_CUB_DPADJ | schweinfurthii | 1.0000 | schweinfurthii | 0.1503 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | verus | 1.0000 | schweinfurthii | 1.0000 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | verus | 0.9826 | verus | 1.0000 |
| MT3_ML_HEAD | schweinfurthii | 1.0000 | verus | 1.0000 |
| MT3_BIEPI | verus | 0.7915 | verus | 1.0000 |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | verus | 1.0000 | schweinfurthii | 1.0000 |
| FP_MAXSHAFT | verus | 1.0000 | schweinfurthii | 1.0000 |
| FP_MINSHAFT | schweinfurthii | 0.7604 | schweinfurthii | 0.9997 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 3.7. *P. t. verus* vs. *P. t. troglodytes*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | troglodytes | 0.8711 | troglodytes | 1.0000 |
| HUM_ML_MID | troglodytes | **0.0005** | troglodytes | **0.0236** |
| HUM_AP_MID | troglodytes | 0.7468 | verus | 1.0000 |
| HUM_SI_HEAD | troglodytes | 0.3466 | troglodytes | 0.1685 |
| HUM_DISTARTWD | troglodytes | 0.1924 | troglodytes | 0.5762 |
| HUM_BIEPI | troglodytes | 1.0000 | verus | 1.0000 |
| *Radius* | | | | |
| RAD_LENGTH | troglodytes | 0.0877 | troglodytes | 0.5278 |
| RAD_ML_MID | troglodytes | **0.0397** | troglodytes | 0.6412 |
| RAD_AP_MID | troglodytes | 1.0000 | verus | 1.0000 |
| RAD_ML_HEAD | troglodytes | 0.8682 | troglodytes | 1.0000 |
| RAD_DISTALWD | troglodytes | 0.6136 | verus | 1.0000 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | troglodytes | 0.6703 | troglodytes | 0.0615 |
| MC_RU_MID | troglodytes | 0.3665 | troglodytes | 1.0000 |
| MC_DP_MID | troglodytes | 0.0583 | troglodytes | 0.6364 |
| MC_RU_HEAD | troglodytes | 0.4402 | troglodytes | 1.0000 |
| MC_BIEPI | troglodytes | 1.0000 | verus | 1.0000 |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | troglodytes | 0.6846 | troglodytes | **0.0125** |
| HP_RU_MAX | troglodytes | **0.0329** | troglodytes | **0.0513** |
| HP_RU_MIN | troglodytes | 0.1198 | troglodytes | 1.0000 |
| HP_RU_BASE | troglodytes | 0.4174 | troglodytes | 0.9533 |
| HP_RU_TROCH | verus | 1.0000 | troglodytes | 1.0000 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | troglodytes | 1.0000 | troglodytes | 0.5991 |
| FEM_ML_MID | verus | 1.0000 | troglodytes | 1.0000 |
| FEM_AP_MID | troglodytes | **0.0008** | troglodytes | **0.0021** |
| FEM_HEAD_HT | troglodytes | **0.0009** | troglodytes | 0.0559 |
| FEM_BICON_WD | troglodytes | 0.3257 | troglodytes | 0.6181 |
| *Tibia* | | | | |
| TIB_LENGTH | troglodytes | **0.0280** | troglodytes | 0.2166 |
| TIB_ML_MID | troglodytes | 0.1768 | troglodytes | 0.6515 |
| TIB_AP_MID | troglodytes | **0.0244** | troglodytes | **0.0058** |
| TIB_PLATEAU | troglodytes | 0.5623 | troglodytes | 0.1413 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | troglodytes | 0.4563 | troglodytes | 1.0000 |
| C_TUB_LENGTH | troglodytes | 0.7284 | verus | 1.0000 |
| C_TUB_HTADJ | troglodytes | 1.0000 | troglodytes | 1.0000 |
| C_TENDON_WD | troglodytes | 1.0000 | verus | 1.0000 |
| C_CUB_WD | troglodytes | 1.0000 | verus | 0.4555 |
| C_CUB_DPADJ | troglodytes | 1.0000 | troglodytes | 0.1358 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | troglodytes | 1.0000 | troglodytes | 0.3857 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | troglodytes | 1.0000 | troglodytes | 0.5825 |
| MT3_ML_HEAD | troglodytes | 0.3711 | verus | 1.0000 |
| MT3_BIEPI | troglodytes | 1.0000 | troglodytes | 1.0000 |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | troglodytes | 0.4214 | troglodytes | **0.0223** |
| FP_MAXSHAFT | troglodytes | 1.0000 | troglodytes | 0.4985 |
| FP_MINSHAFT | troglodytes | **0.0105** | troglodytes | 1.0000 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 3.8. *P. t. schweinfurthii* vs. *P. t. troglodytes*:
Results of comparisons of means and ANOVAs[1] for raw measurements

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | troglodytes | 1.0000 | troglodytes | 1.0000 |
| HUM_ML_MID | troglodytes | 1.0000 | schweinfurthii | 1.0000 |
| HUM_AP_MID | troglodytes | **0.0052** | schweinfurthii | 1.0000 |
| HUM_SI_HEAD | troglodytes | **0.0387** | troglodytes | 1.0000 |
| HUM_DISTARTWD | troglodytes | **0.0465** | troglodytes | 1.0000 |
| HUM_BIEPI | troglodytes | **0.0014** | troglodytes | 0.3389 |
| *Radius* | | | | |
| RAD_LENGTH | troglodytes | 0.1607 | troglodytes | 0.1351 |
| RAD_ML_MID | troglodytes | 1.0000 | troglodytes | 1.0000 |
| RAD_AP_MID | troglodytes | 1.0000 | troglodytes | 0.3903 |
| RAD_ML_HEAD | troglodytes | **0.0001** | troglodytes | **0.0450** |
| RAD_DISTALWD | troglodytes | 0.0865 | troglodytes | 0.2732 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | troglodytes | 0.1575 | troglodytes | 1.0000 |
| MC_RU_MID | troglodytes | **0.0370** | troglodytes | 0.8035 |
| MC_DP_MID | troglodytes | 0.3565 | troglodytes | 0.8791 |
| MC_RU_HEAD | troglodytes | 0.0671 | troglodytes | **0.0268** |
| MC_BIEPI | troglodytes | 0.1227 | troglodytes | **0.0465** |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | troglodytes | **0.0119** | troglodytes | 1.0000 |
| HP_RU_MAX | troglodytes | **0.0123** | troglodytes | 0.2215 |
| HP_RU_MIN | troglodytes | **0.0152** | troglodytes | 1.0000 |
| HP_RU_BASE | troglodytes | **0.0026** | troglodytes | 0.3451 |
| HP_RU_TROCH | troglodytes | 0.7713 | troglodytes | 0.1562 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| FEM_ML_MID | troglodytes | **0.0304** | troglodytes | 0.1439 |
| FEM_AP_MID | troglodytes | 0.3382 | troglodytes | 1.0000 |
| FEM_HEAD_HT | troglodytes | 0.3036 | troglodytes | 1.0000 |
| FEM_BICON_WD | troglodytes | **0.0001** | troglodytes | 0.3386 |
| *Tibia* | | | | |
| TIB_LENGTH | troglodytes | 0.9818 | troglodytes | 1.0000 |
| TIB_ML_MID | troglodytes | **0.0032** | troglodytes | 1.0000 |
| TIB_AP_MID | troglodytes | 0.0652 | troglodytes | 0.2194 |
| TIB_PLATEAU | troglodytes | **0.0018** | troglodytes | 0.7946 |
| | | | | |
| | | | | |

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Calcaneus* | | | | |
| C_LENGTH | troglodytes | 1.0000 | schweinfurthii | 0.8545 |
| C_TUB_LENGTH | troglodytes | 1.0000 | schweinfurthii | 0.4043 |
| C_TUB_HTADJ | troglodytes | 1.0000 | troglodytes | 1.0000 |
| C_TENDON_WD | troglodytes | **0.0326** | troglodytes | 0.2510 |
| C_CUB_WD | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| C_CUB_DPADJ | troglodytes | 1.0000 | schweinfurthii | 1.0000 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | troglodytes | 1.0000 | troglodytes | 0.3985 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | troglodytes | 0.0934 | troglodytes | 0.2944 |
| MT3_ML_HEAD | troglodytes | 0.4035 | schweinfurthii | 1.0000 |
| MT3_BIEPI | troglodytes | 0.1484 | troglodytes | 0.3799 |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | troglodytes | **0.0037** | troglodytes | 0.2381 |
| FP_MAXSHAFT | troglodytes | 0.5849 | troglodytes | 1.0000 |
| FP_MINSHAFT | troglodytes | **0.0443** | schweinfurthii | 1.0000 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. schweinfurthii*, *P. t. troglodytes*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 3.9. Principal components analysis of all variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 33.8413 | 1.8932 | 1.1687 | 0.8607 | 0.5842 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 78.7008 | 4.4029 | 2.7179 | 2.0016 | 1.3585 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| HUMDISTARTWD | 0.9479 | 0.1262 | 0.0646 | -0.0238 | -0.0372 |
| C_LENGTH | 0.9461 | 0.0186 | 0.1456 | -0.0390 | -0.0673 |
| HP_RU_BASE | 0.9456 | -0.1849 | -0.0633 | 0.0289 | -0.1389 |
| HP_RU_TROCH | 0.9438 | -0.0930 | 0.0050 | -0.0307 | -0.1313 |
| TIB_PLATEAU | 0.9429 | 0.1733 | 0.0578 | -0.0193 | -0.0467 |
| TIB_LENGTH | 0.9418 | 0.0051 | 0.2213 | 0.0440 | 0.1401 |
| FEM_BICON_WD | 0.9393 | 0.1895 | 0.0951 | -0.0268 | -0.0867 |
| HUM_BIEPI | 0.9386 | 0.1656 | 0.0847 | -0.0558 | -0.0449 |
| HP_RU_MIN | 0.9336 | -0.0946 | -0.1332 | 0.0332 | -0.0720 |
| FEM_HEAD_HT | 0.9334 | 0.2327 | 0.1304 | -0.0096 | -0.1061 |
| MC_RU_HEAD | 0.9306 | -0.0289 | 0.0353 | 0.0945 | -0.1505 |
| RAD_LENGTH | 0.9263 | 0.0638 | 0.2693 | 0.0436 | 0.0995 |
| HP_RU_MAX | 0.9227 | 0.0779 | -0.1356 | 0.0229 | -0.0925 |
| MT1_LENGTH | 0.9216 | -0.1696 | 0.1402 | 0.0883 | 0.1467 |
| FEM_ML_MID | 0.9212 | 0.0890 | -0.1543 | -0.0684 | 0.1390 |
| HUM_LENGTH | 0.9196 | 0.1088 | 0.2470 | -0.0009 | 0.0611 |
| HP_LENGTH | 0.9190 | -0.1545 | 0.2224 | 0.0465 | 0.0950 |
| RAD_ML_HEAD | 0.9184 | 0.2397 | 0.0481 | -0.0771 | -0.1431 |
| FEM_LENGTH | 0.9169 | 0.1478 | 0.2787 | 0.0434 | 0.0485 |
| C_TUB_HTADJ | 0.9166 | 0.0836 | 0.0219 | -0.0394 | -0.1305 |
| HUM_SI_HEAD | 0.9096 | 0.2486 | 0.0788 | -0.0215 | -0.1085 |
| MC_BIEPI | 0.9064 | -0.2147 | -0.0689 | 0.0582 | -0.1634 |
| HUM_ML_MID | 0.9008 | 0.0838 | -0.1867 | -0.1199 | 0.1971 |
| MT3_ML_HEAD | 0.8939 | -0.1562 | -0.1126 | 0.1736 | -0.1636 |
| RAD_DISTALWD | 0.8938 | 0.0012 | 0.0502 | 0.0298 | 0.0427 |
| C_TENDON_WD | 0.8886 | -0.0705 | -0.0057 | 0.0247 | -0.0055 |
| FP_LENGTH | 0.8878 | -0.2885 | 0.1852 | 0.1281 | 0.0923 |
| TIB_ML_MID | 0.8870 | 0.0343 | -0.2931 | -0.0254 | 0.0960 |
| HUM_AP_MID | 0.8835 | 0.1983 | -0.2133 | -0.0795 | 0.1199 |
| MC_LENGTH | 0.8751 | -0.3219 | 0.2007 | 0.0588 | 0.1215 |
| RAD_AP_MID | 0.8703 | 0.0295 | -0.1929 | -0.0546 | 0.1931 |
| TIB_AP_MID | 0.8670 | 0.1374 | -0.1735 | 0.0040 | 0.1601 |
| MC_DP_MID | 0.8650 | 0.0681 | -0.1052 | 0.0691 | 0.2325 |
| MT3_LENGTH | 0.8619 | -0.3518 | 0.1754 | 0.0949 | 0.1149 |
| C_CUB_WD | 0.8518 | -0.1079 | -0.0315 | -0.1341 | -0.0732 |
| C_TUBLENGTH | 0.8462 | 0.1823 | 0.1942 | -0.0481 | -0.1185 |
| RAD_ML_MID | 0.8437 | 0.2760 | -0.2233 | -0.0580 | 0.0674 |
| FP_MAXSHAFT | 0.8403 | -0.3111 | -0.2543 | 0.0446 | 0.0063 |
| MC_RU_MID | 0.8246 | 0.1023 | -0.1876 | -0.0913 | -0.1747 |
| FEM_AP_MID | 0.7973 | 0.4148 | -0.1929 | 0.0068 | 0.0414 |
| FP_MINSHAFT | 0.7891 | -0.4607 | -0.2472 | 0.1014 | 0.0051 |
| MT3_BIEPI | 0.7808 | -0.4318 | -0.1900 | 0.1091 | -0.1416 |
| C_CUB_DPADJ | 0.3397 | -0.4348 | 0.1020 | -0.8151 | 0.0090 |

Table 3.10. Principal components analysis of forelimb variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 17.3701 | 0.6947 | 0.5429 | 0.4055 | 0.2918 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 82.7148 | 3.3080 | 2.5854 | 1.9310 | 1.3897 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| HUM_BIEPI | 0.9446 | 0.1014 | -0.1463 | 0.0703 | 0.0381 |
| HP_RU_TROCH | 0.9442 | -0.1213 | 0.0459 | 0.0944 | 0.0554 |
| HUMDISTARTWD | 0.9435 | 0.0607 | -0.1160 | 0.0314 | 0.0824 |
| HP_RU_BASE | 0.9420 | -0.2057 | 0.1680 | 0.0520 | 0.0714 |
| HP_RU_MIN | 0.9387 | -0.0715 | 0.1604 | 0.0410 | 0.2144 |
| MC_RU_HEAD | 0.9364 | -0.1443 | 0.0526 | 0.0937 | -0.0417 |
| HP_RU_MAX | 0.9361 | 0.0723 | 0.0787 | 0.1045 | 0.1925 |
| RAD_LENGTH | 0.9255 | -0.0806 | -0.2711 | -0.0587 | -0.0687 |
| RAD_ML_HEAD | 0.9211 | 0.1531 | -0.1797 | 0.1543 | -0.0186 |
| HUM_LENGTH | 0.9170 | -0.0212 | -0.3063 | -0.0094 | -0.0675 |
| HP_LENGTH | 0.9123 | -0.2519 | -0.1070 | -0.0845 | 0.0039 |
| HUM_ML_MID | 0.9122 | 0.1962 | 0.0884 | -0.1595 | 0.0224 |
| MC_BIEPI | 0.9097 | -0.2430 | 0.2151 | 0.1070 | 0.0413 |
| HUM_SI_HEAD | 0.9080 | 0.1470 | -0.2424 | 0.1423 | -0.0043 |
| RAD_DISTALWD | 0.8978 | -0.0678 | -0.0453 | -0.0144 | -0.1317 |
| HUM_AP_MID | 0.8958 | 0.2467 | 0.0857 | -0.0837 | 0.0469 |
| RAD_AP_MID | 0.8793 | 0.1352 | 0.1247 | -0.2529 | -0.1412 |
| MC_LENGTH | 0.8711 | -0.3943 | -0.0213 | -0.1547 | -0.0492 |
| MC_DP_MID | 0.8679 | 0.0560 | 0.0880 | -0.3322 | -0.0410 |
| RAD_ML_MID | 0.8577 | 0.3521 | 0.0898 | -0.0286 | 0.0950 |
| MC_RU_MID | 0.8263 | 0.1151 | 0.2792 | 0.2621 | -0.3553 |

Table 3.11. Principal components analysis of hindlimb variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 16.9045 | 1.3925 | 0.8114 | 0.5992 | 0.3391 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 76.8385 | 6.3295 | 3.6881 | 2.7238 | 1.5413 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| C_LENGTH | 0.9534 | 0.0701 | 0.1175 | -0.1105 | 0.1032 |
| TIB_LENGTH | 0.9432 | 0.0857 | 0.0835 | -0.1843 | -0.1116 |
| TIB_PLATEAU | 0.9386 | 0.2043 | 0.0660 | 0.0246 | 0.0128 |
| FEM_BICON_WD | 0.9357 | 0.2292 | 0.0920 | 0.0061 | 0.0454 |
| MT1_LENGTH | 0.9339 | -0.1023 | -0.0077 | -0.1919 | -0.1462 |
| FEM_HEAD_HT | 0.9233 | 0.2839 | 0.0841 | -0.0307 | 0.0507 |
| FEM_ML_MID | 0.9172 | 0.0992 | -0.0389 | 0.1919 | -0.0861 |
| C_TUB_HTADJ | 0.9169 | 0.1147 | 0.0512 | 0.0126 | 0.1404 |
| FEM_LENGTH | 0.9121 | 0.2243 | 0.1177 | -0.2073 | -0.0417 |
| FP_LENGTH | 0.9084 | -0.2044 | -0.0248 | -0.2415 | -0.1213 |
| MT3_ML_HEAD | 0.9074 | -0.1193 | -0.2115 | 0.0103 | 0.0762 |
| C_TENDON_WD | 0.8973 | -0.0495 | 0.0028 | -0.0023 | 0.1583 |
| TIB_ML_MID | 0.8939 | 0.0357 | -0.1387 | 0.2529 | -0.0859 |
| MT3_LENGTH | 0.8831 | -0.2494 | -0.0025 | -0.2520 | -0.1543 |
| C_CUB_WD | 0.8717 | -0.1075 | 0.0702 | 0.0830 | -0.1273 |
| TIB_AP_MID | 0.8642 | 0.1803 | -0.0876 | 0.2144 | -0.2560 |
| FP_MAXSHAFT | 0.8624 | -0.3250 | -0.1855 | 0.1132 | 0.1434 |
| C_TUBLENGTH | 0.8583 | 0.2119 | 0.1698 | -0.1246 | 0.2614 |
| FP_MINSHAFT | 0.8174 | -0.4370 | -0.2512 | 0.0620 | 0.0952 |
| MT3_BIEPI | 0.8095 | -0.4083 | -0.2117 | 0.0356 | 0.0649 |
| FEM_AP_MID | 0.7868 | 0.4200 | -0.0722 | 0.3012 | 0.0035 |
| C_CUB_DPADJ | 0.3858 | -0.5205 | 0.7064 | 0.2678 | -0.0168 |

Table 3.12. Principal components analysis of long bone variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 17.0781 | 0.7516 | 0.4380 | 0.2577 | 0.2134 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 85.3905 | 3.7579 | 2.1898 | 1.2884 | 1.0670 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| FEM_BICON_WD | 0.9599 | 0.0902 | 0.1438 | -0.1062 | 0.0648 |
| TIB_PLATEAU | 0.9594 | 0.0671 | 0.1315 | -0.1037 | 0.0600 |
| FEM_HEAD_HT | 0.9584 | 0.1364 | 0.1505 | -0.0484 | 0.0204 |
| HUM_BIEPI | 0.9526 | 0.0661 | 0.0346 | 0.0114 | 0.0832 |
| HUMDISTARTWD | 0.9518 | 0.0637 | 0.0337 | 0.0110 | 0.0891 |
| RAD_ML_HEAD | 0.9457 | 0.0764 | 0.1103 | -0.1173 | 0.0329 |
| HUM_SI_HEAD | 0.9407 | 0.0901 | 0.1530 | -0.0995 | 0.0664 |
| TIB_LENGTH | 0.9384 | 0.2213 | -0.1363 | 0.1539 | -0.0531 |
| FEM_LENGTH | 0.9366 | 0.2650 | -0.0237 | 0.1380 | -0.0602 |
| HUM_LENGTH | 0.9358 | 0.2602 | -0.0431 | 0.1110 | -0.0726 |
| FEM_ML_MID | 0.9338 | -0.1774 | -0.0827 | 0.0534 | 0.0767 |
| RAD_LENGTH | 0.9313 | 0.2673 | -0.0809 | 0.1059 | -0.1376 |
| HUM_ML_MID | 0.9202 | -0.2093 | -0.1692 | 0.0112 | 0.0701 |
| HUM_AP_MID | 0.9193 | -0.2420 | 0.0282 | 0.0400 | -0.0309 |
| TIB_AP_MID | 0.9000 | -0.1884 | -0.1113 | -0.1473 | -0.1803 |
| RAD_DISTALWD | 0.8937 | 0.1214 | -0.2000 | -0.2469 | 0.0408 |
| TIB_ML_MID | 0.8907 | -0.2838 | -0.1154 | 0.0819 | 0.0544 |
| RAD_AP_MID | 0.8815 | -0.1845 | -0.2933 | -0.0638 | -0.0541 |
| RAD_ML_MID | 0.8802 | -0.2372 | 0.1339 | 0.2122 | 0.1705 |
| FEM_AP_MID | 0.8404 | -0.2910 | 0.3255 | 0.0091 | -0.2708 |

Table 3.13. Principal components analysis of hand variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 8.5219 | 0.4195 | 0.3086 | 0.2450 | 0.1611 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 85.2186 | 4.1948 | 3.0860 | 2.4496 | 1.6110 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| HP_RU_BASE | 0.9700 | 0.0303 | 0.0684 | -0.0944 | -0.1253 |
| HP_RU_TROCH | 0.9562 | 0.0188 | 0.0182 | -0.0807 | 0.0613 |
| HP_RU_MIN | 0.9541 | -0.1054 | -0.0439 | -0.1979 | 0.0123 |
| MC_RU_HEAD | 0.9499 | 0.0248 | 0.0224 | 0.0521 | -0.1460 |
| MC_BIEPI | 0.9472 | 0.0019 | 0.1562 | -0.0756 | -0.1894 |
| HP_RU_MAX | 0.9245 | -0.2146 | -0.0953 | -0.2054 | 0.1677 |
| HP_LENGTH | 0.9203 | 0.2740 | 0.0290 | 0.0611 | 0.2131 |
| MC_LENGTH | 0.8945 | 0.3780 | 0.0598 | 0.1136 | 0.0216 |
| MC_DP_MID | 0.8611 | -0.0570 | -0.4597 | 0.1870 | -0.0719 |
| MC_RU_MID | 0.8446 | -0.3731 | 0.2280 | 0.2969 | 0.0716 |

Table 3.14. Principal components analysis of foot variables in male and female *Gorilla*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 10.0271 | 0.8130 | 0.7001 | 0.3438 | 0.2763 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 77.1314 | 6.2535 | 5.3857 | 2.6445 | 2.1255 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| C_LENGTH | 0.9406 | 0.0755 | 0.2561 | 0.0139 | -0.0086 |
| MT1_LENGTH | 0.9358 | 0.0541 | 0.0500 | -0.2349 | 0.0534 |
| FP_LENGTH | 0.9333 | 0.0308 | -0.0411 | -0.2823 | 0.0158 |
| MT3_ML_HEAD | 0.9265 | 0.1543 | -0.1271 | 0.0912 | -0.1356 |
| MT3_LENGTH | 0.9205 | -0.0032 | -0.0198 | -0.3230 | 0.0203 |
| FP_MAXSHAFT | 0.9058 | 0.0040 | -0.2698 | 0.1328 | 0.1806 |
| C_TENDON_WD | 0.8997 | 0.0224 | 0.0600 | 0.1636 | 0.1125 |
| C_TUB_HTADJ | 0.8986 | 0.0867 | 0.2268 | 0.1705 | -0.0165 |
| FP_MINSHAFT | 0.8921 | -0.0082 | -0.3585 | 0.0819 | 0.1354 |
| C_CUB_WD | 0.8801 | -0.1049 | 0.0691 | 0.0448 | -0.3981 |
| MT3_BIEPI | 0.8773 | -0.0015 | -0.3477 | 0.0778 | -0.1141 |
| C_TUBLENGTH | 0.8170 | 0.1626 | 0.4690 | 0.0845 | 0.1273 |
| C_CUB_DPADJ | 0.4948 | -0.8567 | 0.1093 | 0.0256 | 0.0526 |

Table 3.15. Pearson correlation analyses of geometric means and PC1 scores from principal components analyses of *Gorilla* (pooled sexes)

| Analysis | Pearson correlation coefficient (r) | Probability (p) |
|---|---|---|
| All variables | 0.9986 | 0.0000 |
| Forelimb | 0.9998 | 0.0000 |
| Hindlimb | 0.9956 | 0.0000 |
| Long bones | 0.9998 | 0.0000 |
| Hand | 0.9997 | 0.0000 |
| Foot | 0.9935 | 0.0000 |

Table 3.16. Principal components analysis of all variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 23.4603 | 3.3803 | 1.9077 | 1.7402 | 1.1960 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 54.5589 | 7.8612 | 4.4366 | 4.0470 | 2.7814 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| FEM_HEAD_HT | 0.8732 | -0.1080 | 0.0634 | -0.1868 | 0.0297 |
| HP_RU_BASE | 0.8643 | 0.2591 | -0.1980 | -0.0445 | 0.0721 |
| HUM_BIEPI | 0.8429 | -0.0258 | 0.1486 | -0.2746 | -0.0330 |
| HUMDISTARTWD | 0.8376 | 0.0386 | 0.1359 | -0.2920 | 0.0467 |
| RAD_ML_HEAD | 0.8362 | 0.0103 | 0.0286 | -0.2864 | 0.1681 |
| TIB_PLATEAU | 0.8305 | -0.0121 | 0.0887 | -0.3565 | 0.0909 |
| HUM_ML_MID | 0.8289 | 0.1543 | 0.2137 | 0.0643 | 0.1008 |
| HP_RU_MAX | 0.8077 | 0.2769 | -0.0123 | 0.1034 | 0.1083 |
| FEM_ML_MID | 0.7995 | 0.1305 | 0.2774 | 0.0179 | 0.0874 |
| MC_RU_HEAD | 0.7986 | 0.2812 | -0.2102 | -0.0446 | 0.0346 |
| MC_BIEPI | 0.7984 | 0.3024 | -0.1517 | -0.0617 | 0.0442 |
| FEM_BICON_WD | 0.7942 | 0.0211 | 0.1319 | -0.3795 | 0.0846 |
| MC_RU_MID | 0.7872 | 0.2116 | -0.0691 | 0.1250 | 0.0059 |
| HUM_SI_HEAD | 0.7857 | 0.0157 | 0.0593 | -0.2018 | 0.1499 |
| HUM_AP_MID | 0.7800 | 0.0393 | 0.2724 | 0.2002 | -0.0379 |
| MT1_LENGTH | 0.7795 | -0.2983 | -0.2068 | 0.1980 | 0.0755 |
| RAD_LENGTH | 0.7738 | -0.4358 | -0.0648 | 0.0212 | 0.1376 |
| MC_DP_MID | 0.7673 | 0.2141 | 0.0568 | 0.1363 | -0.0569 |
| HP_RU_MIN | 0.7649 | 0.3441 | -0.1174 | 0.0052 | 0.1302 |
| FP_LENGTH | 0.7621 | -0.2330 | -0.2052 | 0.3327 | 0.1094 |
| HP_LENGTH | 0.7605 | -0.2748 | -0.1839 | 0.3089 | 0.1354 |
| RAD_DISTALWD | 0.7585 | -0.0261 | 0.0916 | -0.3604 | -0.0366 |
| FP_MINSHAFT | 0.7578 | 0.3256 | -0.1837 | 0.1802 | -0.0639 |
| MT3_LENGTH | 0.7535 | -0.3563 | -0.2407 | 0.2014 | -0.1343 |
| RAD_ML_MID | 0.7472 | 0.1502 | 0.3877 | 0.1826 | -0.0780 |
| HP_RU_TROCH | 0.7430 | 0.1472 | -0.2114 | 0.0568 | 0.1914 |
| FP_MAXSHAFT | 0.7422 | 0.3702 | -0.1242 | 0.1980 | -0.0388 |
| MT3_ML_HEAD | 0.7321 | 0.3123 | -0.2385 | 0.0956 | -0.0944 |
| C_TUB_HTADJ | 0.7219 | -0.1228 | -0.1654 | -0.1329 | -0.0937 |
| RAD_AP_MID | 0.7140 | 0.2108 | 0.2628 | 0.1355 | 0.1155 |
| C_TENDON_WD | 0.7090 | 0.0552 | 0.0298 | -0.2471 | -0.1933 |
| C_LENGTH | 0.6975 | -0.2979 | -0.1353 | -0.0752 | -0.4632 |
| TIB_AP_MID | 0.6913 | -0.1117 | 0.5266 | 0.0395 | -0.0575 |
| HUM_LENGTH | 0.6824 | -0.4839 | 0.0401 | 0.1236 | 0.2596 |
| TIB_LENGTH | 0.6786 | -0.6318 | 0.0332 | 0.0897 | 0.1215 |
| FEM_AP_MID | 0.6765 | -0.0917 | 0.3233 | 0.2672 | -0.1542 |
| MC_LENGTH | 0.6462 | -0.4478 | -0.2473 | 0.1761 | -0.0888 |
| C_CUB_WD | 0.6313 | 0.1889 | -0.2563 | -0.1181 | -0.2706 |
| FEM_LENGTH | 0.6054 | -0.6523 | 0.0255 | -0.0274 | 0.1182 |
| MT3_BIEPI | 0.6029 | 0.3440 | -0.3296 | 0.0749 | -0.2675 |
| TIB_ML_MID | 0.5990 | 0.1945 | 0.4128 | 0.2403 | -0.2892 |
| C_TUB_LENGTH | 0.3458 | -0.4953 | 0.0548 | -0.1744 | -0.5457 |
| C_CUB_DPADJ | 0.2437 | -0.0988 | -0.3291 | -0.4261 | 0.0575 |

Table 3.17. Principal components analysis of forelimb variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 12.4785 | 1.7447 | 1.0143 | 0.9474 | 0.6048 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 59.4216 | 8.3080 | 4.8300 | 4.5113 | 2.8798 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| HP_RU_BASE | 0.8777 | 0.1718 | 0.2674 | 0.0901 | 0.0165 |
| RAD_ML_HEAD | 0.8399 | -0.0473 | 0.0713 | -0.3522 | 0.0827 |
| HUMDISTARTWD | 0.8360 | -0.0149 | 0.0651 | -0.3943 | -0.0056 |
| HUM_BIEPI | 0.8310 | -0.0831 | -0.0140 | -0.3113 | -0.1180 |
| HUM_ML_MID | 0.8182 | 0.1679 | -0.2550 | -0.0307 | -0.0464 |
| MC_BIEPI | 0.8105 | 0.1667 | 0.3324 | 0.1164 | 0.0632 |
| MC_RU_MID | 0.8077 | 0.1516 | 0.0334 | 0.1833 | -0.0649 |
| MC_RU_HEAD | 0.8075 | 0.1548 | 0.3628 | 0.0261 | 0.0311 |
| HP_RU_MAX | 0.8047 | 0.3026 | 0.0169 | 0.1401 | 0.1885 |
| HP_RU_MIN | 0.7904 | 0.3493 | 0.0913 | 0.0861 | 0.0273 |
| MC_DP_MID | 0.7867 | 0.1561 | -0.1270 | 0.1897 | -0.1879 |
| HUM_SI_HEAD | 0.7794 | -0.0937 | -0.0526 | -0.3115 | 0.1343 |
| HP_RU_TROCH | 0.7561 | 0.1027 | 0.2246 | 0.2227 | 0.1338 |
| HUM_AP_MID | 0.7494 | -0.0437 | -0.3583 | 0.0495 | -0.1264 |
| RAD_DISTALWD | 0.7492 | -0.0111 | 0.0924 | -0.3313 | -0.3299 |
| RAD_AP_MID | 0.7320 | 0.1483 | -0.4031 | 0.1006 | 0.1900 |
| RAD_ML_MID | 0.7203 | 0.2604 | -0.4701 | 0.0791 | -0.0877 |
| RAD_LENGTH | 0.7090 | -0.5833 | -0.0110 | -0.0056 | 0.1626 |
| HP_LENGTH | 0.7004 | -0.4378 | 0.0379 | 0.3477 | -0.0753 |
| HUM_LENGTH | 0.6267 | -0.6083 | -0.1234 | 0.0227 | 0.3567 |
| MC_LENGTH | 0.5905 | -0.5931 | 0.0996 | 0.2332 | -0.3700 |

Table 3.18. Principal components analysis of hindlimb variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 11.2044 | 2.0190 | 1.3746 | 1.1640 | 0.9407 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 50.9290 | 9.1772 | 6.2482 | 5.2908 | 4.2761 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| FEM_HEAD_HT | 0.8809 | 0.0569 | -0.0503 | 0.1747 | -0.1123 |
| TIB_PLATEAU | 0.8321 | -0.0162 | -0.0589 | 0.3858 | -0.1806 |
| FEM_BICON_WD | 0.7989 | -0.0264 | -0.1210 | 0.4138 | -0.1585 |
| MT1_LENGTH | 0.7941 | 0.1806 | 0.1316 | -0.2776 | -0.2023 |
| MT3_LENGTH | 0.7818 | 0.2137 | 0.1320 | -0.3073 | -0.0781 |
| FP_LENGTH | 0.7789 | 0.0955 | 0.0621 | -0.3956 | -0.2465 |
| FEM_ML_MID | 0.7711 | -0.1373 | -0.3127 | 0.1123 | -0.0886 |
| C_LENGTH | 0.7709 | 0.2393 | 0.2165 | -0.0823 | 0.3766 |
| C_TUB_HTADJ | 0.7471 | 0.0475 | 0.2039 | 0.1123 | 0.0297 |
| TIB_LENGTH | 0.7393 | 0.5301 | -0.0269 | -0.1113 | -0.1739 |
| FP_MAXSHAFT | 0.7353 | -0.4453 | 0.0401 | -0.1938 | 0.0186 |
| FP_MINSHAFT | 0.7264 | -0.4331 | 0.0900 | -0.2321 | 0.0313 |
| MT3_ML_HEAD | 0.7239 | -0.4125 | 0.1276 | -0.0832 | -0.0003 |
| C_TENDON_WD | 0.7077 | -0.0823 | 0.0530 | 0.3381 | 0.1802 |
| FEM_AP_MID | 0.7018 | 0.0142 | -0.3725 | -0.1586 | 0.0391 |
| TIB_AP_MID | 0.6997 | 0.1184 | -0.5030 | 0.1151 | 0.0599 |
| FEM_LENGTH | 0.6704 | 0.5673 | 0.0358 | -0.0178 | -0.1467 |
| C_CUB_WD | 0.6463 | -0.2988 | 0.2615 | 0.1191 | 0.1469 |
| TIB_ML_MID | 0.6173 | -0.2342 | -0.4455 | 0.0237 | 0.2132 |
| MT3_BIEPI | 0.6172 | -0.4633 | 0.2130 | -0.1522 | 0.1586 |
| C_TUB_LENGTH | 0.4149 | 0.5554 | 0.0977 | 0.0154 | 0.6327 |
| C_CUB_DPADJ | 0.2811 | 0.0439 | 0.6203 | 0.3892 | -0.1699 |

Table 3.19. Principal components analysis of long bone variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 12.2165 | 1.7845 | 1.2729 | 0.7592 | 0.5765 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 61.0825 | 8.9226 | 6.3644 | 3.7960 | 2.8824 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| FEM_HEAD_HT | 0.8824 | -0.0758 | -0.1482 | 0.0459 | -0.0879 |
| HUMDISTARTWD | 0.8731 | 0.0487 | -0.2268 | -0.0560 | 0.0236 |
| HUM_BIEPI | 0.8697 | 0.0163 | -0.1841 | -0.0488 | 0.0808 |
| RAD_ML_HEAD | 0.8499 | -0.0157 | -0.2779 | -0.1839 | -0.0673 |
| TIB_PLATEAU | 0.8361 | 0.0274 | -0.3763 | 0.1786 | 0.0462 |
| HUM_ML_MID | 0.8260 | 0.2541 | 0.0656 | 0.0031 | -0.1702 |
| FEM_BICON_WD | 0.8159 | 0.0549 | -0.4205 | 0.2166 | 0.0510 |
| FEM_ML_MID | 0.8096 | 0.1930 | 0.0319 | -0.0996 | -0.2223 |
| HUM_SI_HEAD | 0.7967 | 0.0453 | -0.2189 | -0.2334 | -0.2171 |
| RAD_DISTALWD | 0.7762 | 0.0374 | -0.3121 | 0.0791 | 0.1834 |
| RAD_LENGTH | 0.7761 | -0.4629 | 0.1194 | -0.0337 | 0.0128 |
| HUM_AP_MID | 0.7707 | 0.1919 | 0.2993 | 0.0054 | -0.3259 |
| TIB_AP_MID | 0.7639 | 0.1349 | 0.1978 | 0.2421 | 0.2982 |
| TIB_LENGTH | 0.7608 | -0.5374 | 0.2004 | 0.1033 | 0.0743 |
| RAD_ML_MID | 0.7425 | 0.3985 | 0.2665 | -0.1286 | 0.1777 |
| HUM_LENGTH | 0.7259 | -0.5247 | 0.2708 | -0.1724 | -0.0108 |
| FEM_AP_MID | 0.7017 | 0.1802 | 0.3567 | 0.3716 | -0.2497 |
| FEM_LENGTH | 0.6944 | -0.6207 | 0.1667 | 0.0800 | 0.0576 |
| RAD_AP_MID | 0.6798 | 0.2170 | 0.2145 | -0.5277 | 0.2173 |
| TIB_ML_MID | 0.6191 | 0.4582 | 0.3011 | 0.1693 | 0.2187 |

Table 3.20. Principal components analysis of hand variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 6.5325 | 1.0599 | 0.5647 | 0.4510 | 0.3673 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 65.3254 | 10.5985 | 5.6472 | 4.5097 | 3.6732 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| HP_RU_BASE | 0.9191 | 0.1014 | -0.1008 | 0.0190 | -0.0241 |
| MC_BIEPI | 0.8636 | 0.1364 | -0.2465 | 0.2381 | -0.1057 |
| MC_RU_HEAD | 0.8555 | 0.0789 | -0.2757 | 0.2383 | -0.1284 |
| MC_RU_MID | 0.8289 | 0.1301 | 0.2342 | 0.2695 | 0.1658 |
| HP_RU_MAX | 0.8287 | 0.2744 | 0.0938 | -0.3051 | 0.1341 |
| HP_RU_MIN | 0.8185 | 0.3051 | 0.2573 | 0.0037 | 0.2474 |
| HP_RU_TROCH | 0.8036 | 0.0336 | -0.3590 | -0.3561 | 0.0122 |
| MC_DP_MID | 0.7829 | -0.0390 | 0.3951 | -0.1075 | -0.4606 |
| HP_LENGTH | 0.7201 | -0.5860 | 0.0054 | -0.1411 | 0.0595 |
| MC_LENGTH | 0.6236 | -0.7024 | 0.0547 | 0.1147 | 0.1286 |

Table 3.21. Principal components analysis of foot variables in male and female *Pan*

Latent Roots (Eigenvalues)

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 6.3795 | 1.5275 | 1.1127 | 0.8581 | 0.6027 |

Percent of Total Variance Explained

| 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|
| 49.0728 | 11.7503 | 8.5592 | 6.6006 | 4.6362 |

Component loadings

| | 1 | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|
| C_LENGTH | 0.7997 | -0.3683 | -0.1885 | 0.1162 | -0.1419 |
| MT1_LENGTH | 0.7798 | -0.3098 | 0.3237 | -0.2019 | 0.1992 |
| MT3_LENGTH | 0.7781 | -0.3103 | 0.3225 | -0.1440 | 0.0422 |
| FP_LENGTH | 0.7752 | -0.2456 | 0.4148 | -0.2232 | 0.0483 |
| MT3_ML_HEAD | 0.7569 | 0.2735 | 0.1798 | -0.0161 | -0.2712 |
| FP_MINSHAFT | 0.7549 | 0.4255 | 0.0384 | 0.1418 | 0.1020 |
| FP_MAXSHAFT | 0.7541 | 0.4627 | 0.0179 | 0.1370 | 0.1346 |
| C_TUB_HTADJ | 0.7346 | -0.1163 | -0.2279 | 0.1355 | 0.0976 |
| MT3_BIEPI | 0.6879 | 0.3370 | 0.0790 | 0.0812 | -0.5115 |
| C_TENDON_WD | 0.6674 | 0.0511 | -0.3560 | 0.0903 | 0.2805 |
| C_CUB_WD | 0.6654 | 0.3002 | -0.2565 | 0.0292 | 0.1963 |
| C_TUB_LENGTH | 0.4393 | -0.6704 | -0.3123 | 0.3772 | -0.1721 |
| C_CUB_DPADJ | 0.3465 | 0.0148 | -0.5603 | -0.7196 | -0.1368 |

Table 3.22. Pearson correlation analyses of geometric means and PC1 scores from principal components analyses of *Pan* (pooled sexes)

| Analysis | Pearson correlation coefficient (r) | Probability (p) |
|---|---|---|
| All variables | 0.9962 | 0.0000 |
| Forelimb | 0.9982 | 0.0000 |
| Hindlimb | 0.9880 | 0.0000 |
| Long bones | 0.9961 | 0.0000 |
| Hand | 0.9990 | 0.0000 |
| Foot | 0.9784 | 0.0000 |

Figure 3.1. Principal components analysis of all variables for *Gorilla*, plotted by sex and species

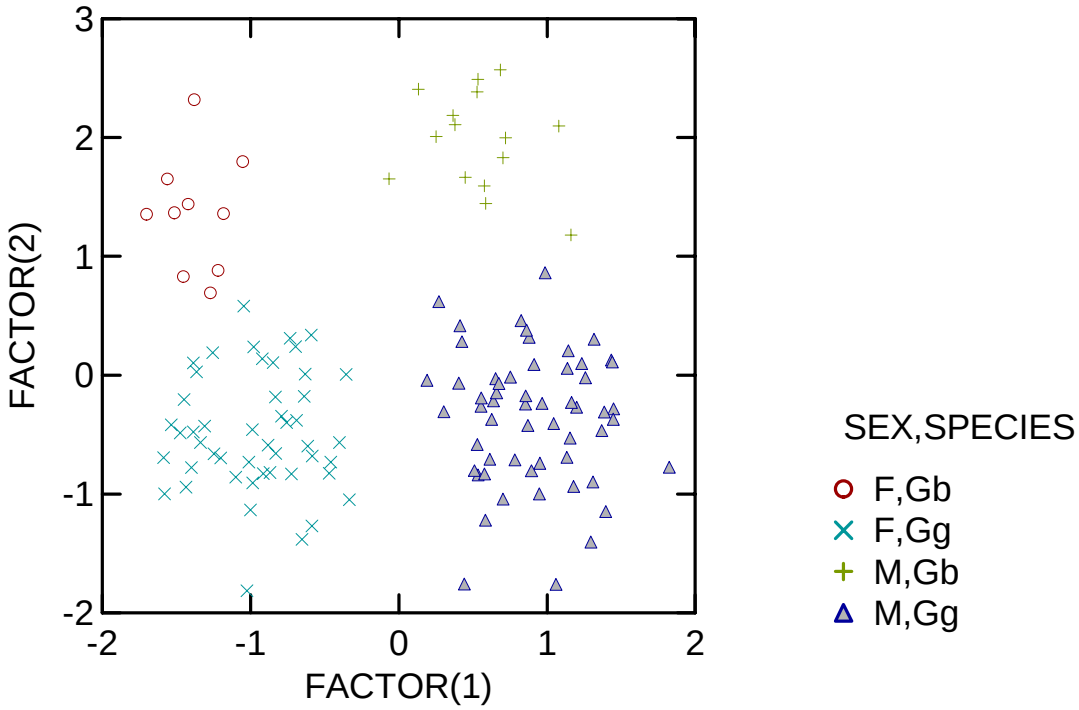


Figure 3.2. Principal components analysis of all variables for *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

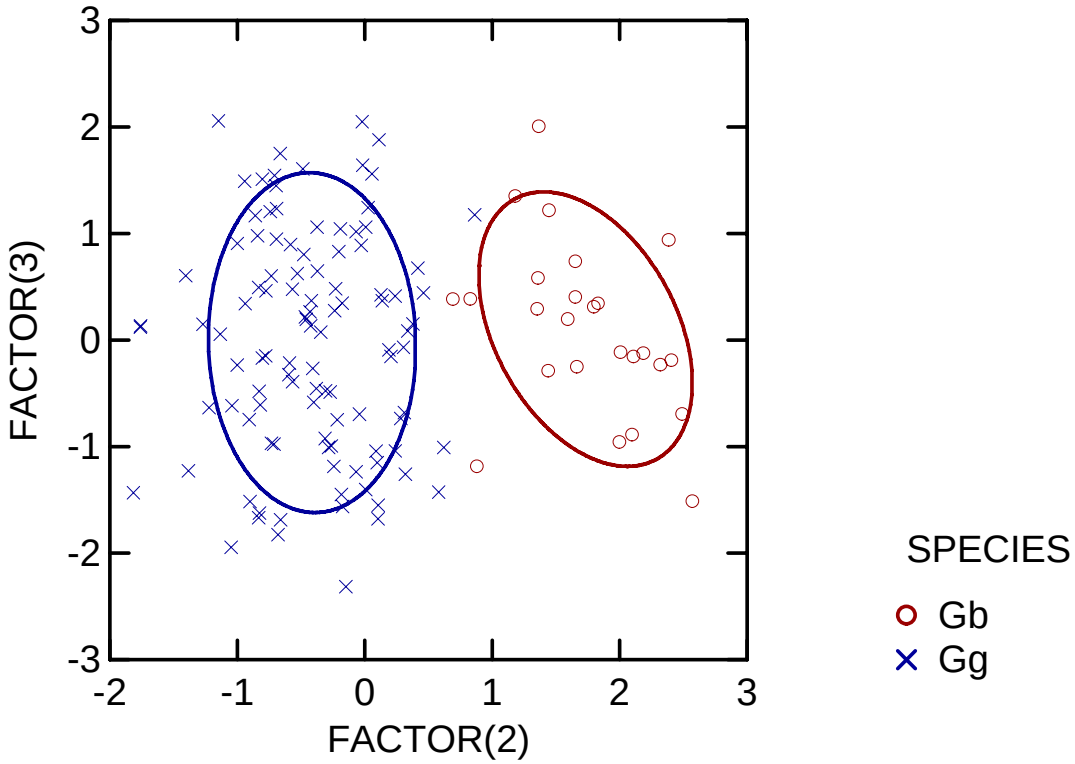


Figure 3.3. Principal components analysis of all variables for *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

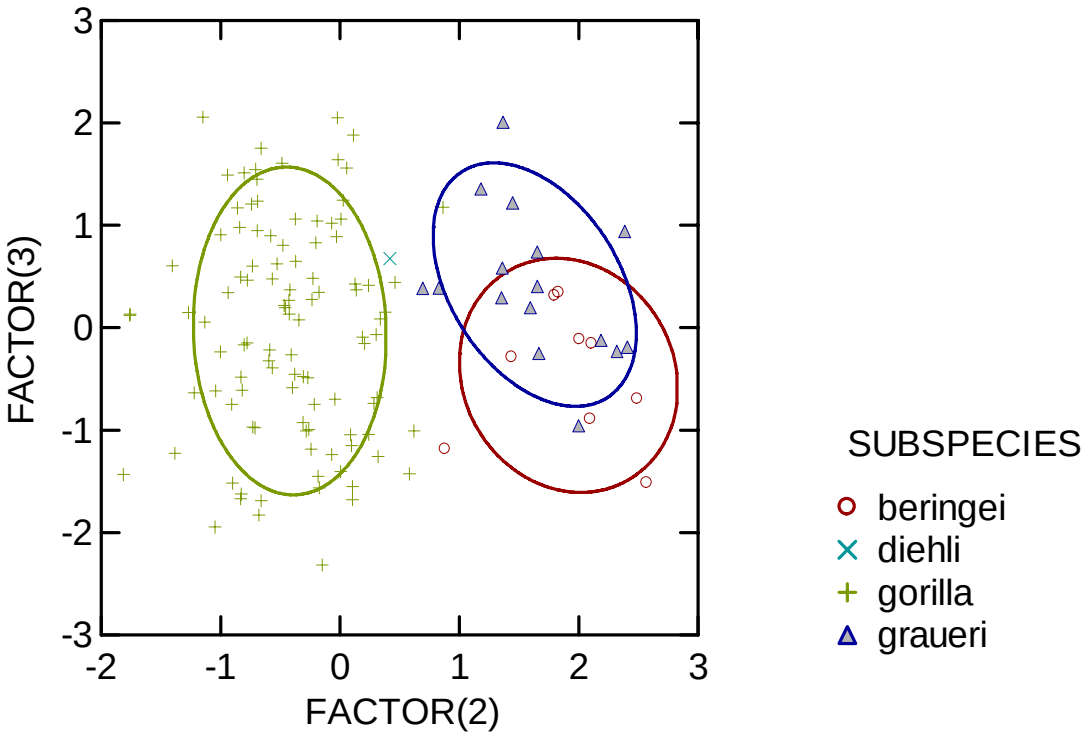


Figure 3.4. Principal components analysis of all variables for *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

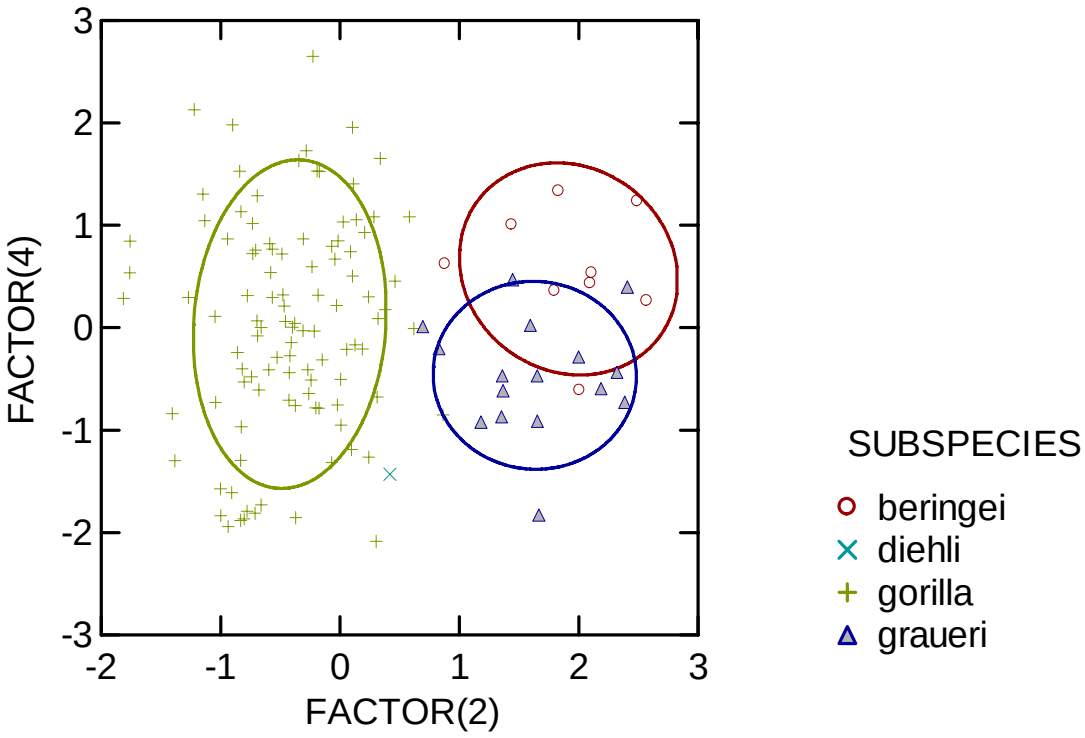


Figure 3.5. Principal components analysis of all variables for *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

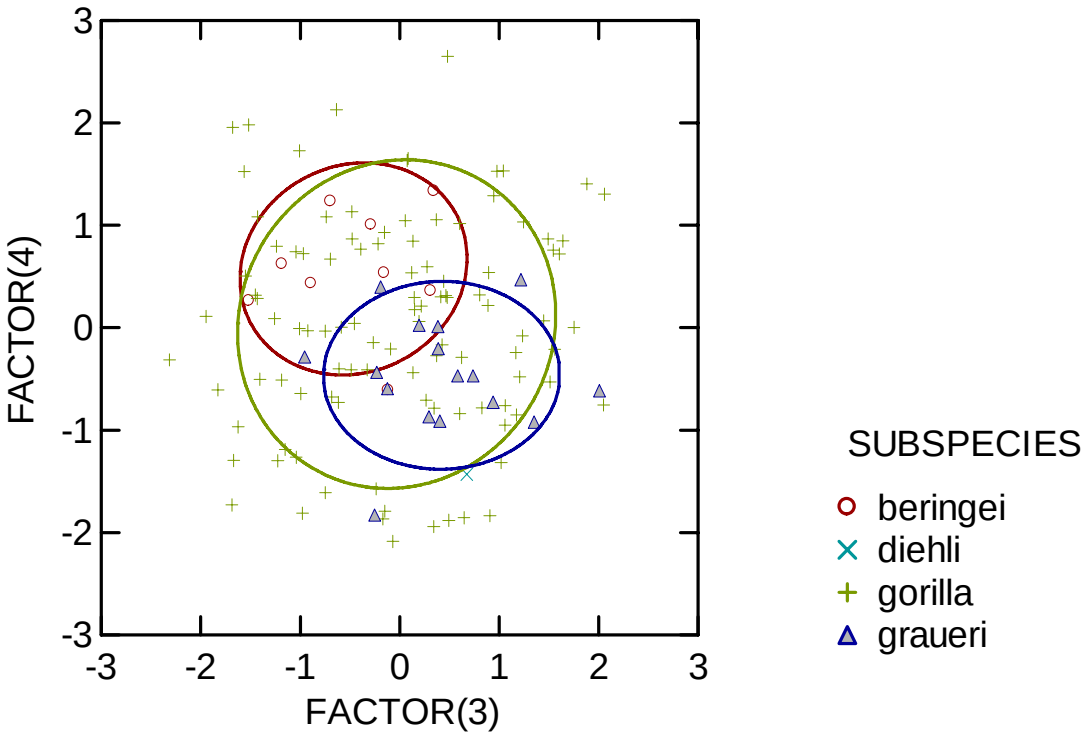


Figure 3.6. Principal components analysis of forelimb variables from *Gorilla*, plotted by sex and species

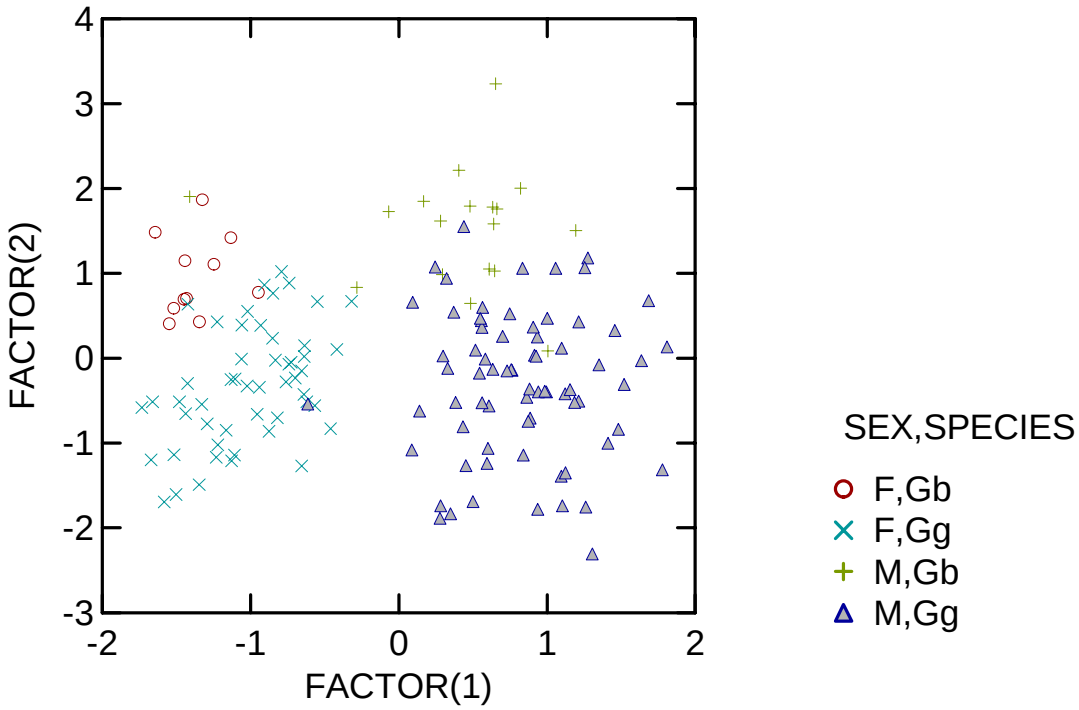


Figure 3.7. Principal components analysis of forelimb variables from *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

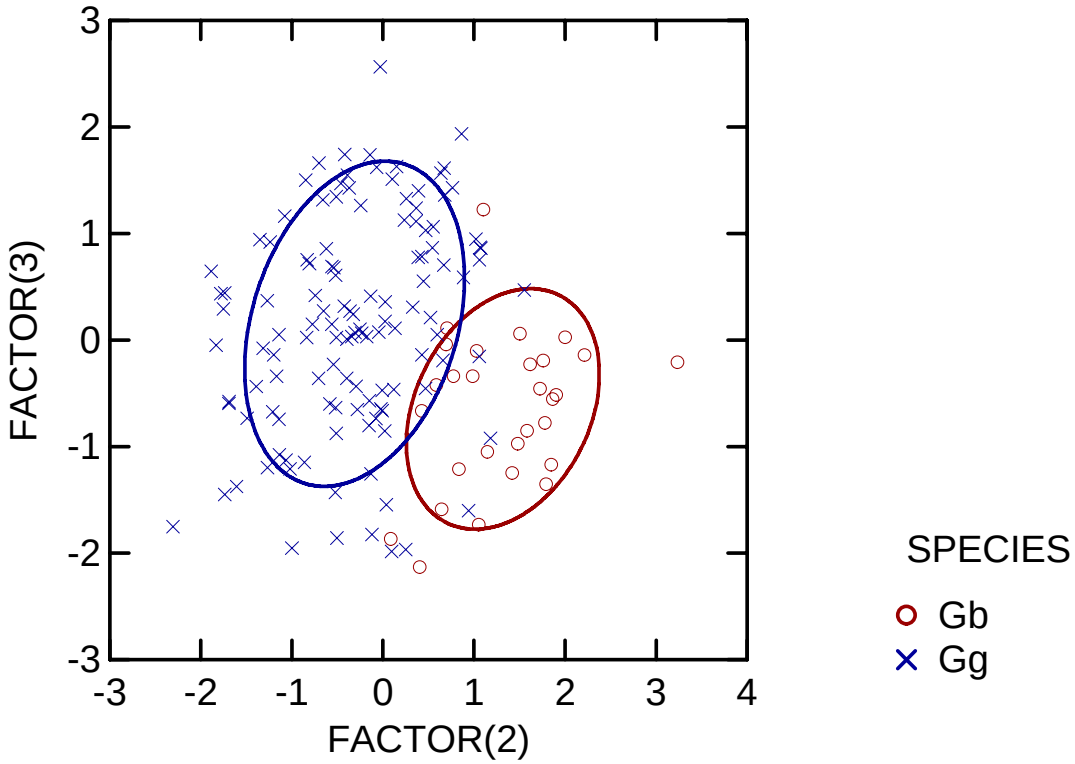


Figure 3.8. Principal components analysis of forelimb variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

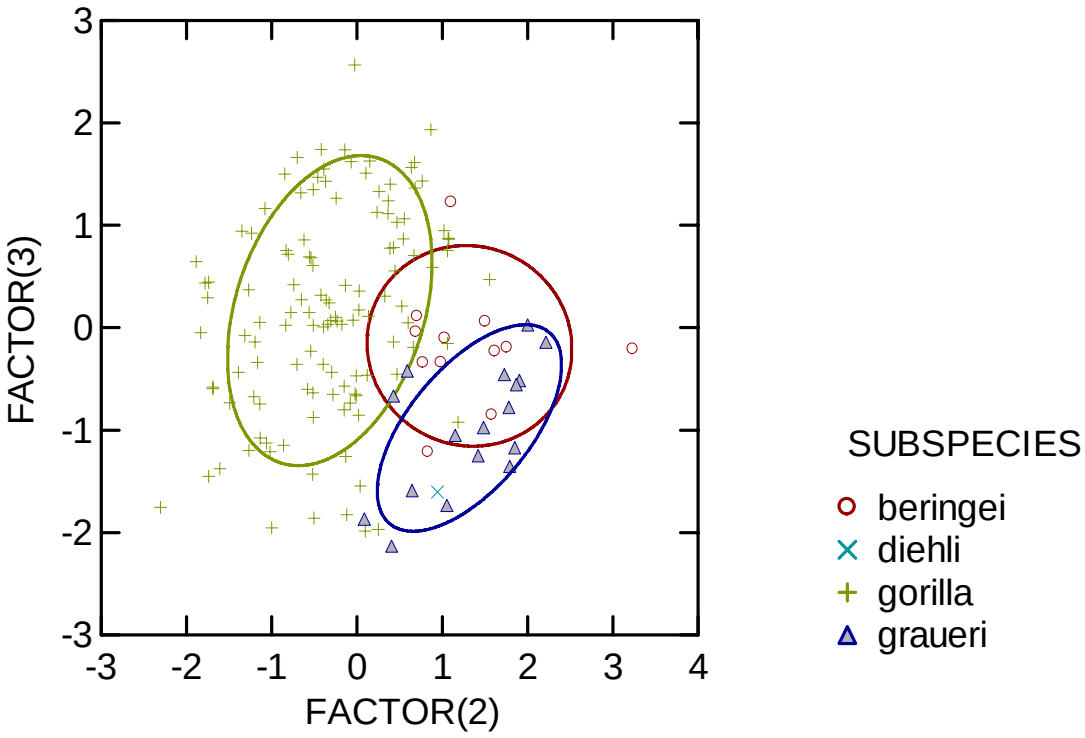


Figure 3.9. Principal components analysis of hindlimb variables from *Gorilla*, plotted by sex and species

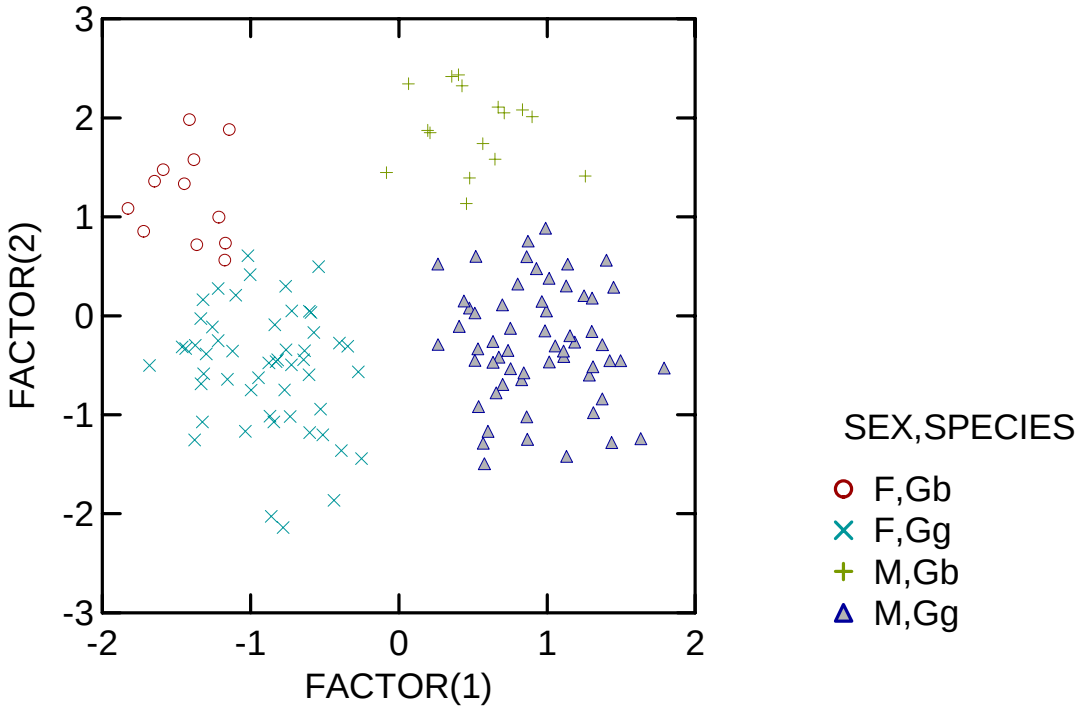


Figure 3.10. Principal components analysis of hindlimb variables from *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

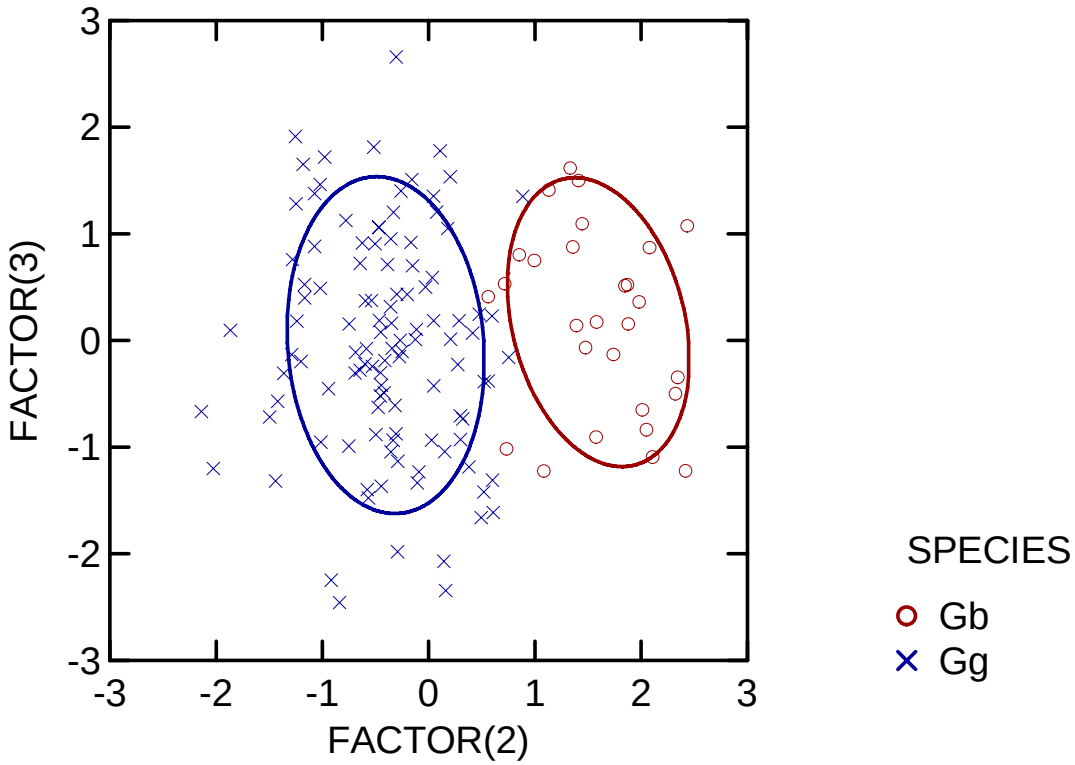


Figure 3.11. Principal components analysis of hindlimb variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

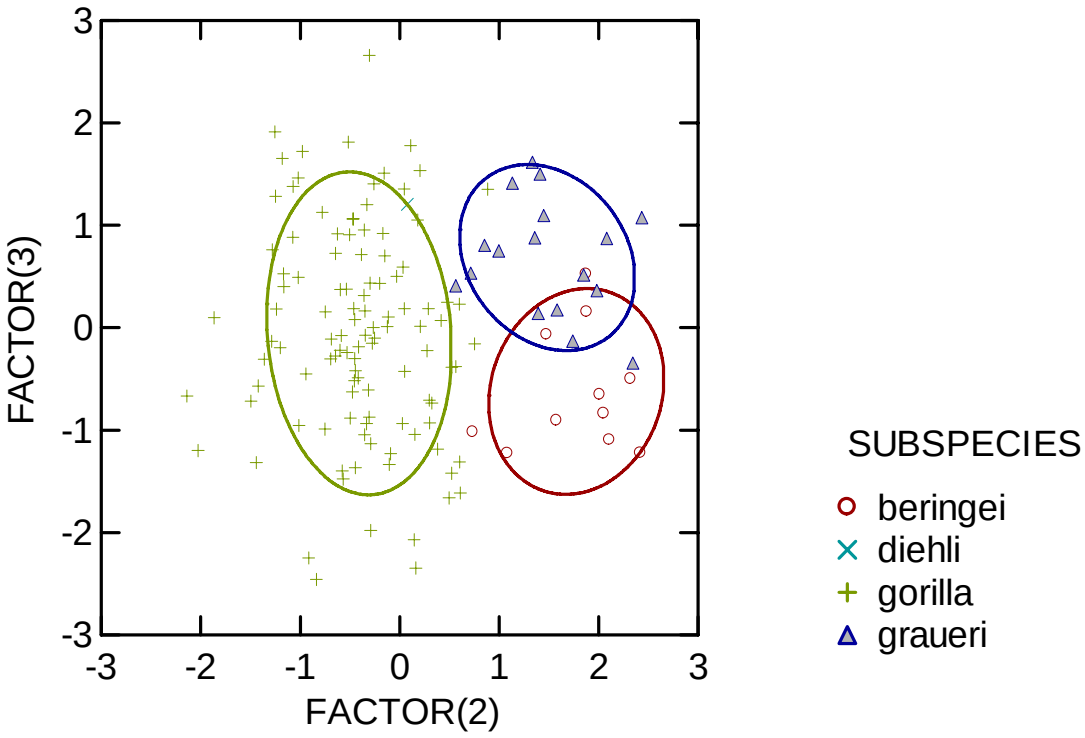


Figure 3.12. Principal components analysis of long bone variables from *Gorilla*, plotted by sex and species

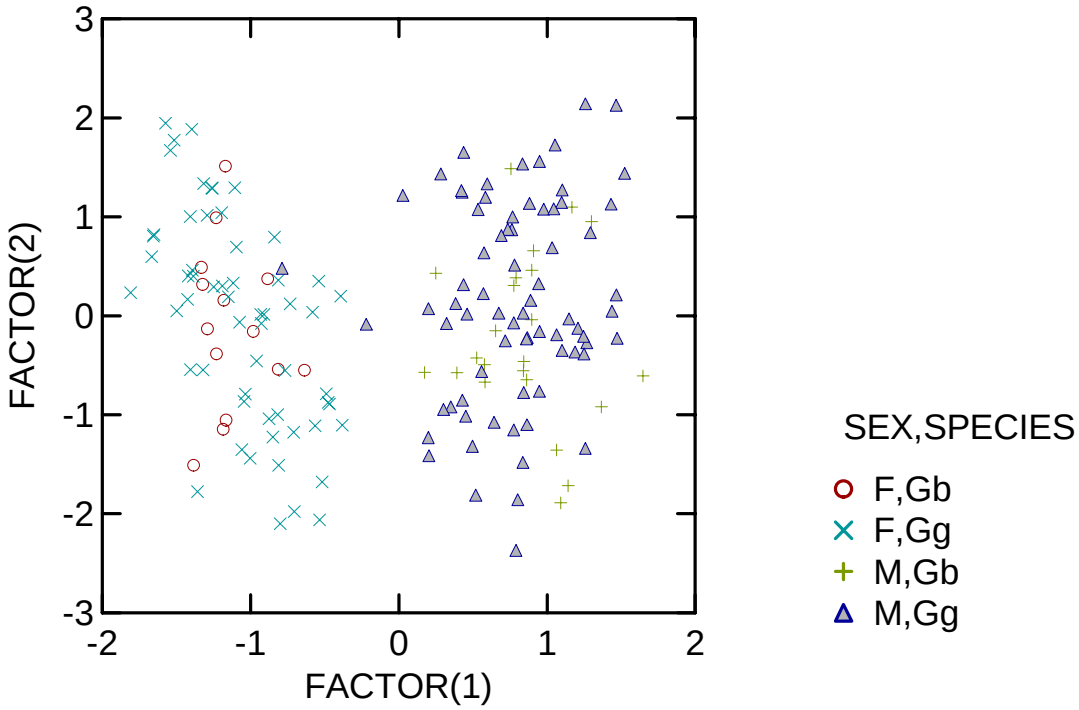


Figure 3.13. Principal components analysis of long bone variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

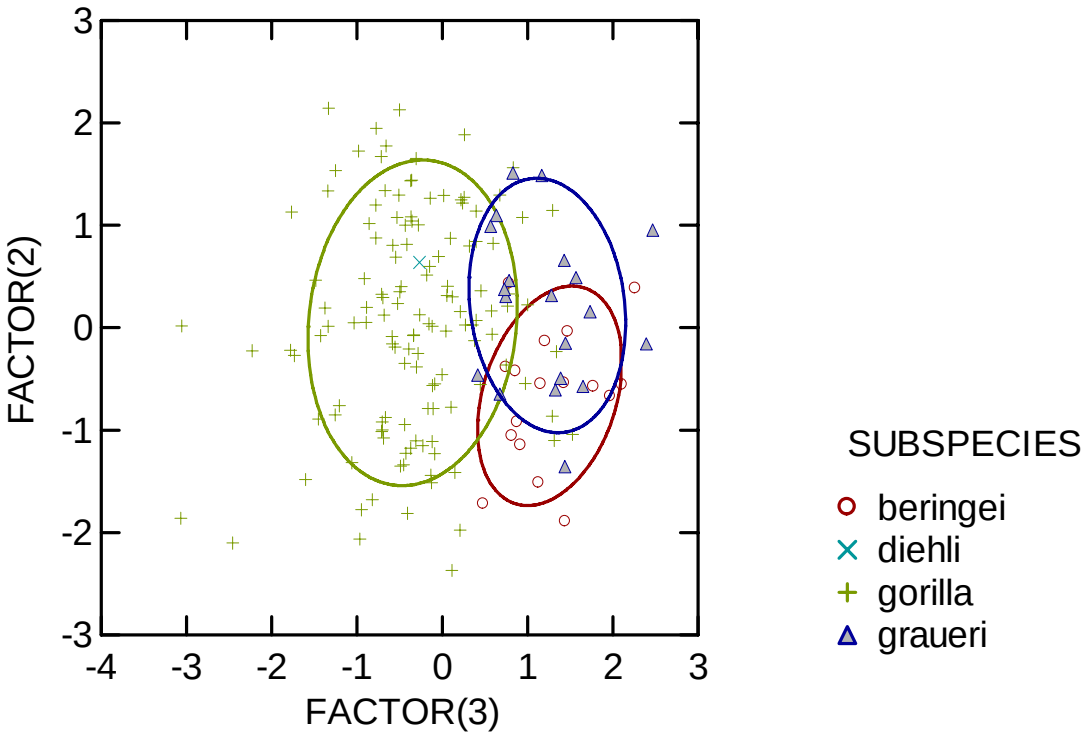


Figure 3.14. Principal components analysis of long bone variables from *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

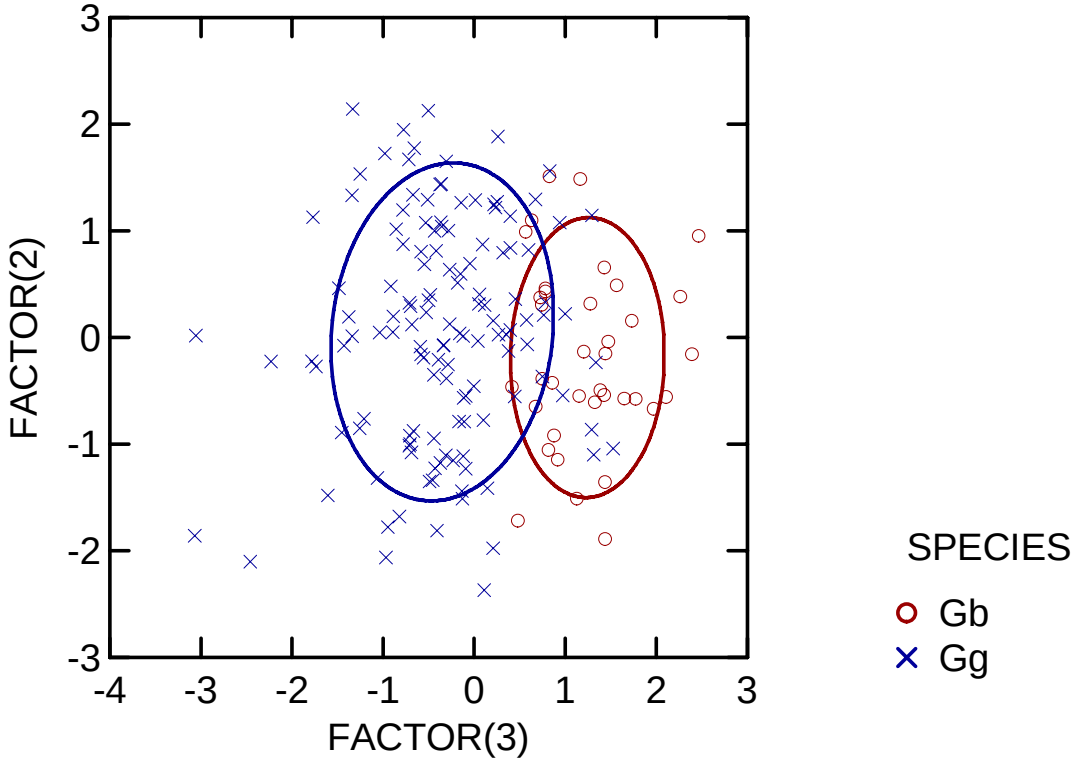


Figure 3.15. Principal components analysis of hand variables from *Gorilla*, plotted by sex and species

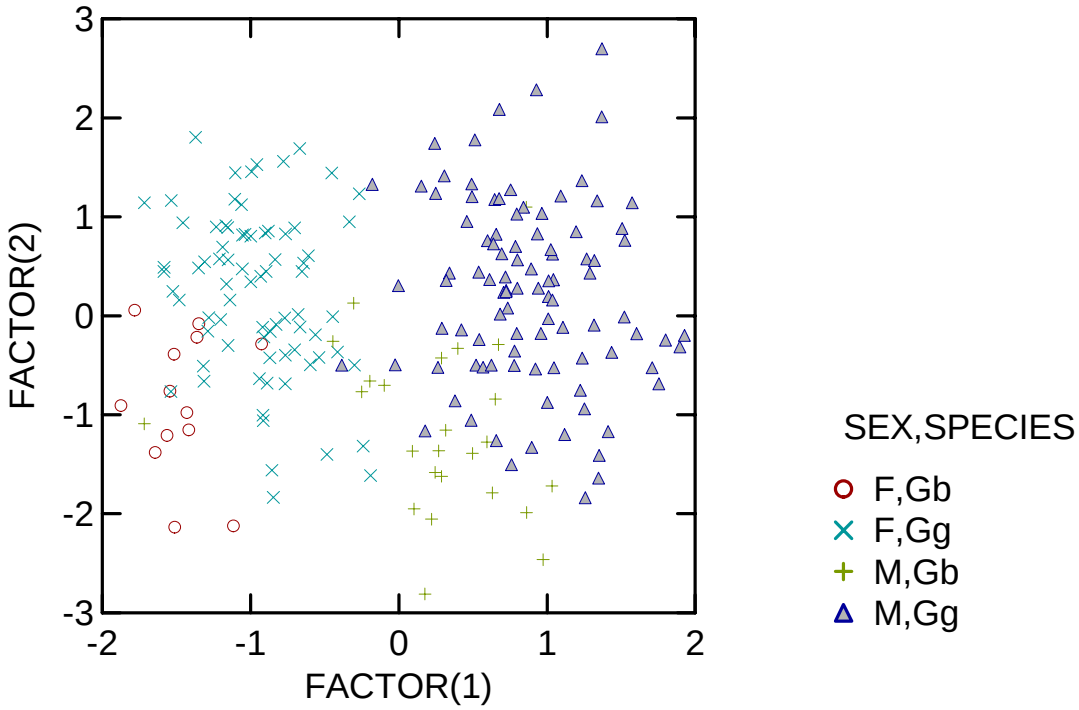


Figure 3.16. Principal components analysis of hand variables from *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

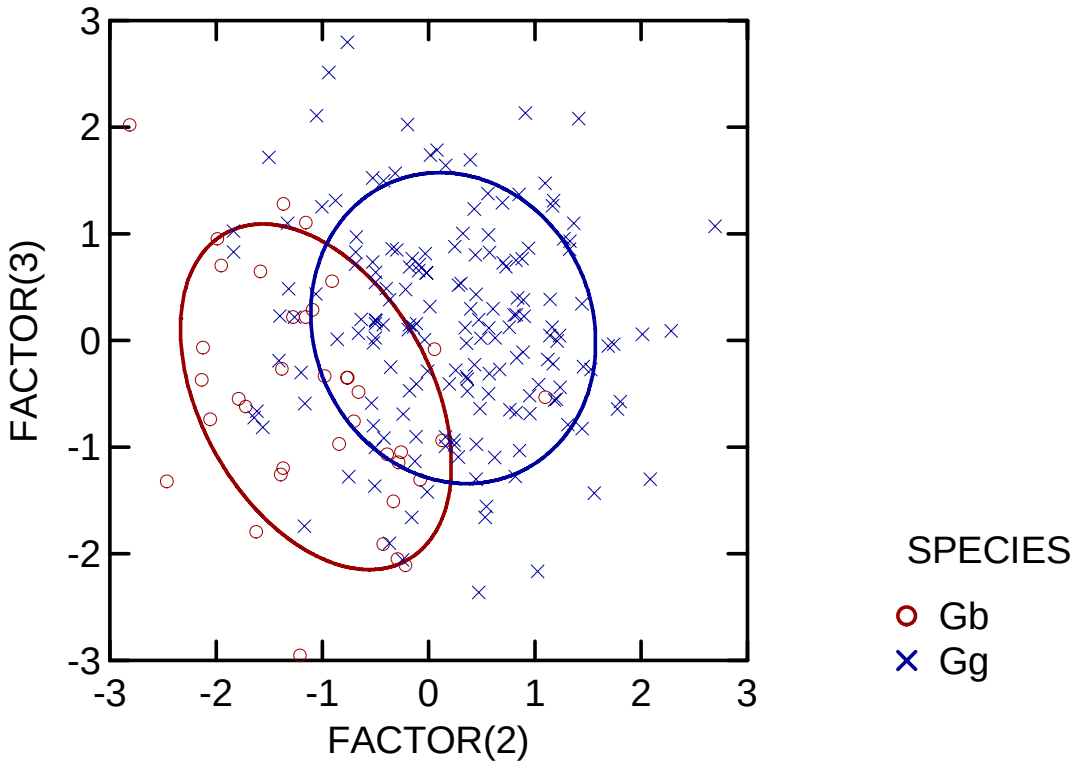


Figure 3.17. Principal components analysis of hand variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

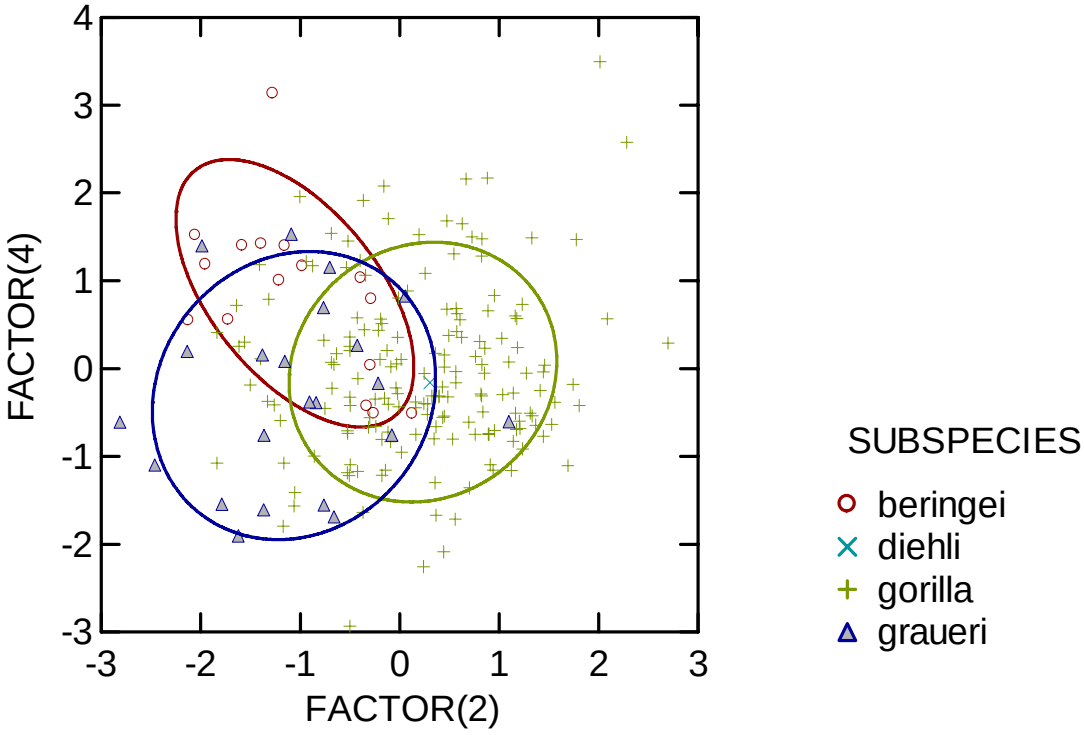


Figure 3.18. Principal components analysis of hand variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

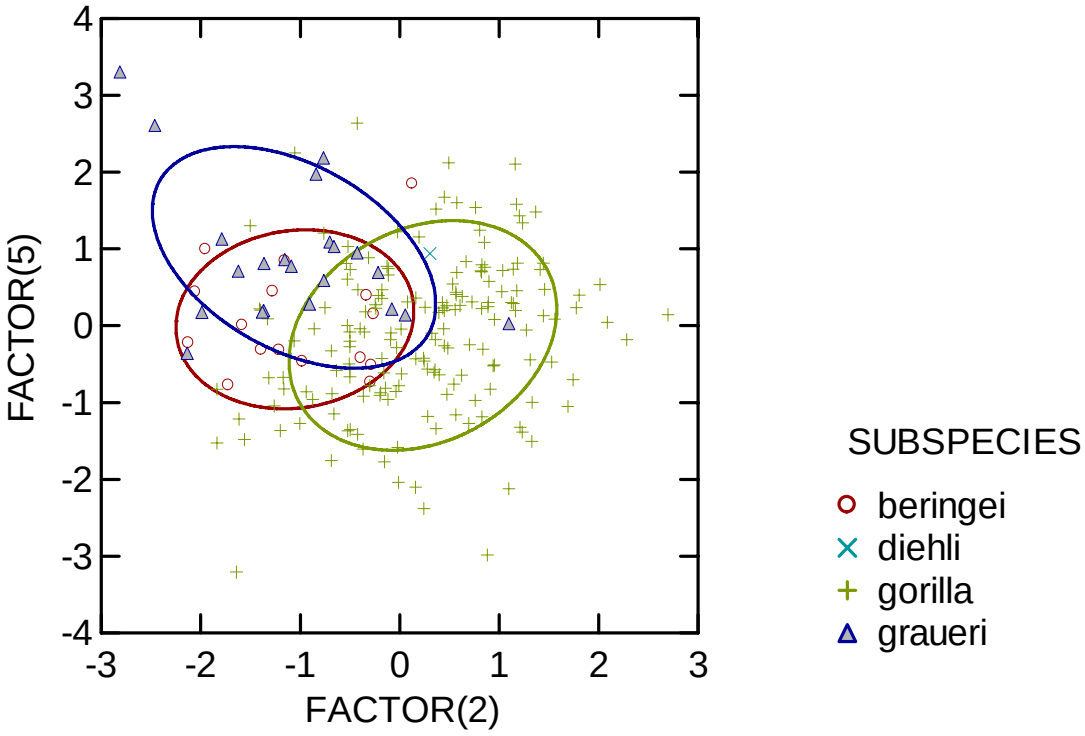


Figure 3.19. Principal components analysis of hand variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

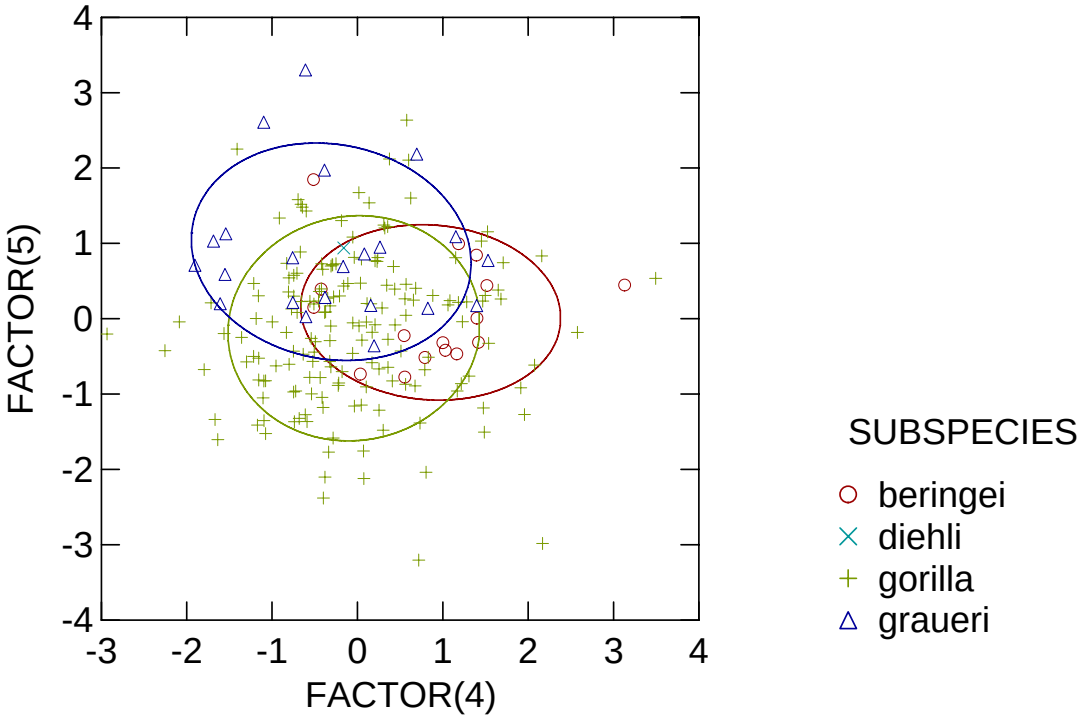


Figure 3.20. Principal components analysis of foot variables from *Gorilla*, plotted by sex and species

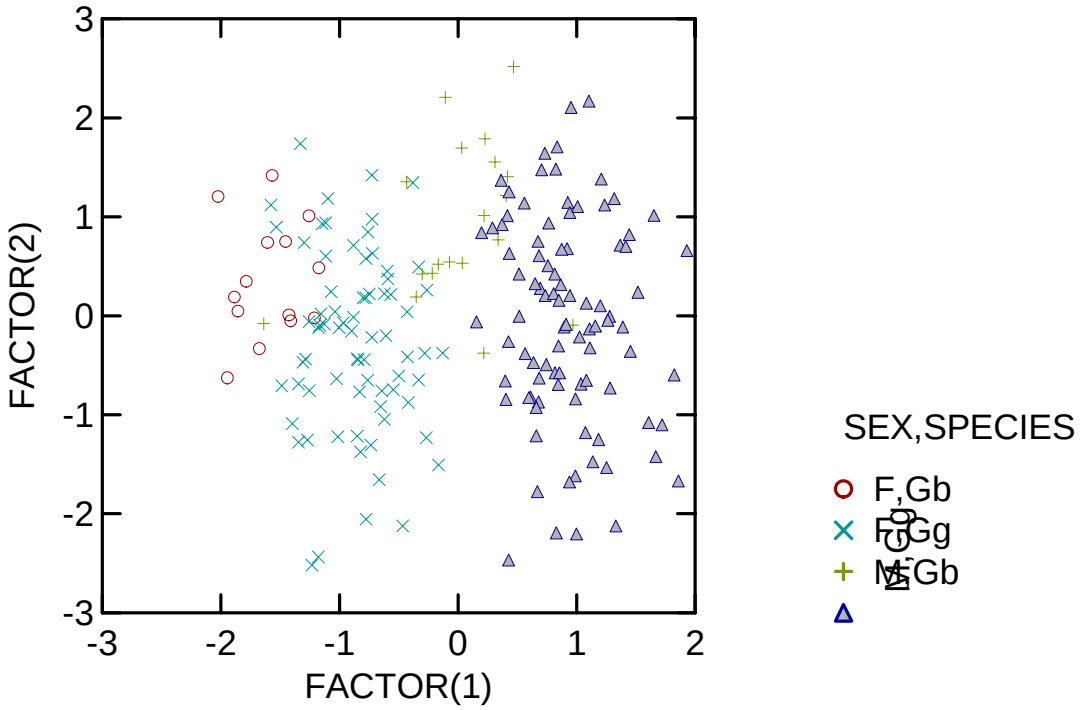


Figure 3.21. Principal components analysis of foot variables from *Gorilla*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

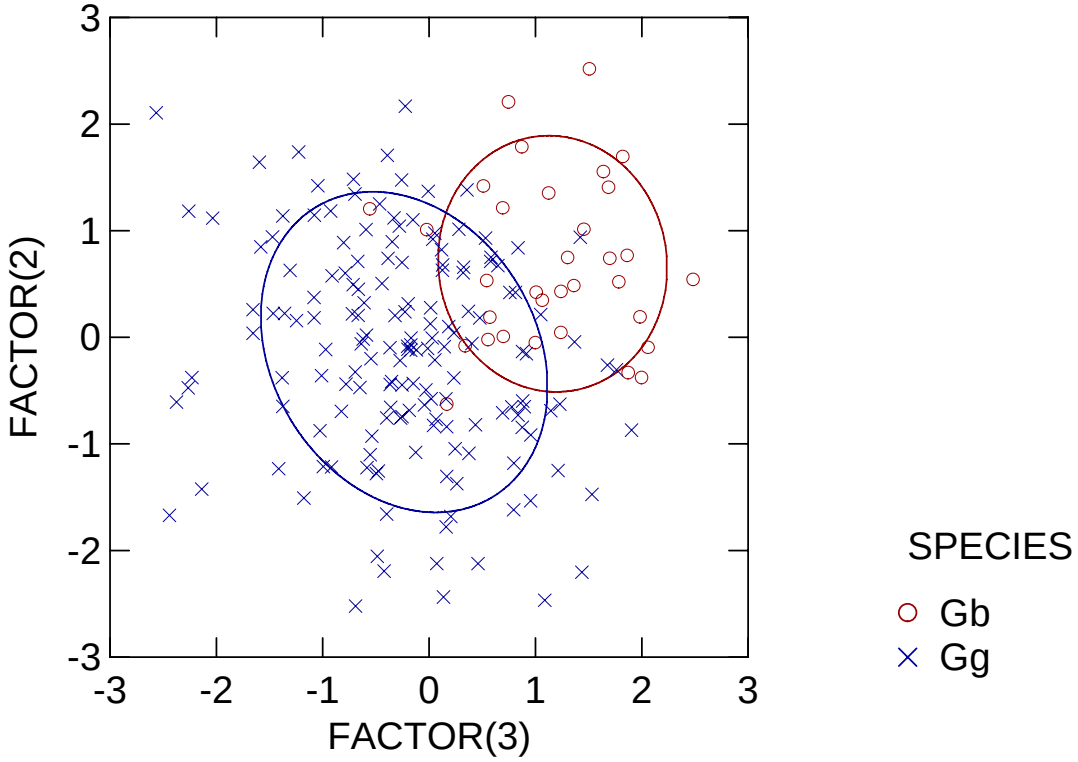


Figure 3.22. Principal components analysis of foot variables from *Gorilla*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

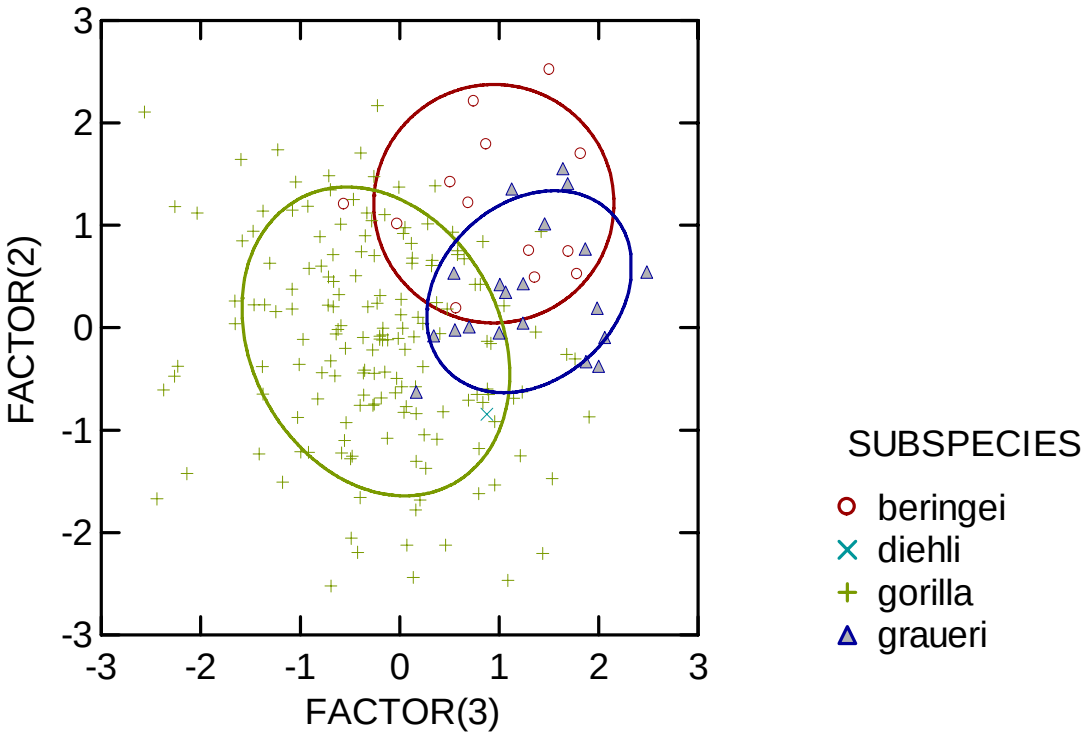


Figure 3.23. Principal components analysis of all variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

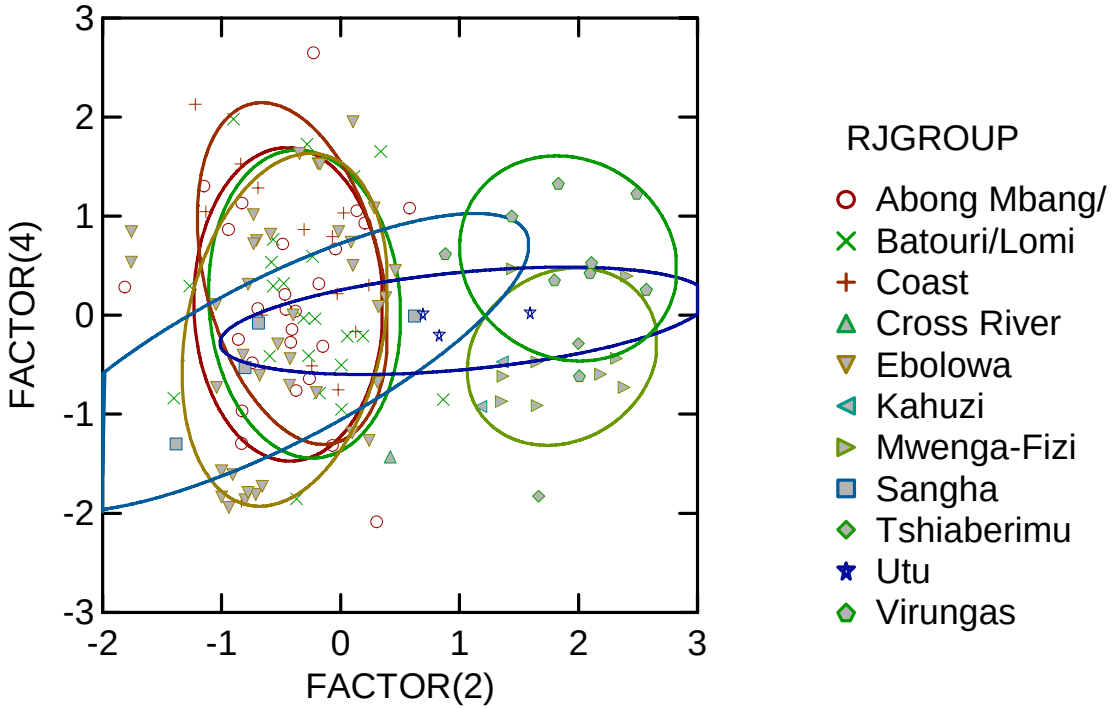


Figure 3.24. Principal components analysis of forelimb variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

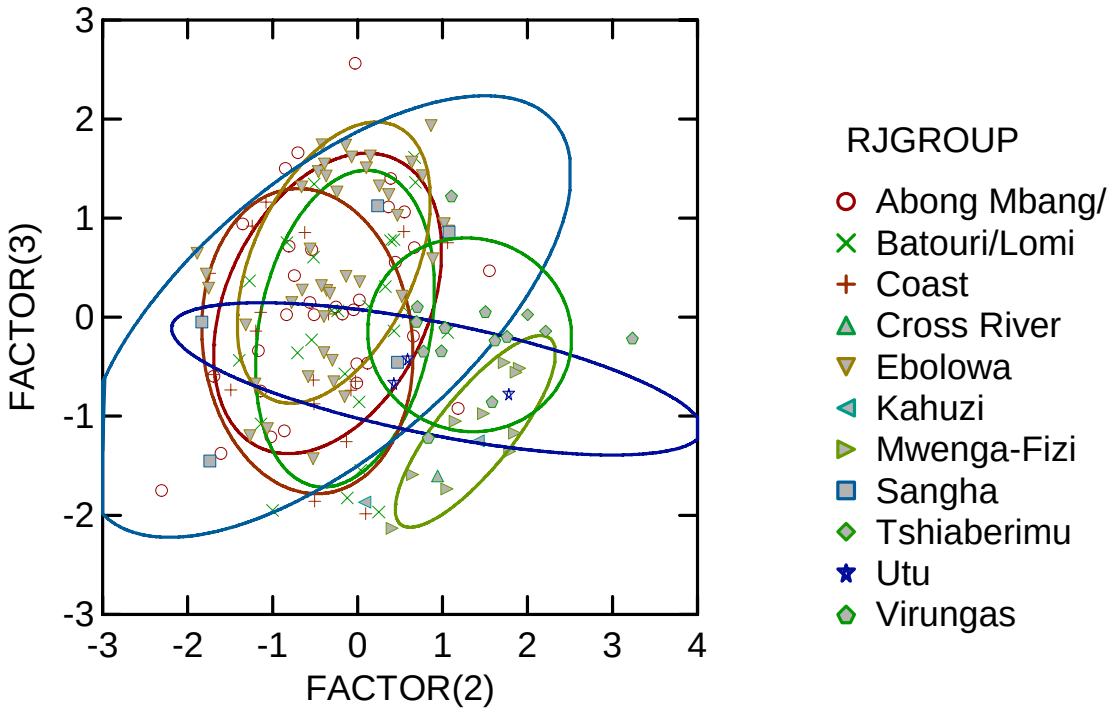


Figure 3.25. Principal components analysis of hindlimb variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

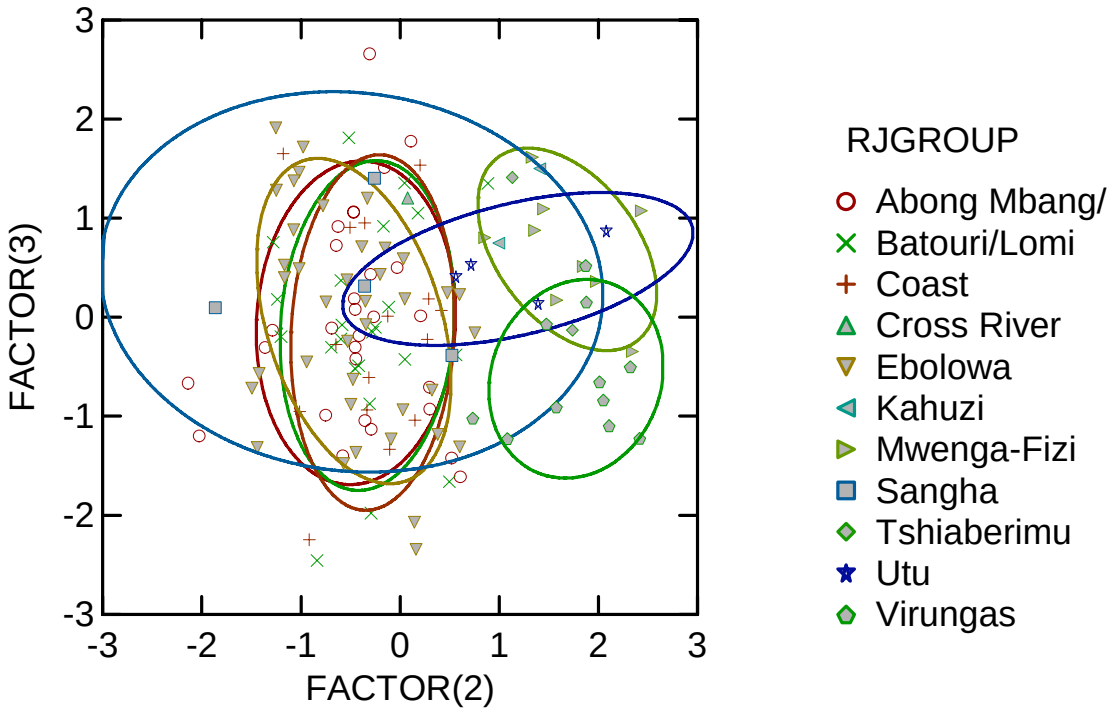


Figure 3.26. Principal components analysis of long bone variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

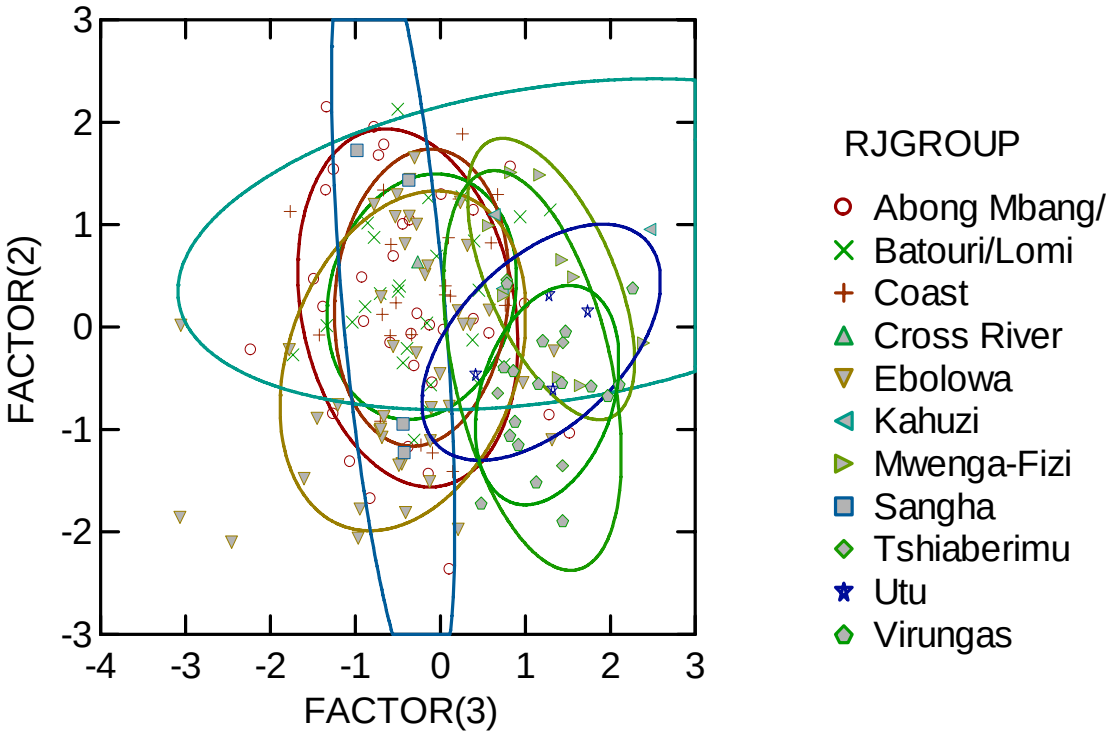


Figure 3.27. Principal components analysis of hand variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

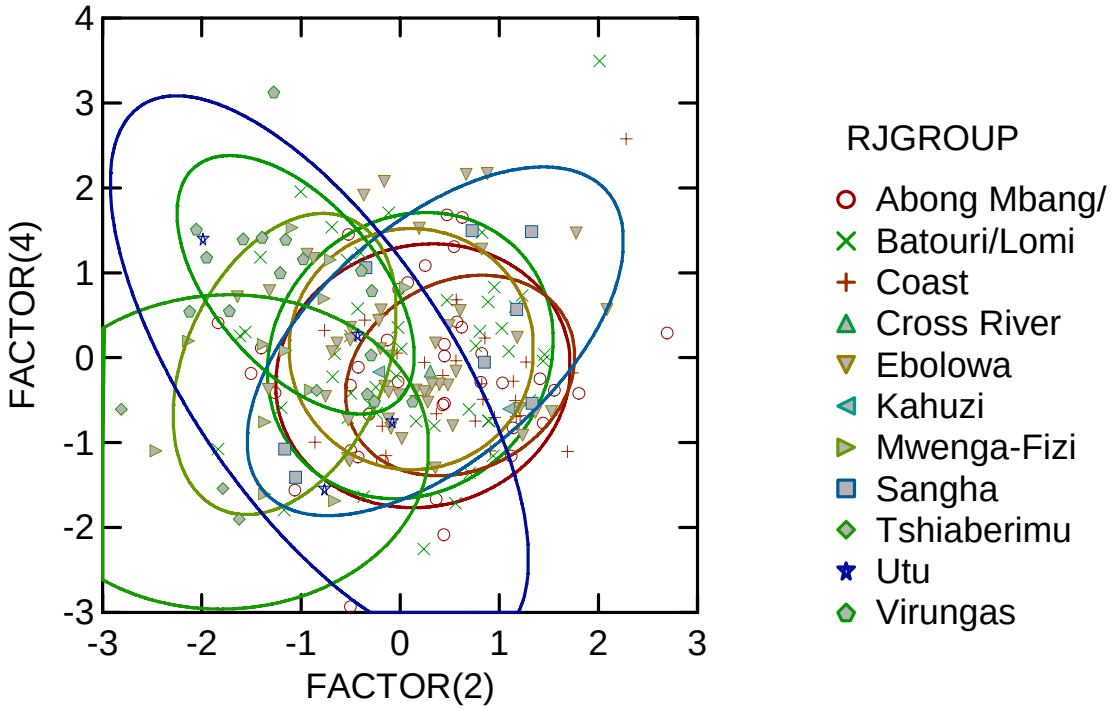


Figure 3.28. Principal components analysis of foot variables from *Gorilla*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes the subspecies of *G. beringei* is on the y-axis. The confidence ellipses for the samples are set at 68.27%.

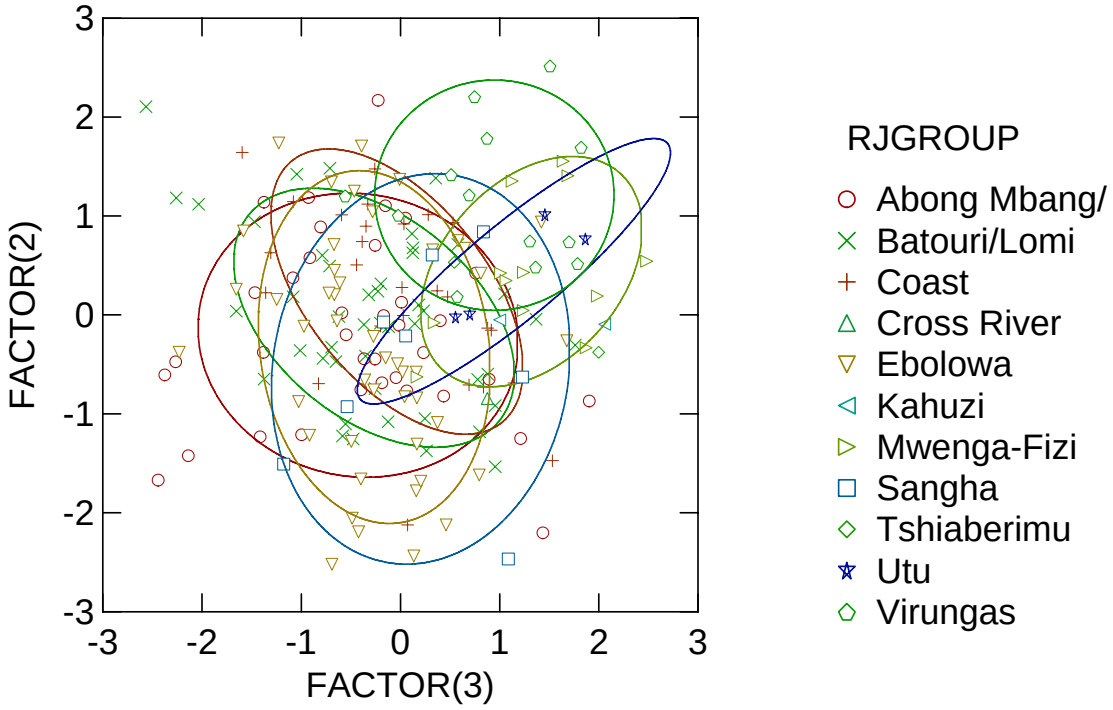


Figure 3.29. Principal components analysis of all variables from *Pan*, plotted by sex and species

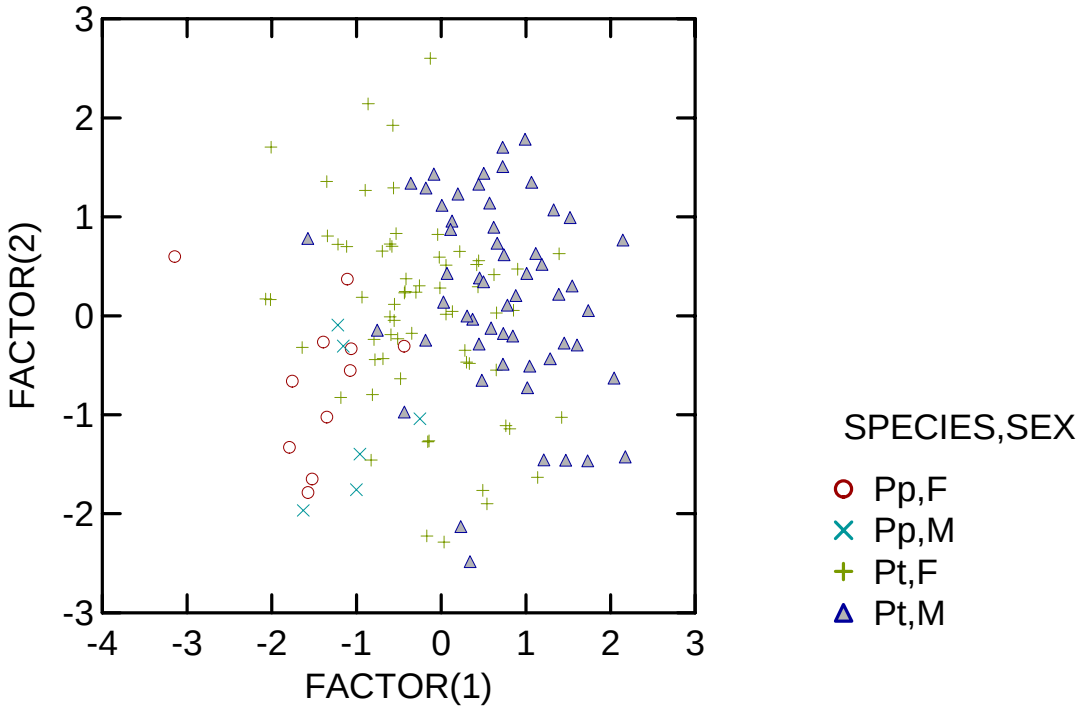


Figure 3.30. Principal components analysis of all variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

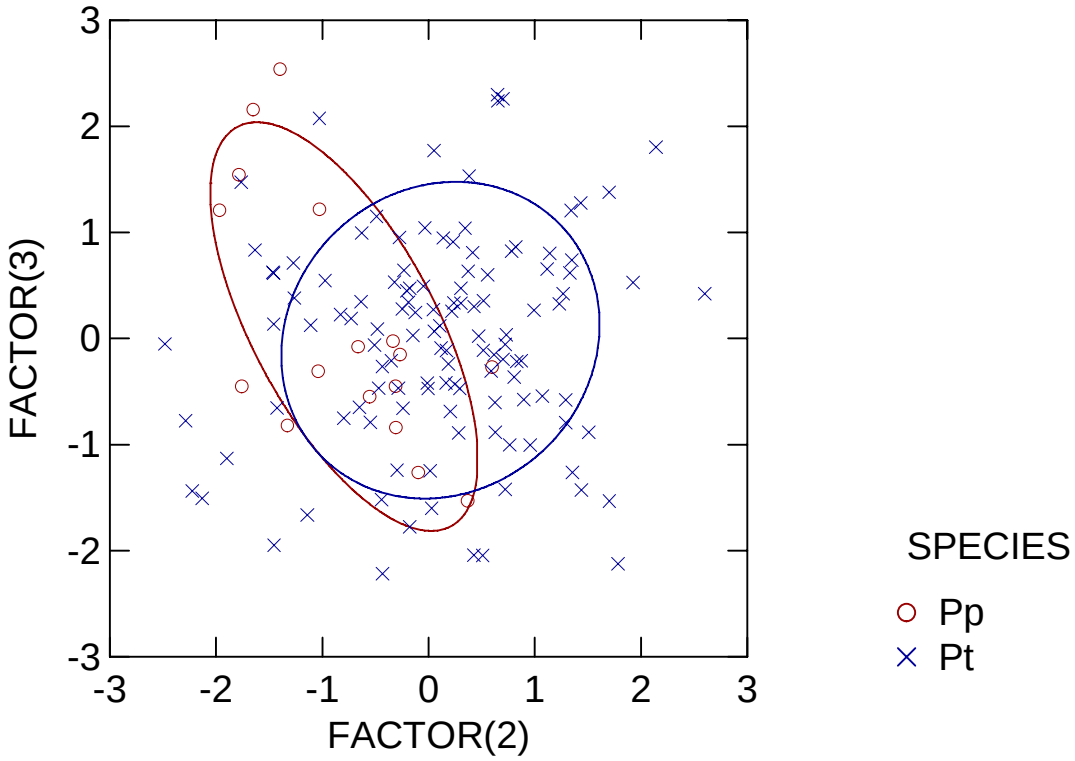


Figure 3.31. Principal components analysis of all variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

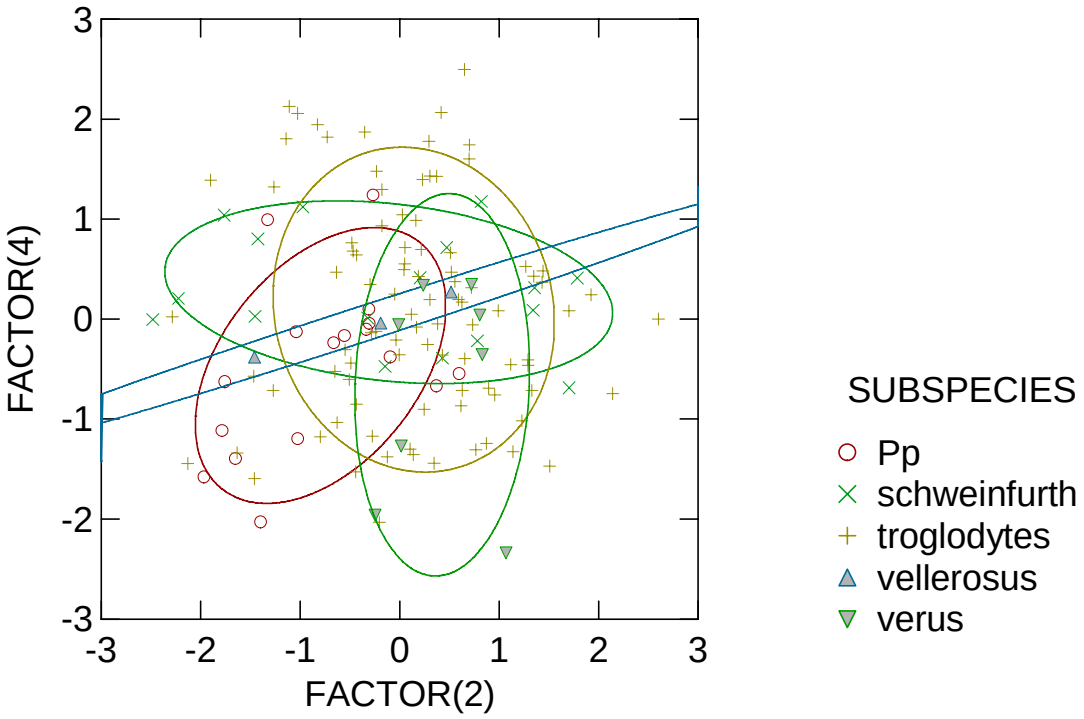


Figure 3.32. Principal components analysis of forelimb variables from *Pan*, plotted by sex and species

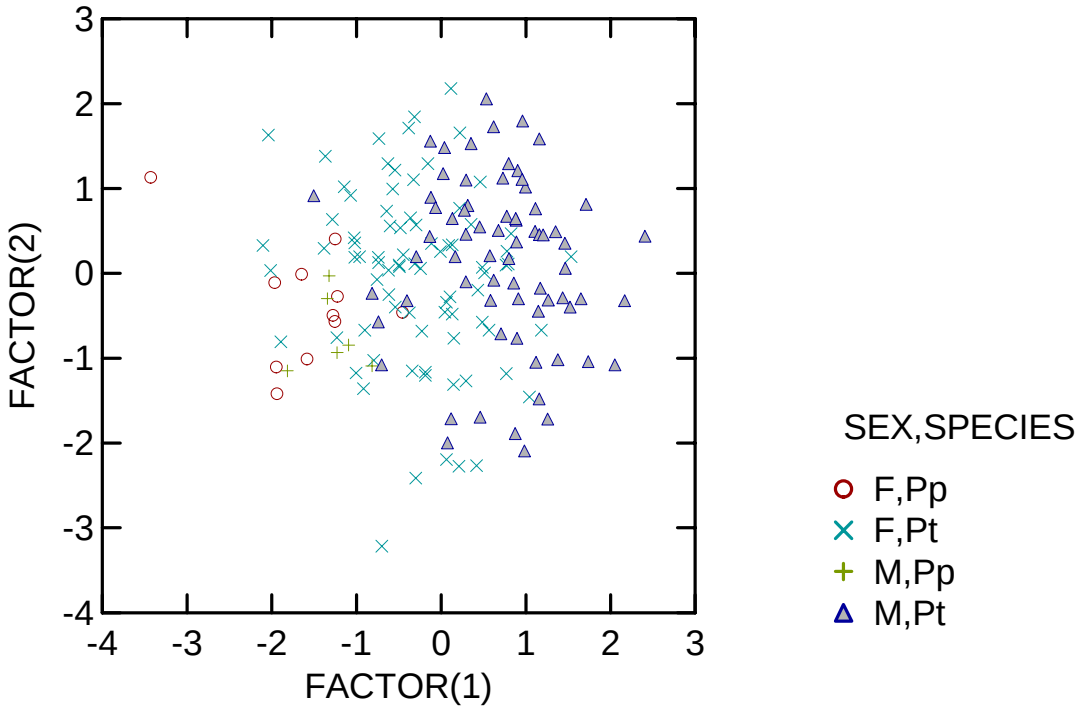


Figure 3.33. Principal components analysis of forelimb variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

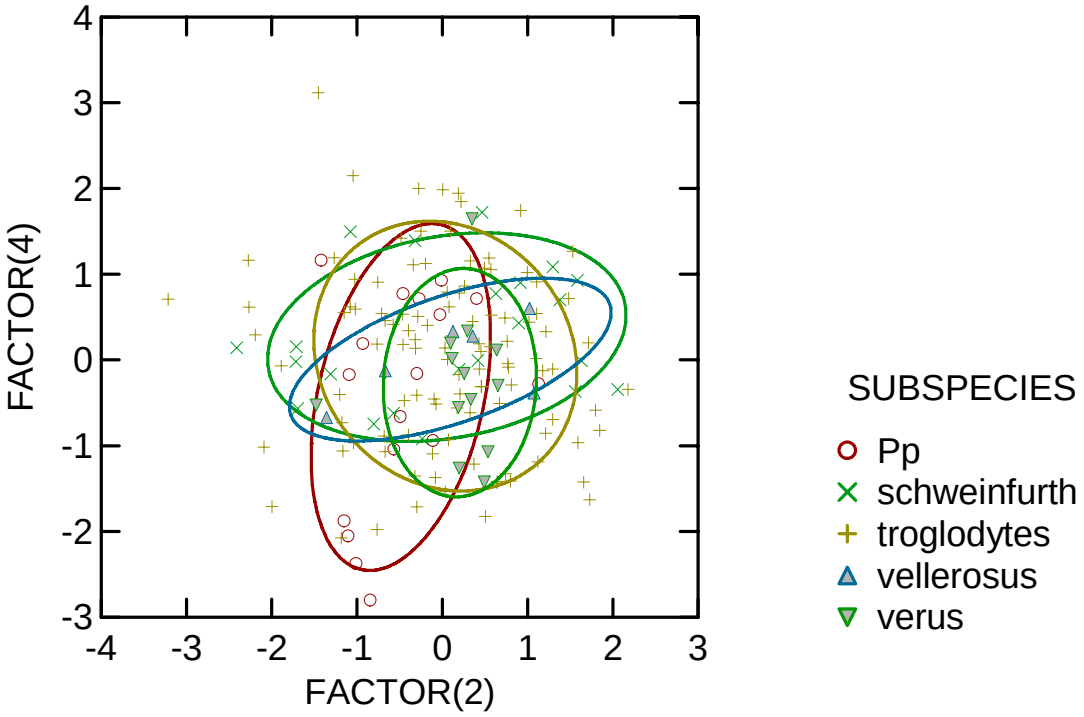


Figure 3.34. Principal components analysis of forelimb variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

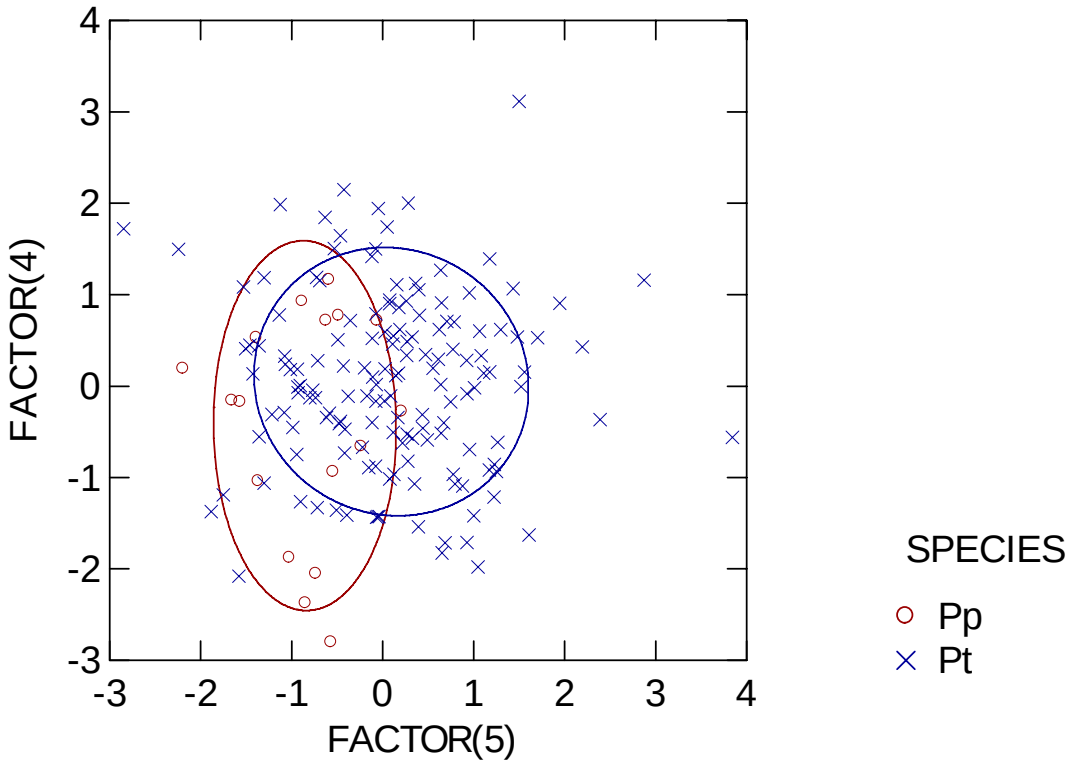


Figure 3.35. Principal components analysis of hindlimb variables from *Pan*, plotted by sex and species

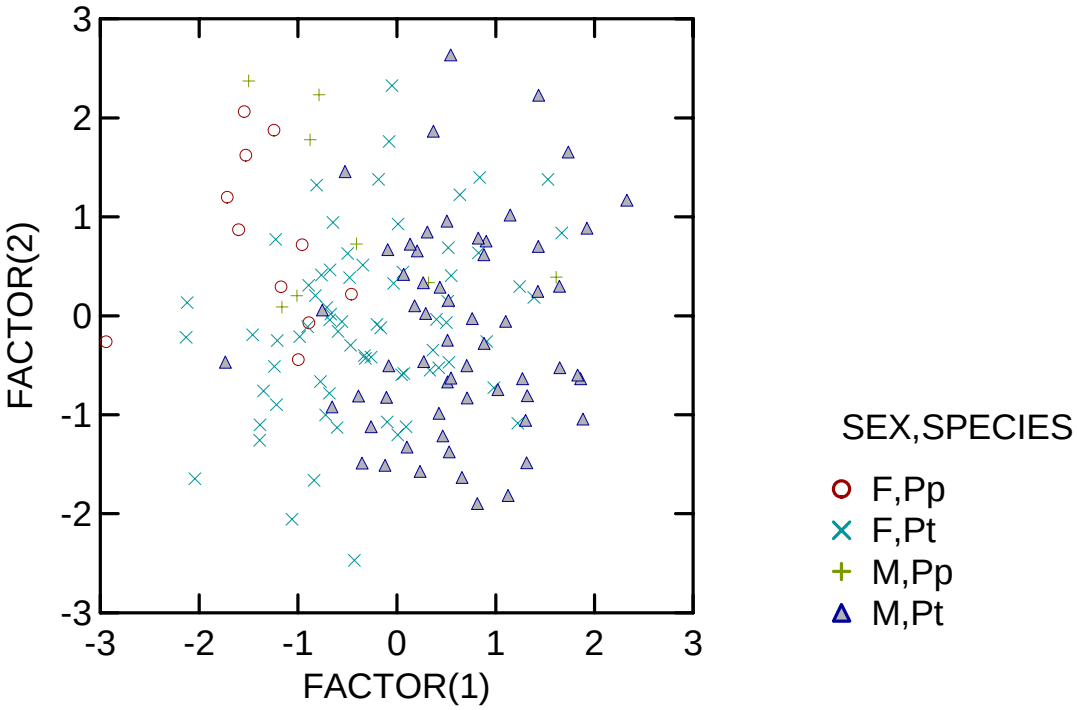


Figure 3.36. Principal components analysis of hindlimb variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

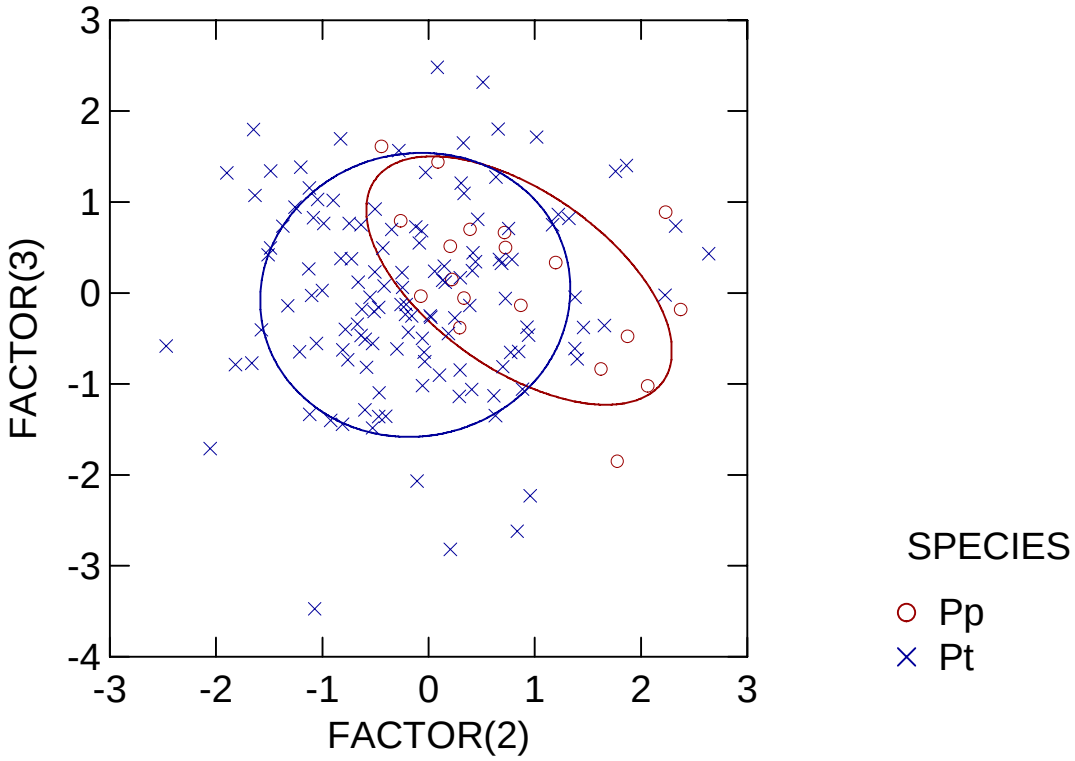


Figure 3.37. Principal components analysis of hindlimb variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

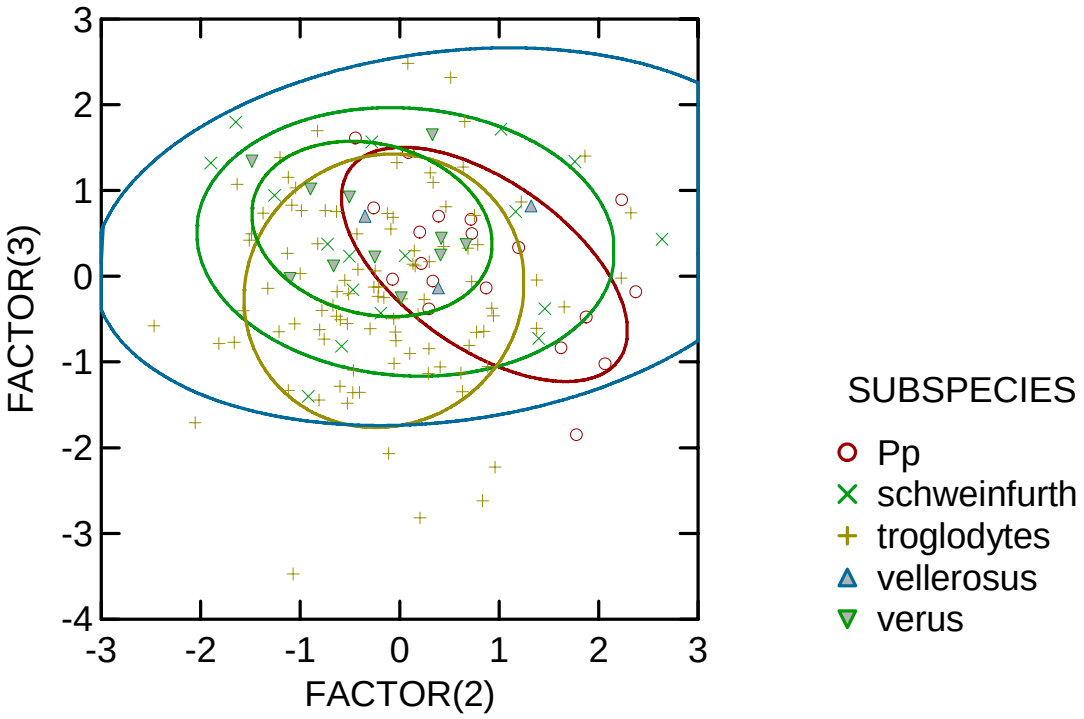


Figure 3.38. Principal components analysis of long bone variables from *Pan*, plotted by sex and species

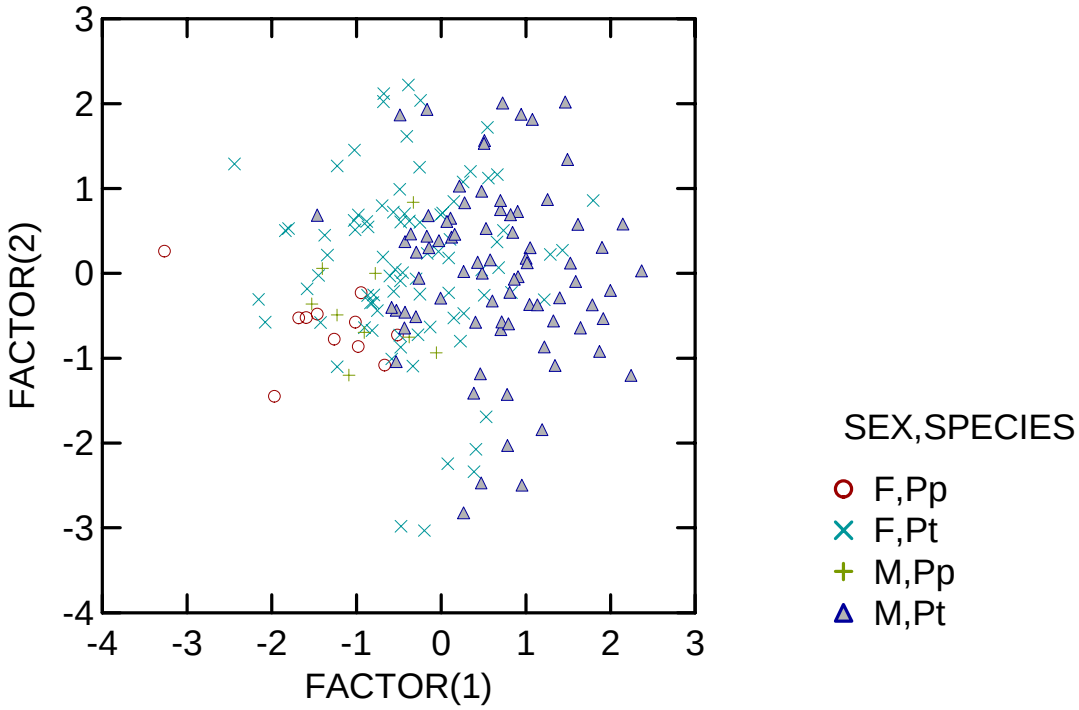


Figure 3.39. Principal components analysis of long bone variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

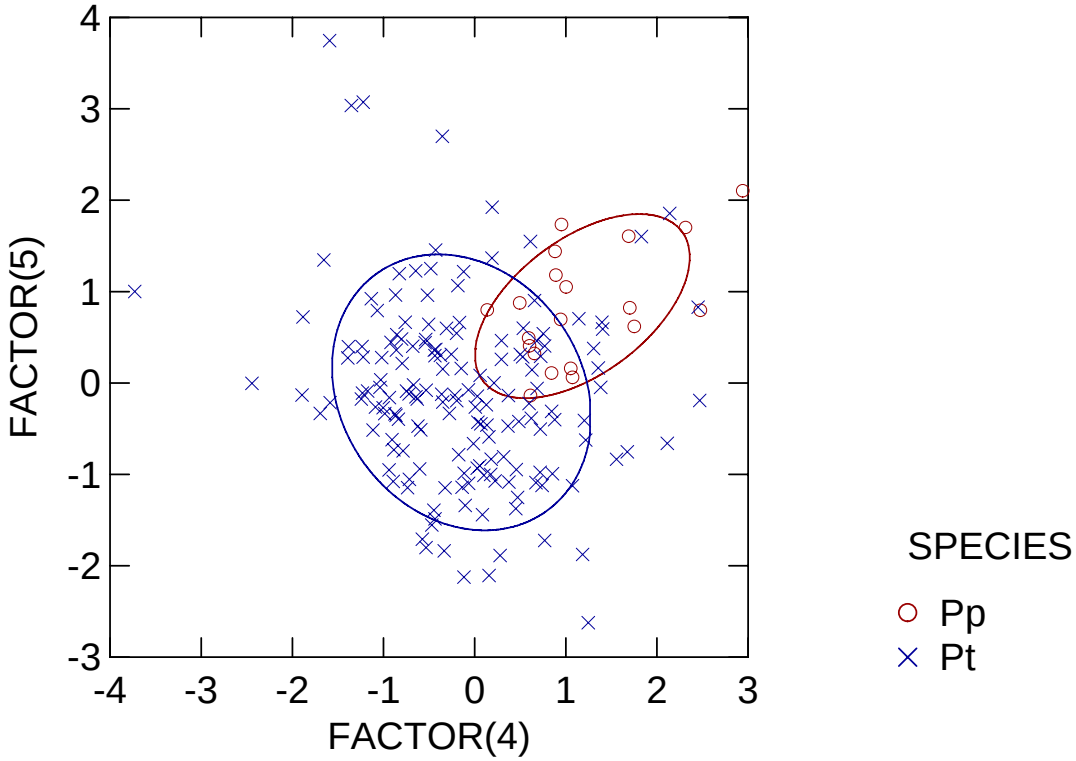


Figure 3.40. Principal components analysis of long bone variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

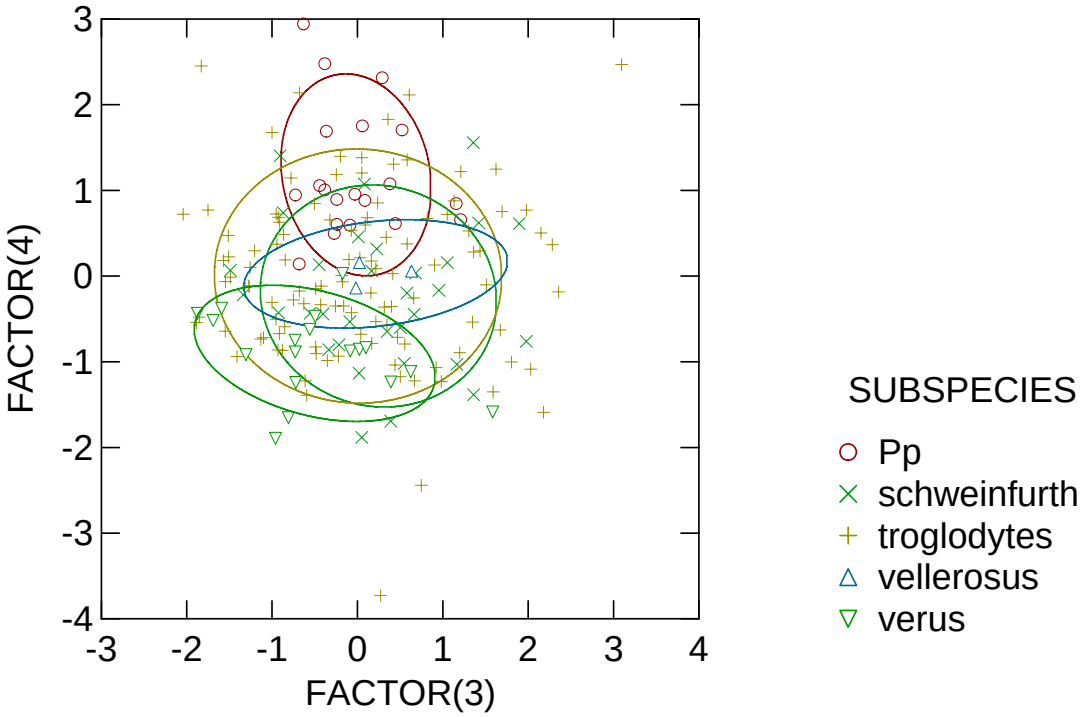


Figure 3.41. Principal components analysis of long bone variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

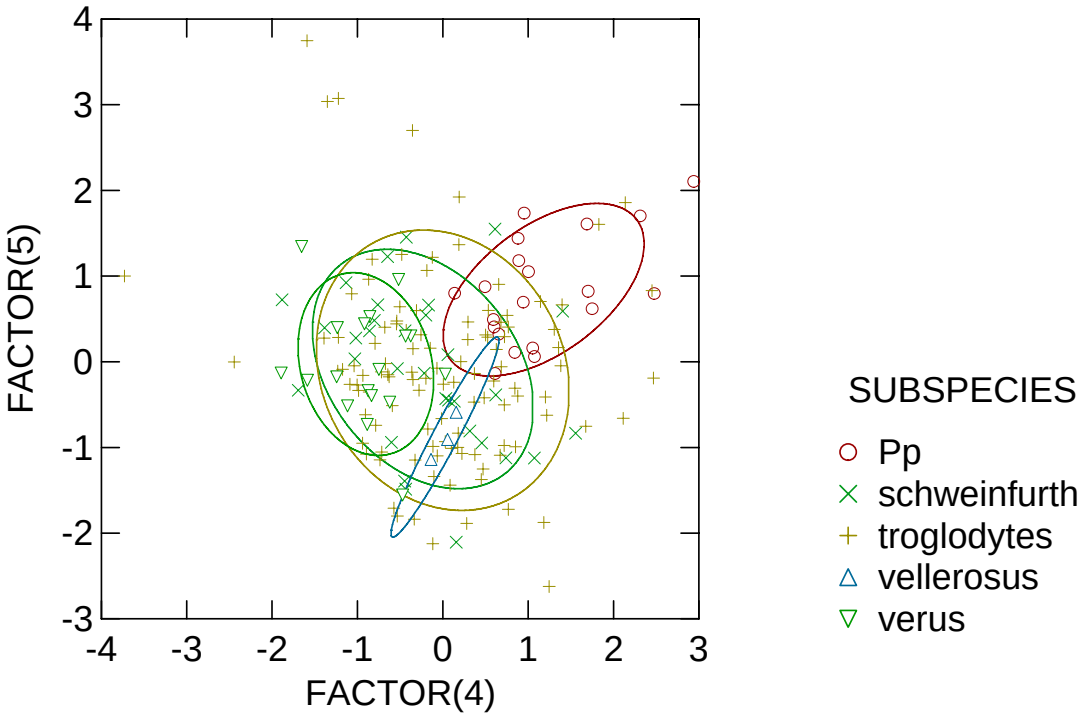


Figure 3.42. Principal components analysis of hand variables from *Pan*, plotted by sex and species

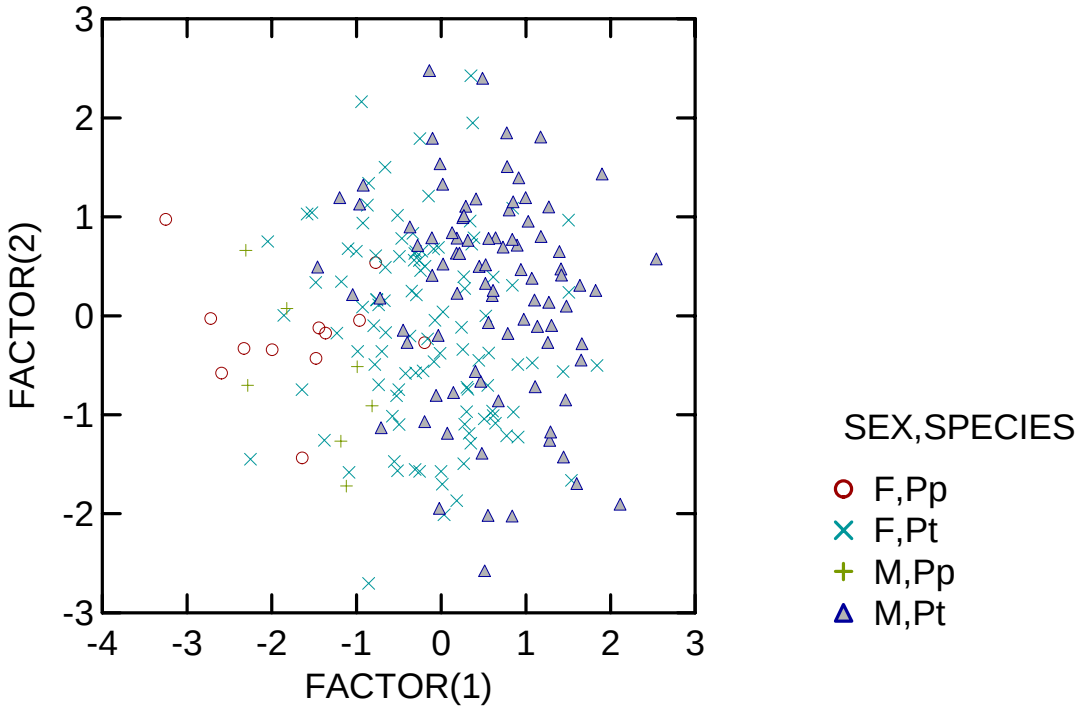


Figure 3.43. Principal components analysis of hand variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

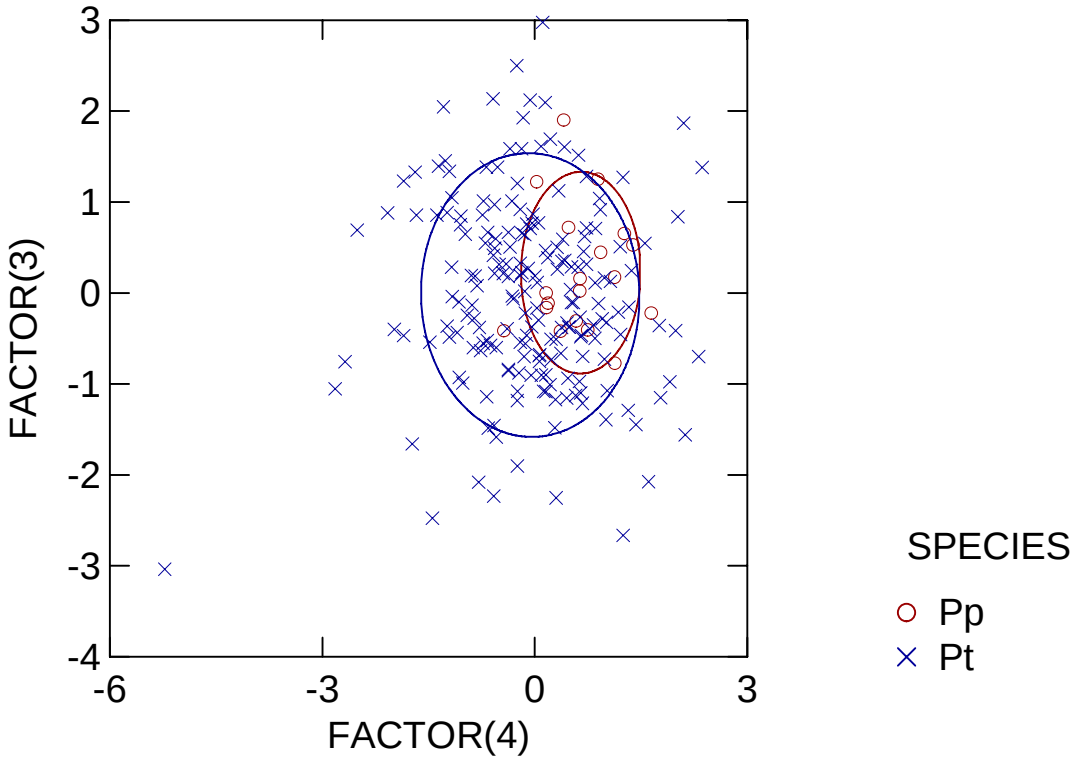


Figure 3.44. Principal components analysis of hand variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

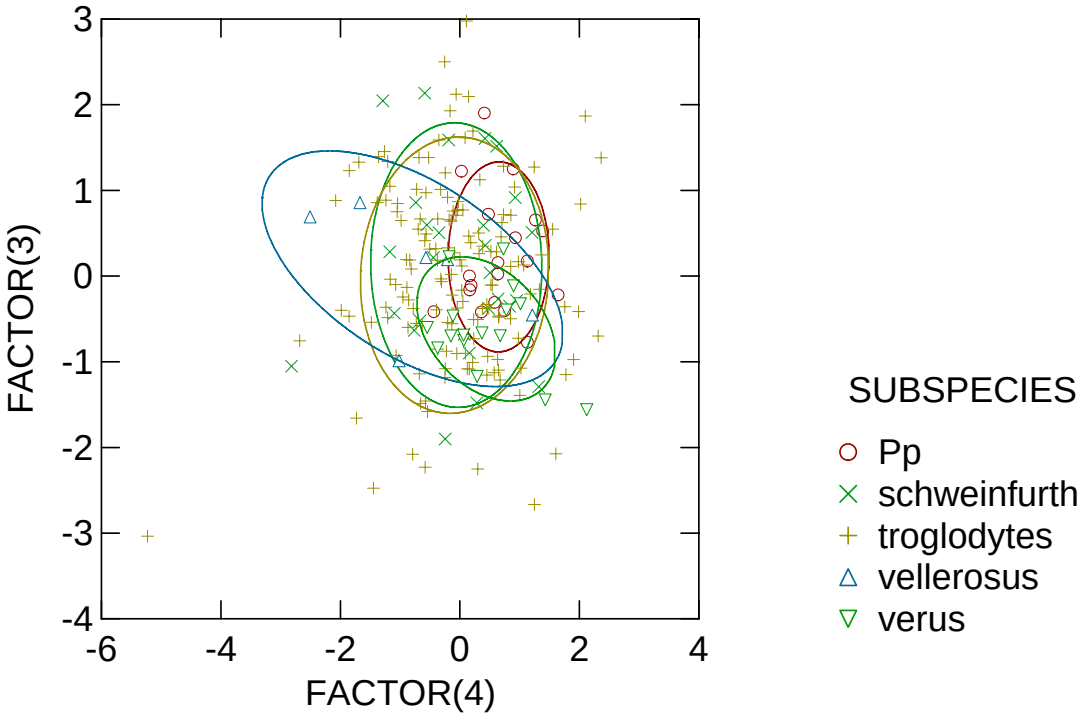


Figure 3.45. Principal components analysis of foot variables from *Pan*, plotted by sex and species

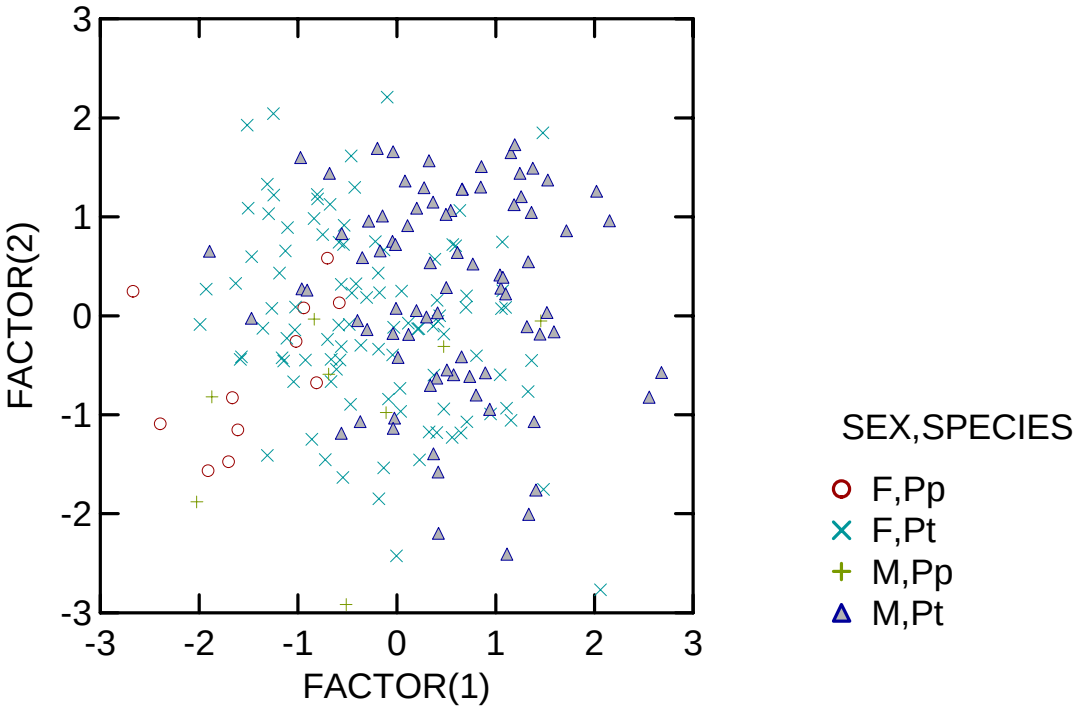


Figure 3.46. Principal components analysis of foot variables from *Pan*, plotted by species. The confidence ellipses for the samples are set at 68.27%.

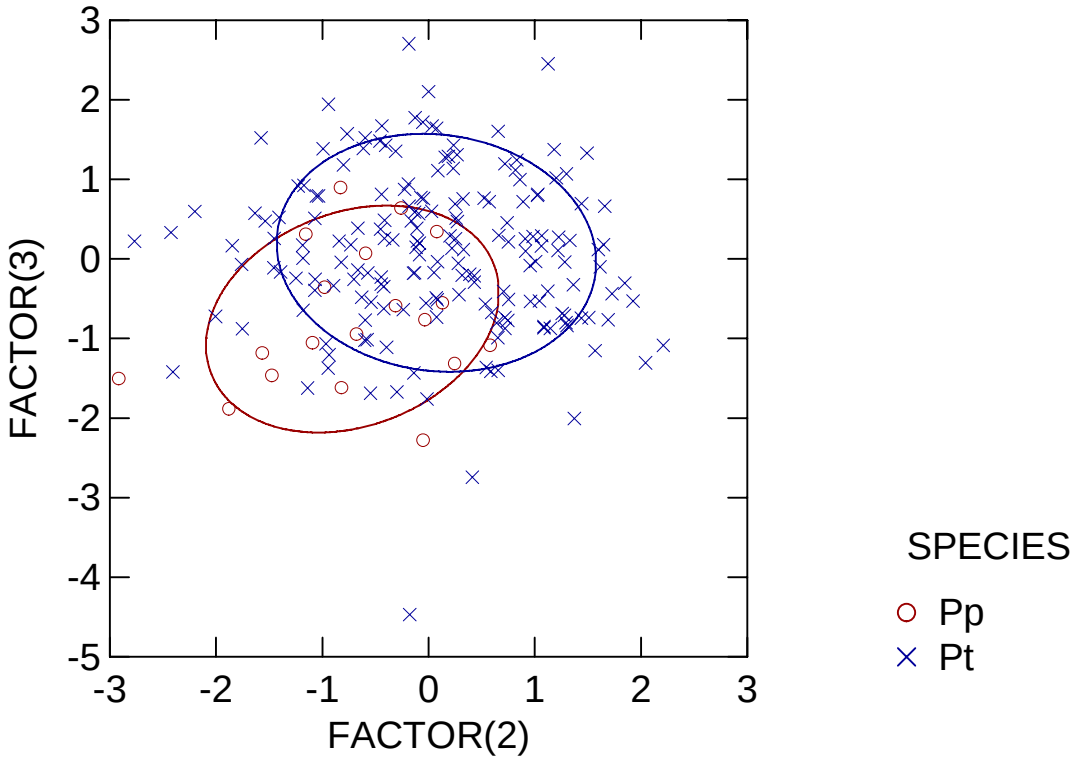


Figure 3.47. Principal components analysis of foot variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

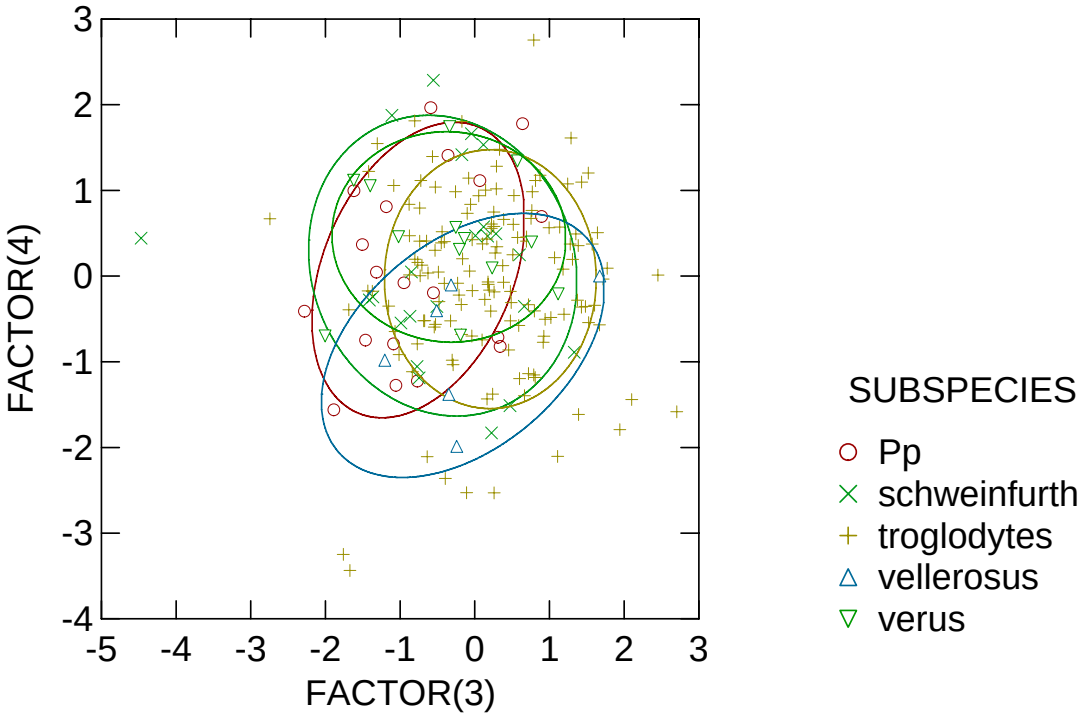


Figure 3.48. Principal components analysis of foot variables from *Pan*, plotted by subspecies. The confidence ellipses for the samples are set at 68.27%.

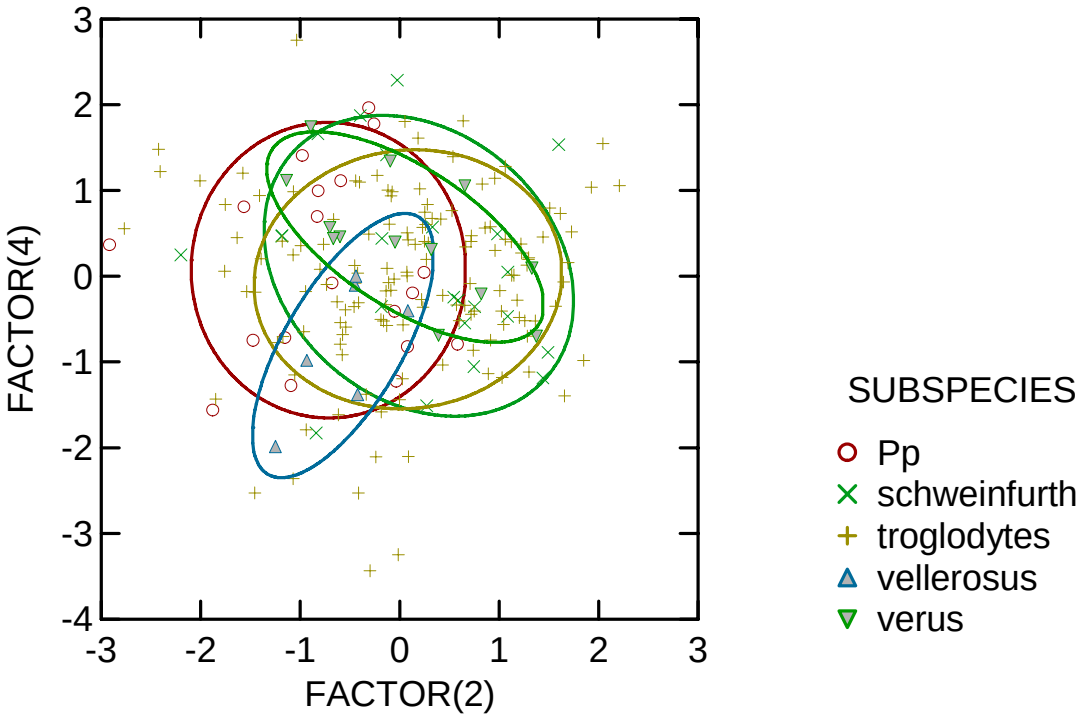


Figure 3.49. Principal components analysis of all variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.

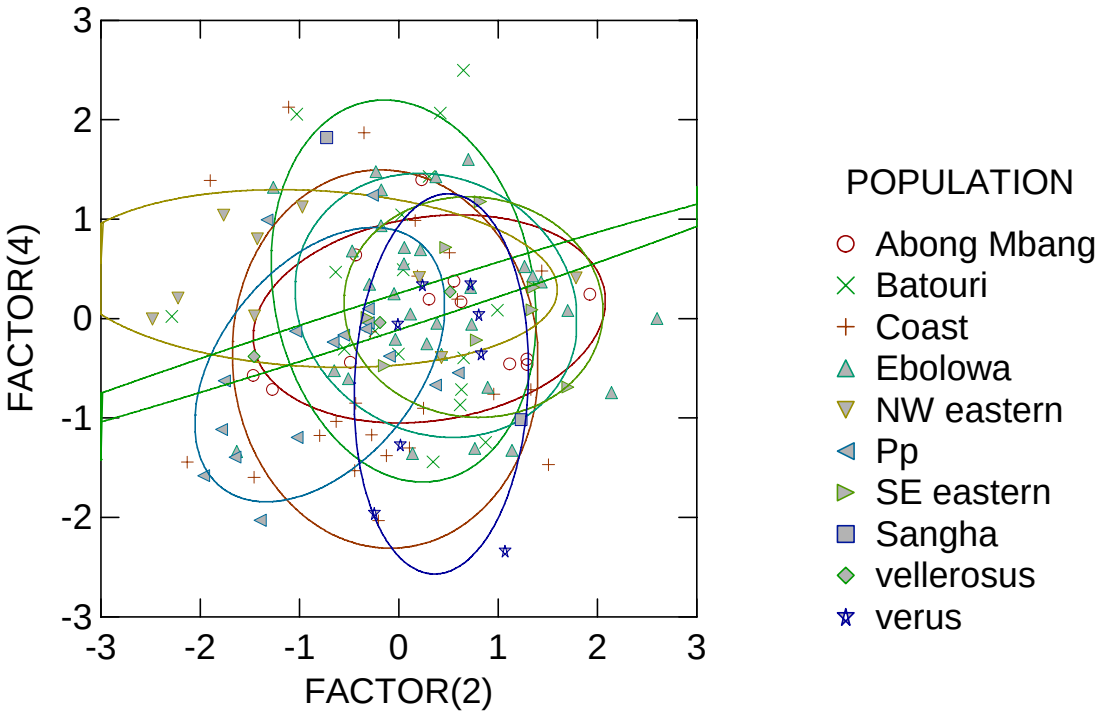


Figure 3.50. Principal components analysis of forelimb variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.

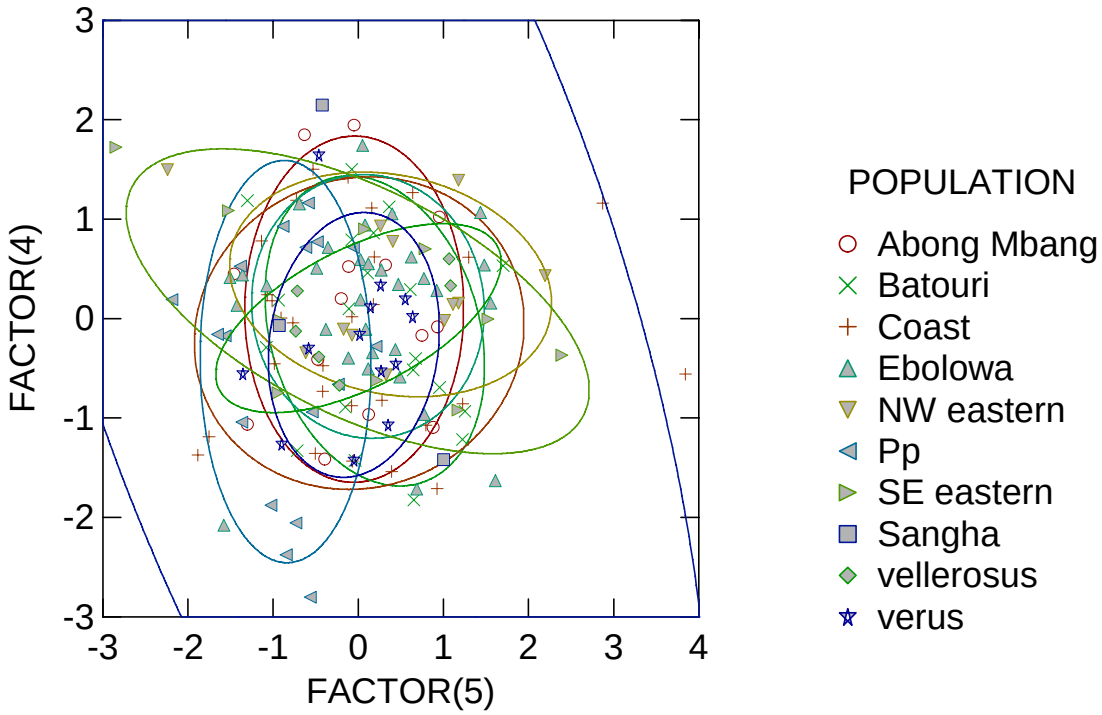


Figure 3.51. Principal components analysis of hindlimb variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.

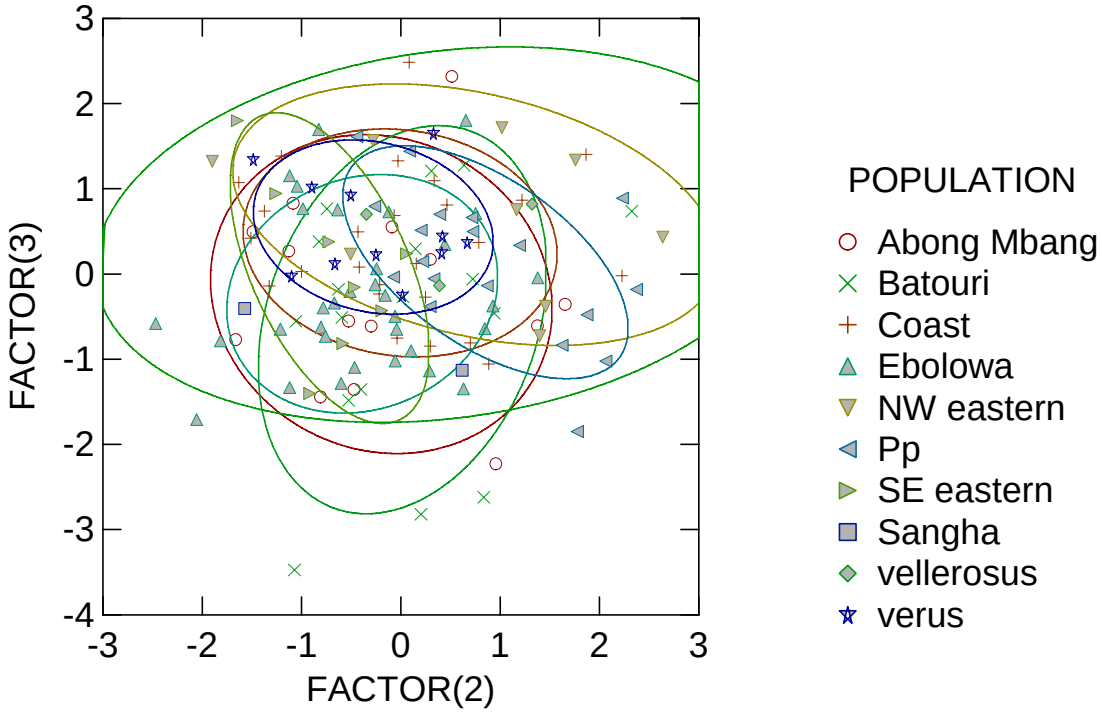


Figure 3.52. Principal components analysis of long bone variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.

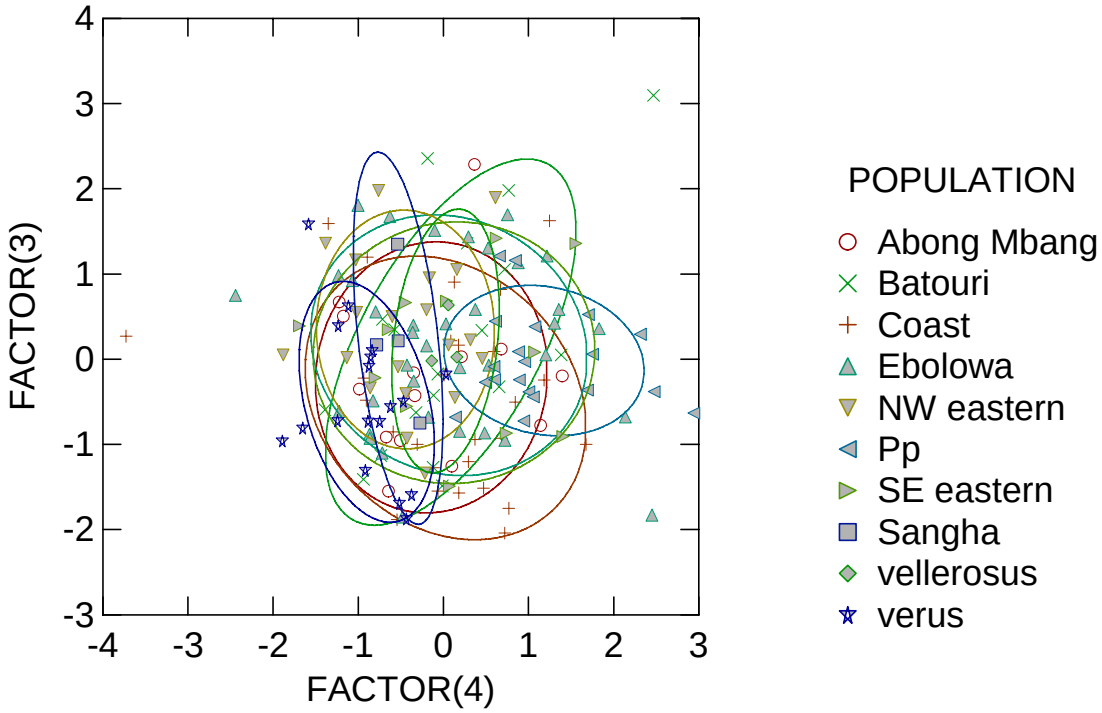


Figure 3.53. Principal components analysis of hand variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.

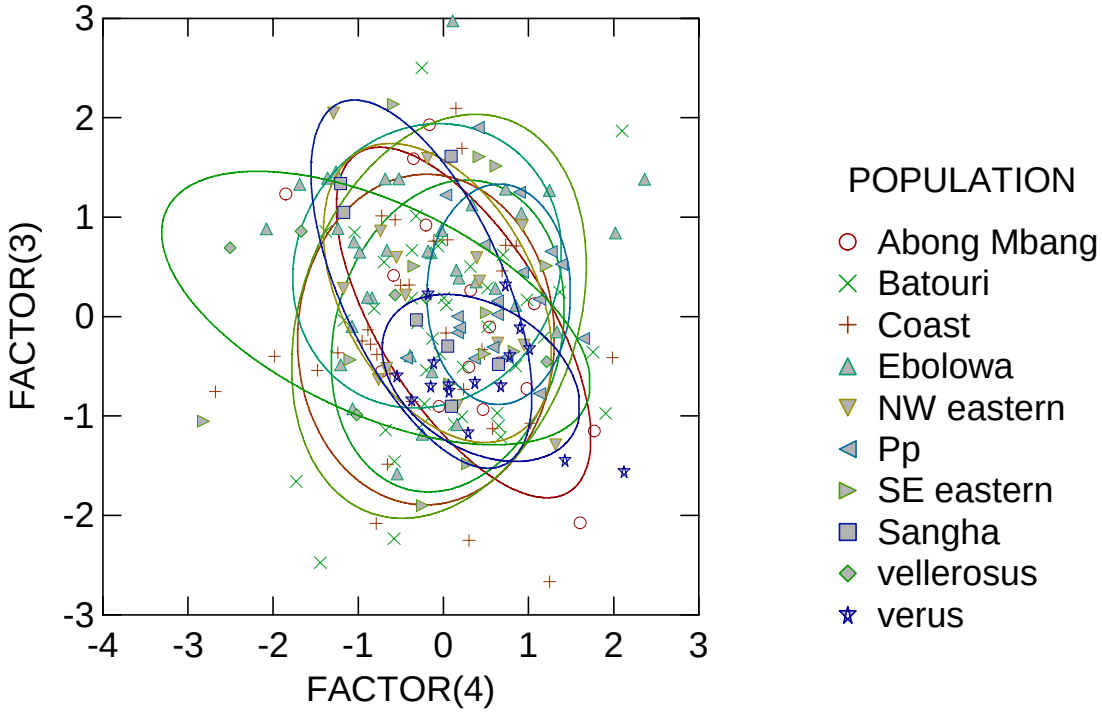
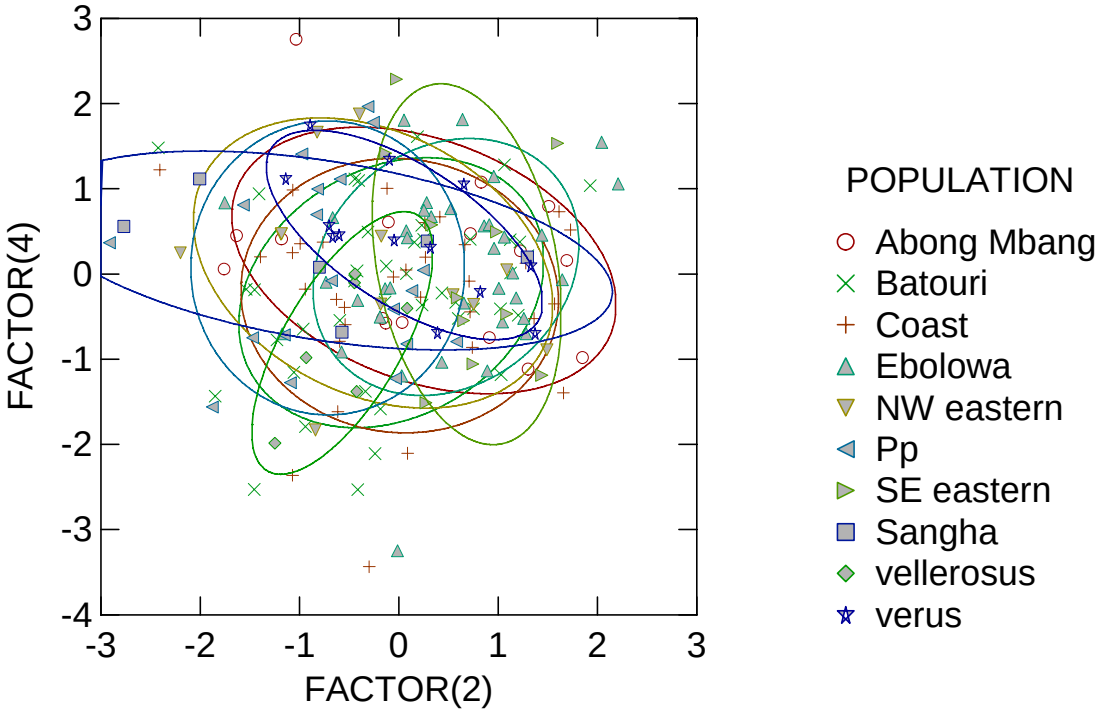


Figure 3.54. Principal components analysis of foot variables from *Pan*, plotted by population. The component that best distinguishes the species is on the x-axis, and the component that best distinguishes *P. t. verus* from *P. t. schweinfurthii* and *P. t. troglodytes* is on the y-axis. If the two components are the same, then the y-axis is the component that distinguishes *P. t. verus* second-best, after the component on the x-axis. The confidence ellipses for the samples are set at 68.27%.



# Geographic Variation in the Forelimb and Hindlimb Skeletons of African Apes

by

Rebecca S. Jabbour

Vol. II

A dissertation submitted to the Graduate Faculty in Anthropology in partial fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

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# CHAPTER 4

## RESULTS: Analyses of ratios of hand and foot bone measurements

This chapter reports results of the analyses of hand and foot ratios. The primary goal of this set of analyses is to address the same questions and predictions about patterns of geographic variation that are addressed by the analyses of raw measurements; however, because the hand and foot ratios were selected for their proposed functional significance, using these variables also has the potential to facilitate exploration of the relationship between geographic variation and adaptation in African apes. Definitions of these ratios can be found in Tables 2.5 (listed by skeletal element) and 2.6 (listed by proposed functional significance). Literature sources for these ratios and their functional interpretations are given in Appendix 1.

These hand and foot bone ratios were selected for analysis because they were thought likely to reflect the relative frequency of positional behaviors that are either characteristically arboreal (climbing and suspension) or characteristically terrestrial (knuckle-walking). For the sake of this chapter's readability, variables that are proposed to reflect the relative frequency of characteristically arboreal positional behaviors are referred to as "arboreal variables", and variables that are proposed to reflect the relative frequency of characteristically terrestrial positional behaviors are referred to as "terrestrial variables". This is not meant to imply that the functional significance of these variables is known or assumed. The ratios are designed so that, if the proposed relationship between morphology and positional behavior does exist, higher values reflect a greater frequency of the positional behavior.

The chapter is organized into three main sections. The first section describes the results of the comparisons of means. The second section describes the results of the multivariate analyses. The final section brings together and compares the results of the various analyses to look for patterns in the observed geographic variation.

Names of ratios are abbreviated in the tables accompanying this chapter. The descriptive names to which these abbreviations refer may be located in Tables 2.5 and 2.6, but the reader may find it easier to consult Appendix 3, Table 2, for a simple list of abbreviations, each followed by its descriptive name.

## Comparisons of means

Comparisons of means using univariate statistics were performed between genera, species, subspecies, and populations. Males and females were analyzed separately. This section is divided into separate subsections for comparisons between *Gorilla* and *Pan*, comparisons within *Gorilla*, and comparisons within *Pan*.

Comparisons of means between genera and between species were conducted using two-sample t-tests. Bonferroni corrections were applied to adjust for multiple tests, and differences between groups are described as "significant" only when Bonferroni-corrected p-values are less than or equal to 0.05. Results also include uncorrected p-values, as their inclusion sometimes provides a better appreciation for patterns in the observed variation. References to "low uncorrected p-values" describe uncorrected p-values less than or equal to 0.05.

Comparisons of means at the subspecies and population levels were accomplished with one-way ANOVAs. Results are based on post hoc significance tests of pairwise comparisons, using a Bonferroni adjustment.

## *Gorilla* and *Pan* compared

### Hand

Results of the two-sample t-tests comparing hand ratios in *Gorilla* and *Pan* are summarized in Table 4.1.

Of the four hand variables proposed to reflect arboreal locomotor behaviors ("arboreal variables"), the *Pan* mean is significantly greater than the *Gorilla* mean for two of them, the hand phalanx flexor sheath ridge size ratio (HPFS) and the phalanx-metacarpal length ratio (XPMC), in both males and females. The *Gorilla* mean is significantly greater than the *Pan* mean for the hand phalanx arch height ratio (HPAH) in both sexes. The metacarpal arch height ratio (MCAH) is not significantly different in either sex.

Of the nine hand variables proposed to reflect terrestrial locomotion ("terrestrial variables"), the *Pan* mean is significantly greater than the *Gorilla* mean, in both sexes, for five of them, the ratios of metacarpal biepicondylar width (MCB), hand phalanx midshaft diameter (HPMD), hand phalanx base width (HPBD), hand phalanx trochlear width (HPTW), and hand phalanx glenoid plate tubercle size (HPGT). Of the remaining four terrestrial hand variables, the ratios of metacarpal midshaft diameter (MCM), metacarpal dorsal ridge height (MCDR), metacarpal head shape (MCHS), and hand power arm:load arm (XHPL), the *Gorilla* mean is significantly greater for all comparisons except that for MCDR in females, which has a low uncorrected p-value.

*Gorilla* and *Pan* are significantly different in both sexes for eleven of the thirteen hand ratios, with extremely small Bonferroni-corrected p-values for almost all of these comparisons. The genus means are significantly different in males, but not in females,

for a twelfth hand variable. For each of the thirteen variables, the same genus has the greater mean in both males and females. Despite the distinctions between genera, there is no clear functional signal in these differences, as each genus has the higher mean for half of the arboreal variables and about half of the terrestrial variables.

Foot

Results of the two-sample t-tests comparing foot ratios in *Gorilla* and *Pan* are summarized in Table 4.2.

Of the six arboreal foot variables, three are significantly different in both males and females, and two more are significantly different in females only. The *Gorilla* mean is significantly greater than the *Pan* mean for the cuboid facet shape ratio of the calcaneus (CCFS) in both males and females and for the foot phalanx arch height ratio (FPAH) in females. The *Pan* mean is significantly greater for the cuboid facet depth ratio of the calcaneus (CCFD) and the phalanx-metatarsal length ratio (XPMT) in both sexes and for the metatarsal arch height ratio (MTAH) in females. The arch height ratios of the foot phalanx and metatarsal (FPAH and MTAH) are not significantly different in males, but, in both cases, the male means differ in the same direction as the significantly different female means, with low uncorrected p-values. One arboreal foot variable, the foot phalanx flexor sheath ridge size ratio (FPFS), is not significantly different in either males or females.

Of the three terrestrial foot variables, a significant difference between genera is evident in two. In both the metatarsal biepicondylar width ratio (MTB) and the calcaneal tuberosity-metatarsal length ratio (XCMT), the *Gorilla* mean is significantly greater than

the *Pan* mean in both sexes. The calcaneal tendon facet width ratio (CCTW) is not significantly different in either males or females.

*Gorilla* and *Pan* are significantly different in both sexes for five of the nine foot ratios, with extremely small Bonferroni-corrected p-values for all of these comparisons. Two further foot variables are significantly different in females but not in males, with low uncorrected p-values for the male comparisons. In each of the nine cases, the same genus has the greater mean in both males and females. There is no clear pattern in which genus has the greater mean for arboreal foot variables. The *Gorilla* mean is greater for both of the terrestrial foot variables that show significant differences between the genera.

Summary of differences between *Gorilla* and *Pan*

Many significant differences in hand bone morphology are found between *Gorilla* and *Pan*. The third metacarpal of *Gorilla* has a greater dorso-palmar diameter in relation to radio-ulnar diameter at midshaft in both sexes, a greater head width in relation to head height in both sexes, greater head height in relation to third proximal hand phalanx length in both sexes, and a greater dorsal ridge height in relation to head height in males. The third proximal hand phalanx of *Gorilla* has a greater arch height in relation to bone length in both sexes. The *Pan* third metacarpal has a greater biepicondylar width in relation to head width in both sexes. The *Pan* third proximal hand phalanx has a greater length relative to third metacarpal length, a greater dorso-palmar diameter relative to radio-ulnar diameter at midshaft, more flaring flexor sheath ridges, a wider base relative to minimum shaft width, a wider trochlea relative to minimum shaft width, and greater projection of glenoid plate tubercles relative to base height, all in both sexes.

*Gorilla* and *Pan* are also significantly different in many features of the foot skeleton. The *Gorilla* third metatarsal has a greater biepicondylar width relative to head width in both sexes, and its third proximal hand phalanx has a greater arch height relative to bone length in females. In both sexes, the *Gorilla* calcaneus has a longer tuberosity relative to third metatarsal length and a taller cuboid facet relative to cuboid facet width. The *Pan* third metatarsal has a greater arch height relative to bone length in females. In both sexes of *Pan*, the length of the third proximal foot phalanx is greater relative to third metatarsal length, and the depth of the cuboid facet of the calcaneus is greater relative to its width.

In terms of the differences in positional behavior frequencies and substrate/superstrate use that these variables are proposed to reflect, results are quite inconsistent. Each genus has significantly higher values for multiple variables in both arboreal and terrestrial categories.

### *Gorilla*

#### Species

Hand

Results of the two-sample t-tests comparing hand ratios in the two species of *Gorilla* are summarized in Table 4.3.

Of the four arboreal hand variables, three are significantly different between *Gorilla* species in one or both sexes. The *G. beringei* mean is significantly greater for the phalanx-metacarpal length ratio (XPMC) in both sexes and for the hand phalanx flexor sheath ridge size ratio (HPFS) for males only, although it is also greater, with a low

uncorrected p-value, for HPFS in females. The *G. gorilla* mean is significantly greater for the hand phalanx arch height ratio (HPAH) in both sexes.

Of the nine terrestrial hand variables, three are significantly different in one or both sexes. The *G. gorilla* mean is significantly greater for the metacarpal biepicondylar width ratio (MCB) and the hand phalanx based width ratio (HPBD) in both sexes and for the hand phalanx glenoid plate tubercle size ratio (HPGT) in males, although it is also non-significantly greater for HPGT in females.

The two species of *Gorilla* are significantly different in both sexes for four of the thirteen hand variables in this study and in males only for two further hand variables. *Gorilla gorilla* has the greater mean for all three terrestrial hand variables that show a significant difference between species and also for one of the three significantly different arboreal hand variables.

Foot

Results of the two-sample t-tests comparing foot ratios in the two species of *Gorilla* are summarized in Table 4.4.

Of the six arboreal foot variables, four are significantly different between *Gorilla* species in one or both sexes. The *G. beringei* mean is significantly greater for the metatarsal arch height ratio (MTAH) and the foot phalanx flexor sheath ridge size ratio (FPFS) in both sexes and for the phalanx-metatarsal length ratio (XPMT) in males, with a non-significantly greater mean for XPMT in females. The *G. gorilla* mean is significantly greater for the cuboid facet depth ratio of the calcaneus (CCFD) in both sexes.

Of the three terrestrial foot variables, two are significantly different between species. The *G. gorilla* mean is greater for the metatarsal biepicondylar width ratio (MTB) in both sexes, while the *G. beringei* mean is greater for the calcaneal tuberosity-metatarsal length ratio (XCMT) in both sexes.

Five out of nine foot variables show a significant difference between *Gorilla* species in both sexes, and a further foot variable shows a significant difference in males only. There is no clear pattern in which species has the higher mean for either arboreal or terrestrial variables.

Summary of differences between *G. beringei* and *G. gorilla*

The two species of *Gorilla* are distinguished by a number of significantly different features of the hand. In *G. beringei*, the third proximal hand phalanx is longer relative to third metacarpal length in both sexes, and its flexor sheath ridges are more flaring in males. The third metacarpal of *G. gorilla* has a greater biepicondylar width relative to head width in both sexes. The third proximal hand phalanx of *G. gorilla* has a greater arch height relative to bone length and a wider base relative to minimum shaft width in both sexes, and it has greater glenoid plate tubercle projection relative to base height in males.

Foot features also differ significantly between the *Gorilla* species. The third metatarsal of *G. beringei* has a higher arch relative to bone length in both sexes, and its third proximal foot phalanx has more flaring flexor sheath ridges in both sexes and is longer relative to third metatarsal length in males. The *G. beringei* calcaneal tuberosity is longer relative to third metatarsal length in both sexes. In both sexes of *G. gorilla*, the

third metatarsal biepicondylar width is greater relative to head width, and the cuboid facet of the calcaneus is deeper relative to its width.

Of the three features of the hand and foot that show no significant differences between the genera, two also show no significant differences between the species of *Gorilla*. These features are third metacarpal arch height relative to bone length and calcaneal tendon facet width relative to tuberosity height. The flaring of the flexor sheath ridges on the third proximal foot phalanx is significantly different between the *Gorilla* species in both sexes but not between *Gorilla* and *Pan*.

In terms of functional interpretations, results are inconsistent, as they were in the comparisons between genera. Each species of *Gorilla* has significantly higher values than the other for multiple arboreal variables and at least one terrestrial variable.

**Subspecies**

Univariate comparisons of hand and foot ratios among *Gorilla* subspecies were accomplished with one-way ANOVAs including all three of the subspecies for which samples are adequate for analysis: *G. b. beringei, G. b. graueri*, and *G. g. gorilla*. Results of post hoc tests of pairwise comparisons are reported in Tables 4.5 – 4.10. As comparisons of means between *G. g. gorilla* and the two *G. beringei* subspecies are similar to the univariate differences between *G. gorilla* and *G. beringei* summarized in the section above on species-level comparisons, they are not summarized in text form.

Hand

Results of post hoc significance tests for comparisons of *G. b. beringei* and *G. b. graueri*, from one-way ANOVAs comparing *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla* on the basis of hand ratios, are summarized in Table 4.5.

Of the four arboreal hand variables, a significant difference is found in only one. The *G. b. graueri* mean is significantly greater for phalanx-metacarpal length ratio (XPMC) in males only, although it is non-significantly greater in females.

Of the nine terrestrial hand variables, three variables show a significant difference in one sex. The *G. b. beringei* mean is greater for the metacarpal head shape ratio (MCHS) in males and the hand phalanx glenoid plate tubercle size ratio (HPGT) in females. The *G. b. graueri* mean is greater for the metacarpal biepicondylar width ratio (MCB) in males. For all three variables, the same subspecies has the greater mean in both males and females, although only one sex shows a significant difference.

Four of the thirteen hand variables show a significant difference between these subspecies, but no variable is significantly different in both sexes. The *G. b. graueri* mean is greater for the one significantly different arboreal variable and also for one of the three significantly different terrestrial variables.

Foot

Results of post hoc significance tests for comparisons of *G. b. beringei* and *G. b. graueri*, from one-way ANOVAs comparing *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla* on the basis of foot variables, are summarized in Table 4.6.

Of the six arboreal foot variables, one is significantly different between these subspecies. The *G. b. graueri* mean is significantly greater for the foot phalanx flexor sheath ridge size ratio (FPFS) in both males and females.

Of the three terrestrial foot variables, two are significantly different in one sex. The *G. b. graueri* mean is significantly greater for the metatarsal biepicondylar width ratio (MTB) and the calcaneal tendon facet width ratio (CCTW) in females only; it is non-significantly greater for both variables in males.

Three of the nine foot variables are significantly different in at least one sex. The *G. b. graueri* sample has the greater mean for all three of these variables.

Summary of differences between *G. b. beringei* and *G. b. graueri*

Several features of the hand differ significantly between the two subspecies of *G. beringei*, but each only in one sex. In *G. b. beringei*, the third metacarpal has a wider head relative to head height in males, and the third proximal hand phalanx has greater projection of the glenoid plate tubercles relative to base height in females. In *G. b. graueri*, the third metacarpal has a greater biepicondylar width relative to head width in males, and the third proximal hand phalanx is longer relative to third metacarpal length in males.

Three features of the foot differ significantly between the two subspecies, as well. The greater expression of each feature is seen in *G. b. graueri*. Its third metatarsal has a greater biepicondylar width relative to head width in females, its third proximal foot phalanx has more flaring flexor sheath ridges in both sexes, and its calcaneal tendon facet is wider relative to tuberosity height in females.

Of the three features with no significant differences between *Gorilla* and *Pan*, two are among those that differ significantly between subspecies of *G. beringei*. These features are the flaring of the flexor sheath ridges on the third proximal foot phalanx and the width of the calcaneal tendon facet relative to tuberosity height. Only the third

metacarpal arch height relative to bone length is not significantly different in either sex when comparing genera, species of *Gorilla*, or subspecies of *G. beringei*.

Of the seven features that are significantly different between subspecies of *G. beringei*, five are also significantly different between the species of *Gorilla*. The two features that are significantly different between subspecies of *G. beringei* but not species of *Gorilla* are the measures of third metacarpal head width and calcaneal tendon facet width.

Functional signals, based on the proposed significance of the analyzed ratios, are consistent for arboreal variables but not for terrestrial variables. Both arboreal variables that show significant differences between the subspecies have greater values in *G. b. graueri*, but greater values for significantly different terrestrial variables are split evenly between *G. b. beringei* and *G. b. graueri*.

**Populations**

At the population level, comparisons of means were made only among the three *Gorilla* populations from west-central Africa used in direct comparisons between *Gorilla* and *Pan*: Coast, Cameroon Interior, and Ebolowa. Univariate comparisons of these three populations of *G. g. gorilla* were conducted using one-way ANOVAs. Results are reported as post hoc tests of pairwise comparisons using a Bonferroni correction. No tables of univariate results are provided, as there are few significant differences, and they can be presented adequately in the text.

Hand

Of the four arboreal hand variables, one shows significant differences between populations. In both males and females, the phalanx-metacarpal length ratio (XPMC) is significantly greater in the Cameroon Interior group than in the Ebolowa group ($p = 0.0000$ for males; $p = 0.0496$ for females), and in males it is significantly greater in the Cameroon Interior group than in the Coast group ($p = 0.0406$).

Of the nine terrestrial hand variables, three show significant differences between populations, and significant differences are only found among the females. The Cameroon Interior group has a significantly greater mean than the Ebolowa group for the metacarpal head shape ratio (MCHS) ($p = 0.0061$) and the hand phalanx trochlear width ratio (HPTW) ($p = 0.0078$), and it has a significantly greater mean than the Coast group for the metacarpal head shape ratio (MCHS) ($p = 0.0130$), as well. The Ebolowa group has a significantly greater mean than the Cameroon Interior group for the metacarpal biepicondylar width ratio (MCB) ($p = 0.0224$).

The Cameroon Interior group stands out for being one of the two groups in every one of these comparisons, and it is more different from the Ebolowa population than it is from the Coast population. The Cameroon Interior mean is greater in every comparison showing a significant difference, except one.

Foot

Of the six arboreal foot variables, one shows a significant difference in one comparison of groups. The Cameroon Interior males have a significantly greater mean than the Ebolowa males for the phalanx-metatarsal length ratio (XPMT) ($p = 0.0177$).

Of the three terrestrial foot variables, two show a significant difference in one comparison of groups each. In males, the Ebolowa mean is significantly greater than the

Cameroon Interior mean for the metatarsal biepicondylar width ratio (MTB) ($p = 0.0121$). In females, the Coast mean is significantly greater than the Ebolowa mean for the calcaneal tuberosity-metatarsal length ratio (XCMT) ($p = 0.0346$).

Summary of differences among populations of *Gorilla*

Of ten univariate comparisons between populations that yield a significant difference, nine include the Cameroon Interior group, and it appears to be more different from the Ebolowa group than from the Coast group. Although there are ten comparisons with significant differences, there are only seven variables with significant differences, as two variables (the phalanx-metacarpal length ratio and the metacarpal head shape ratio [XPMC and MCHS]) provide multiple significant differences between groups. Six of the seven variables provide significant differences between the Cameroon Interior group and at least one other group. In four of those six variables, the Cameroon Interior mean is greater than that of the group or groups from which it is significantly different. The other two variables have a significantly greater mean in the Ebolowa group than in the Cameroon Interior group; these are the biepicondylar width ratios of the metacarpal and metatarsal (MCB and MTB), which are homologous variables of the hand and foot.

Of the seven variables that show significant differences between populations, three are inter-element length ratios: phalanx-metacarpal, phalanx-metatarsal, and calcaneal tuberosity-metatarsal length ratios (XPMC, XPMT, and XCMT). Two of these (XPMC and XPMT) are homologous ratios of the hand and foot. Further, two more of the seven significantly different variables are biepicondylar width ratios of the metacarpal and metatarsal, which constitute another pair of homologous ratios of the hand and foot. This suggests that differences between the populations in hand and foot morphology may

have fewer sources of variation than the initial count of seven significantly different variables would suggest.

Interestingly, the five ratios mentioned above that are either inter-element length ratios or biepicondylar width ratios are all among the ratios that are significantly different between the species of *Gorilla*. Further, both of the biepicondylar width ratios (MCB and MTB) and one of the three inter-element length ratios (XPMC) are among the seven ratios with significant differences between the two subspecies of *G. beringei*. This suggests that certain kinds of variables are especially prone to vary between geographic groups of *Gorilla*.

### *Pan*

#### Species

Hand

Results of the two-sample t-tests comparing hand ratios in the two species of *Pan* are summarized in Table 4.11.

Of the four arboreal hand variables, two exhibit a significant difference between the two species of *Pan*. In both the hand phalanx flexor sheath ridge size ratio (HPFS) and the phalanx-metacarpal length ratio (XPMC), the *P. troglodytes* mean is significantly greater than the *P. paniscus* mean in both sexes.

Of the nine terrestrial hand variables, only one shows a significant difference between species. The *P. troglodytes* mean is significantly greater for the hand phalanx glenoid plate tubercle size ratio (HPGT) in both sexes.

The two species of *Pan* have significantly different means in both sexes for three out of thirteen hand variables. Two are arboreal variables and one is a terrestrial variable. The *P. troglodytes* mean is greater for all three of these variables.

Foot

Results of the two-sample t-tests comparing foot ratios in the two species of *Pan* are summarized in Table 4.12.

Of the six arboreal foot variables, two show significant differences between the species in one or both sexes. The *P. troglodytes* mean is significantly greater for the phalanx-metatarsal length ratio (XPMT) in both sexes and for the metatarsal arch height ratio (MTAH) in females; it is also non-significantly greater for MTAH in males, with a low uncorrected p-value.

Of the three terrestrial foot variables, one is significantly different in one sex. The mean is significantly greater in *P. paniscus* males for the calcaneal tuberosity-metatarsal length ratio (XCMT), and it is non-significantly greater for XCMT in *P. paniscus* females, with a low uncorrected p-value.

Three out of nine foot variables in the study are significantly different, in one or both sexes, between the two species of *Pan*. *Pan troglodytes* has the higher mean for both arboreal foot variables with significant differences, and *P. paniscus* has the higher mean for the one terrestrial foot variable with a significant difference.

Summary of differences between *P. paniscus* and *P. troglodytes*

Significant differences between species of *Pan* are found in three features of the hand, all in both sexes. The third proximal hand phalanx of *P. troglodytes* is longer

relative to the third metacarpal, has greater flaring of flexor sheath ridges, and has greater projection of the glenoid plate tubercles relative to base height.

The species differ significantly in three features of the foot, as well. The *P. troglodytes* third metatarsal arch height is greater relative to bone length in females, and its third proximal hand phalanx is longer relative to third metatarsal length in both sexes. The *P. paniscus* calcaneal tuberosity is longer relative to third metatarsal length in males.

The three variables that are not significantly different between genera are also not significantly different between species of *Pan*. All six of the variables that are significantly different between species of *Pan*, in at least one sex, are also significantly different between species of *Gorilla*, in at least one sex. These six variables include the three inter-element length ratios, two of which (phalanx-metacarpal and phalanx-metatarsal ratios) are homologous ratios of the hand and foot.

When potential functional interpretations are considered, all significantly different arboreal variables present a consistent signal, having greater values in *P. troglodytes*, but greater values for the two significantly different terrestrial variables are split between *P. troglodytes* and *P. paniscus*.

**Subspecies**

Analyses of *Pan* subspecies are limited to subspecies of *P. troglodytes*, as no subspecies of *P. paniscus* have been identified. Univariate comparisons of *P. troglodytes* subspecies were accomplished with one-way ANOVAs including all three of the subspecies for which samples are available for both sexes: *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*. Results are reported as post hoc tests of pairwise comparisons.

*P. t. troglodytes* vs. *P. t. schweinfurthii*

Hand

Results of post hoc significance tests for comparisons of *P. t. troglodytes* and *P. t. schweinfurthii*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of hand ratios, are summarized in Tables 4.13.

Only one out of the thirteen hand variables is significantly different between these two subspecies. *P. t. schweinfurthii* has a significantly greater mean for the hand phalanx midshaft diameter ratio (HPMD) in males only, while it has a non-significantly greater mean for HPMD in females.

Foot

Results of post hoc significance tests for comparisons of *P. t. troglodytes* and *P. t. schweinfurthii*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of foot ratios, are summarized in Table 4.14.

Of nine foot variables, not one is significantly different in either males or females.

*P. t. troglodytes* vs. *P. t. verus*

Hand

Results of post hoc significance tests for comparisons of *P. t. troglodytes* and *P. t. verus*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of hand ratios, are summarized in Table 4.15.

Of four arboreal hand variables, one is significantly different in a single sex. The *P. t. troglodytes* mean is significantly greater for the hand phalanx flexor sheath ridge size ratio (HPFS) in females, while it is greater, but not significantly so, in males.

Of nine terrestrial hand variables, one is significantly different in a single sex. The *P. t. verus* mean is significantly greater for the hand phalanx midshaft diameter ratio (HPMD) in males; it is non-significantly greater in females.

Foot

Results of post hoc significance tests for comparisons of *P. t. troglodytes* and *P. t. verus*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of foot ratios, are summarized in Table 4.16.

Of six arboreal foot variables, three are significantly different in a single sex each. The *P. t. troglodytes* mean is significantly greater for the cuboid facet shape ratio of the calcaneus (CCFS) in males and the phalanx-metatarsal length ratio (XPMT) for females; it is non-significantly greater for each of these variables in the opposite sex. The *P. t. verus* mean is significantly greater for the foot phalanx flexor sheath ridge size ratio (FPFS) in males, but the *P. t. troglodytes* mean is non-significantly greater for FPFS in females.

No significant differences are found in the terrestrial foot variables.

*P. t. schweinfurthii* vs. *P. t. verus*

Hand

Results of post hoc significance tests for comparisons of *P. t. schweinfurthii* and *P. t. verus*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of hand ratios, are summarized in Table 4.17.

No significant differences in hand variables are found between the two subspecies.

Foot

Results of post hoc significance tests for comparisons of *P. t. schweinfurthii* and *P. t. verus*, from one-way ANOVAs comparing *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* on the basis of foot ratios, are summarized in Table 4.18.

Of six arboreal foot variables, one is significantly different between subspecies. The *P. t. verus* mean is significantly greater for the foot phalanx flexor sheath ridge size ratio (FPFS) in males and non-significantly greater for FPFS in females.

No significant differences are found in the terrestrial foot variables.

Summary of differences among subspecies of *P. troglodytes*

Few significant differences in hand and foot morphology are seen among the subspecies of *P. troglodytes*. Comparisons of *P. t. troglodytes* and *P. t. verus* yielded several significant differences, while comparisons between *P. t. troglodytes* and *P. t. schweinfurthii* and *P. t. schweinfurthii* and *P. t. verus* yielded only one significant difference each.

Five hand and foot features were significantly different between *P. t. troglodytes* and *P. t. verus*, each in only one sex. In *P. t. troglodytes*, the third proximal hand phalanx has greater flaring of the flexor sheath ridges in females, the third proximal foot phalanx is longer relative to third metatarsal length in females, and the cuboid facet of the calcaneus is taller relative to its width in males. In *P. t. verus*, the third proximal hand phalanx has a greater dorso-palmar diameter relative to radio-ulnar diameter at midshaft in males, and the third proximal foot phalanx has more flaring flexor sheath ridges in males. Among the significantly different arboreal variables, each subspecies has the

greater value for at least one variable. Only one terrestrial variable is significantly different between the subspecies.

When *P. t. troglodytes* and *P. t. schweinfurthii* are compared, the third proximal hand phalanx of *P. t. schweinfurthii* has a significantly greater dorso-palmar diameter relative to radio-ulnar diameter at midshaft in males. This ratio is also significantly greater in *P. t. verus* males compared to *P. t. troglodytes* males, indicating that it is particularly small relative to the other subspecies in *P. t. troglodytes* males. When *P. t. schweinfurthii* and *P. t. verus* are compared, the third proximal foot phalanx of *P. t. verus* has significantly greater flaring of the flexor sheath ridges in males. This ratio is also significantly greater in *P. t. verus* males compared to *P. t. troglodytes* males, indicating that *P. t. verus* males have particularly flaring flexor sheath ridges of the third proximal foot phalanges relative to males of the other subspecies.

Although the three variables that are not significantly different between the two genera are also not significantly different between the two species of *Pan*, one of them, the foot phalanx flexor sheath ridge size ratio (FPFS), is significantly different between subspecies of *P. troglodytes*. This ratio is also significantly different between species and subspecies of *Gorilla*. Of the five variables that differ significantly between subspecies of *P. troglodytes*, only two of them are also significantly different between species of *Pan*. These two are the hand phalanx flexor sheath ridge size ratio (HPFS) and the phalanx-metatarsal length ratio (XPMT). Note that XPMT is an inter-element length ratio; this type of variable appears to commonly vary between geographic groups analyzed here.

**Populations**

At the population level, comparisons of means were made only among the three *Pan* populations from west-central Africa used in direct comparisons between *Gorilla* and *Pan*: Coast, Cameroon Interior, and Ebolowa. Univariate comparisons of these three populations of *P. t. troglodytes* were conducted using one-way ANOVAs, and only one significant difference was found, based on post hoc tests of pairwise comparisons using a Bonferroni correction. Among females, the mean for the hand phalanx base width ratio (HPBD) in the Cameroon Interior group is significantly greater than the mean for HPBD in the Ebolowa group ($p = 0.0065$). This variable is not significantly different between species or subspecies of *Pan*, but it is significantly different between *Gorilla* and *Pan* and between species of *Gorilla*. No tables of univariate results are provided.

**Multivariate analyses**

Multivariate analyses of hand and foot bone ratios include discriminant function analysis (DFA) and principal components analysis (PCA). Analyses at the levels of genus, species, subspecies, and population are conducted using DFA. Additional analyses at the level of subspecies are conducted using PCA. Separate analyses are conducted for males and females, and hand and foot variables are analyzed separately.

For both types of multivariate analysis, the results report variables that contribute most to the separation of groups. The same arbitrary cutoff point is used for both to determine which variables are reported. For the PCAs, the list of variables with the highest loadings on each component includes all variables having loadings (correlations to the component) with absolute values of 0.40 or greater. For the DFAs, the list of

variables that contribute most to discriminating the groups includes all variables having coefficients with absolute values of 0.40 or greater.

Graphs are used to illustrate some, but not all, results. All PCA results are accompanied by graphs, because PCA results rely on visual assessment. Only DFAs involving more than two groups are graphically illustrated, as discrimination between two groups can be adequately presented using text and tables. The population-level DFAs are not accompanied by graphs for several reasons explained in the text.

### *Gorilla* and *Pan* compared

Two sets of discriminant function analyses were performed on the *Gorilla* and *Pan* samples together, one by genus (two groups, *Gorilla* and *Pan*) and one by species (four groups, *G. gorilla*, *G. beringei*, *P. troglodytes*, and *P. paniscus*). The analyses by genus explore how well the two genera can be discriminated and which variables contribute the most to this discrimination. The analyses by species look at whether the structuring of species-level variation in hand and foot variables, as revealed by discriminant function analysis, reflects current taxonomy. In other words, are the species of each genus more similar to one another than they are to the species of the other genus?

#### *Gorilla* and *Pan* analyzed by genus

Hand

Analysis of male *Gorilla* and *Pan* hands finds the forward and backward stepwise models and the complete model to all discriminate between genera with a 100% rate of correct classification (Wilks' lambda $p = 0.0000$). The forward and backward stepwise models are identical and are reported here, in preference to the complete model, because

they have the advantage of requiring fewer variables for the same rate of correct classification. Nine variables are selected by the models. The variables that contribute the most to discriminating the groups are the ratios of hand phalanx midshaft diameter (HPMD), hand power arm:load arm (XHPL), metacarpal head shape (MCHS), hand phalanx arch height (HPAH), and hand phalanx flexor sheath ridge size (HPFS), in order of magnitude (Table 4.19).

When female *Gorilla* and *Pan* hands are analyzed, the forward and backward stepwise models and the complete model all discriminate between genera with a 100% rate of correct classification (Wilks' lambda p = 0.0000). The forward and backward stepwise models are the same, with nine variables selected, and are reported here. The variables that contribute the most to discriminating the groups are the ratios of hand power arm:load arm (XHPL), metacarpal head shape (MCHS), hand phalanx midshaft diameter (HPMD), and metacarpal midshaft diameter (MCM) (Table 4.19).

Three hand ratios are among those that contribute the most to the discrimination between genera in both males and females: hand phalanx midshaft diameter (HPMD), hand power arm:load arm (XHPL), and metacarpal head shape (MCHS).

Foot

Male *Gorilla* and *Pan* feet are discriminated with a 100% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise and complete models. The forward and backward stepwise models are the same and are reported here. Seven variables are selected by the models. The variables that contribute most to the models are the calcaneal tuberosity-metatarsal length ratio (XCMT) and the metatarsal biepicondylar width ratio (MTB) (Table 4.20).

For female feet, the two genera are also discriminated with a 100% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise and complete models. The forward and backward stepwise models are identical, selecting seven variables, and are reported here. The calcaneal tuberosity-metatarsal length ratio (XCMT) contributes the most to this separation between groups (Table 4.20).

One foot variable, the calcaneal tuberosity-metatarsal length ratio (XCMT), dominates the functions that discriminate between the genera in both sexes.

Summary of hand and foot

In both males and females, *Gorilla* and *Pan* specimens are discriminated from one another 100% of the time using either hand or foot variables. No graphs are provided to illustrate the results of these analyses, because only two groups were analyzed, resulting in only one function and, consequently, only one axis to plot.

The hand and foot ratios that are among those that contribute most to the discriminant function in both males and females all have significantly different means in both sexes. The metacarpal head shape ratio (MCHS), the hand power arm:load arm ratio (XHPL), and the calcaneal tuberosity-metatarsal length ratio (XCMT) are significantly greater in *Gorilla*, while the hand phalanx midshaft diameter ratio (HPMD) is significantly greater in *Pan*. These are all "terrestrial variables", but this is unlikely to explain their especially prominent contributions to discriminating the genera, as one of the hand variables varies in the opposite direction from the others.

*Gorilla* and *Pan* analyzed by species

Hand

Male hands from the two species of *Gorilla* and the two species of *Pan* are discriminated at the species level with a 96% rate of correct classification (Wilks' lambda p = 0.0000) by forward and backward stepwise and complete models. Despite having the same rate (rounded) of correct classification, the complete model correctly classifies one more specimen than the stepwise models do, and the results of the complete model are reported here (Table 4.21, Figure 4.1).

All four species are quite well-discriminated by the model, with the lowest rate of correct classification belonging to *Pan troglodytes*, at 94%. All misclassified cases are assigned to the other species of the same genus. Function 1 separates *Gorilla* and *Pan*, and the variables that contribute the most to this separation of genera are the ratios of hand power arm:load arm (XHPL), hand phalanx midshaft diameter (HPMD), metacarpal head shape (MCHS), and hand phalanx arch height (HPAH). Function 2 separates the two species within each genus, and the variables that contribute the most to this species-level separation are the ratios of phalanx-metacarpal length (XPMC), hand phalanx flexor sheath ridge size (HPFS), metacarpal biepicondylar width (MCB), and hand phalanx arch height (HPAH). For Function 2, *P. paniscus* and *G. gorilla* each has a higher canonical score of group means than its congener, indicating that they differ in similar ways from their congeners. The species are arrayed on Function 2 from *G. beringei* at lower values to *P. paniscus* at higher values. Function 3 separates *P. paniscus* from the other three species, and this function is dominated by the hand phalanx glenoid plate tubercle size ratio (HPGT) and the metacarpal head shape ratio (MCHS).

Female hands are discriminated at the species level with an 89% rate of correct classification (Wilks' lambda p = 0.0000) by the complete model, which is only 1% better

than the stepwise models. The results of the complete model are reported here (Table 4.22, Figure 4.2).

All four species are discriminated well by the model, with *G. beringei* having the lowest rate of correct classification, at 85%. All misclassified cases except one are assigned to the other species of the same genus. As with the analysis of male hands, Function 1 separates *Gorilla* and *Pan*. The variables that contribute most to this separation are the ratios of hand power arm:load arm (XHPL), metacarpal head shape (MCHS), hand phalanx midshaft diameter (HPMD), and metacarpal midshaft diameter (MCM). Function 2 separates the two species within each genus, as with the males; *P. paniscus* and *G. gorilla* once again have higher canonical scores of group means than their congeners, indicating that the congeners differ in similar ways based on this function, and the four species are arrayed from *G. beringei* at lower values to *P. paniscus* at higher values. Function 2 receives its largest contributions from the phalanx-metacarpal length ratio (XPMC) and the hand phalanx arch height ratio (HPAH). Function 3 does not further separate any of the groups.

In both males and females, the species of *Gorilla* and *Pan* are well-discriminated. Function 1 separates the two genera, and Function 2 separates the two species within each genus. On Function 2, *P. paniscus* and *G. gorilla* vary in the same direction relative to *P. troglodytes* and *G. beringei*, in both sexes. Three ratios are among those that contribute most to discrimination of genera in Function 1 in both sexes: hand power arm:load arm (XHPL), hand phalanx midshaft diameter (HPMD), and metacarpal head shape (MCHS). Two ratios are among those that contribute most to discrimination of

species in Function 2 in both sexes: phalanx-metacarpal length (XPMC) and hand phalanx arch height (HPAH).

Foot

Male feet from the two species of *Gorilla* and the two species of *Pan* are discriminated at the species level with a 92% rate of correct classification (Wilks' lambda p = 0.0000) by forward and backward stepwise and complete models. The results of the stepwise models, which are identical, are reported here (Table 4.23, Figure 4.3). Eight variables are selected by the models.

*Pan paniscus*, with a 63% rate of correct classification (five of eight cases correct), is not as well-discriminated as the other three species, which have correct classification rates of 90 – 96%. All misclassified cases are assigned to the other species of the same genus. Function 1 separates *Gorilla* and *Pan* and is heavily dominated by the calcaneal tuberosity-metatarsal length ratio (XCMT). Function 2 primarily separates *G. beringei* from the other three taxa, and also provides some separation of *Pan* species, relying largely on the ratios of foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), metatarsal arch height (MTAH), and foot phalanx arch height (FPAH) to do so. Function 3 slightly separates *P. paniscus* from the other three species, mostly based on the phalanx-metatarsal length ratio (XPMT) and the foot phalanx flexor sheath ridge size ratio (FPFS).

Female feet are discriminated at the species level with an 89% rate of correct classification (Wilks' lambda p = 0.0000) by forward and backward stepwise and complete models. All three models are identical, and all nine foot variables are included in the stepwise, as well as the complete, models (Table 4.24, Figure 4.4).

The species of *Gorilla* are discriminated better than the species of *Pan*. *Gorilla gorilla* and *G. beringei* are each classified with a 93% success rate, while the rate for *P. troglodytes* is 86% and for *P. paniscus* is 82%. All misclassified cases except one are assigned to the other species of the same genus. Function 1, once again, separates the genera and is heavily dominated by the calcaneal tuberosity-metatarsal length ratio (XCMT). Function 2 primarily separates *G. beringei* from the other taxa, also separating *Pan* species to some extent, based mostly on the ratios of foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), and metatarsal arch height (MTAH). Function 3 provides very little separation of groups.

In both males and females, the overall rate of correct classification is good for the species of *Gorilla* and *Pan*, but the *Gorilla* species are better-discriminated than the *Pan* species, and *P. paniscus* has the lowest rate of correct classification. Even so, all misclassified cases except one are assigned to the other species of the same genus, indicating that the genus-level discrimination is quite robust. In both sexes, Function 1 separates the two genera and is dominated by the calcaneal tuberosity-metatarsal length ratio (XCMT). Function 2 primarily separates *G. beringei* from the other species in both sexes, emphasizing the contributions of the ratios of foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), and metatarsal arch height (MTAH).

Summary of hand and foot

Analysis of both hand and foot variables shows that variation among the four species of African ape is structured in agreement with current taxonomy. In both males and females, and in both hands and feet, Function 1 separates the two genera. Function 2 separates the two species of each genus in the analyses of hand variables, and it primarily

separates *G. beringei* from the other species in the analyses of foot variables. If *P. paniscus* is accepted as a valid species of *Pan*, and if morphological variation in hand and foot bones has any bearing on species-level systematics in African apes, the discrimination of species on Function 2 lends support to the validity of the recently-instituted species *G. beringei*. In every analysis, Function 2 separates the two species of *Gorilla* more than it separates the two species of *Pan*. This can be verified by consulting the canonical scores of group means supplied for each analysis (Tables 4.21 – 4.24).

The variables that contribute most, across both sexes, to discrimination between genera when analyzed by species are the same as those that contribute most to discrimination between genera when analyzed by genus. These variables are briefly discussed in the summary of the analyses by genus. With regard to species-level discrimination, two ratios of the hand and three ratios of the foot are among those that contribute most to differentiating the species in both sexes, and they do not overlap with the four variables that contribute most to separating the genera in both sexes. The hand variables are the phalanx-metacarpal length (XPMC) and hand phalanx arch height (HPAH) ratios. The phalanx-metacarpal length ratio (XPMC) is significantly different between species of *Gorilla* and between species of *Pan*, in comparisons of both males and females. The hand phalanx arch height ratio (HPAH) is significantly different between species of *Gorilla*, in both sexes, but is not significantly different between species of *Pan* in either sex. The foot variables are the ratios of foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), and metatarsal arch height (MTAH). All three of these variables are significantly different between species of *Gorilla* in both sexes, but only the metatarsal arch height (MTAH) has a significant

difference between species of *Pan*, and this difference is present only in females (with a low uncorrected p-value in males). Not surprisingly, the function that separates species on the basis of foot variables primarily separates the species of *Gorilla*.

### *Gorilla*

Discriminant function analyses and PCAs are used to reveal patterns of geographic variation within the genus *Gorilla*. Variation at the levels of species, subspecies, and population is evaluated using DFA. Principal components analysis is used to complement the subspecies-level DFAs and to explore patterns of clustering among populations.

#### Species

Discriminant function analysis is used to examine how well the two species of *Gorilla*, *G. beringei* and *G. gorilla*, can be differentiated and which variables contribute most to differentiating them.

##### Hand

Using male hand variables, the two species of *Gorilla* are discriminated with a 98% rate of correct classification (Wilks' lambda p = 0.0000) by forward and backward stepwise models. The stepwise models are slightly more successful than the complete model. The results of the forward and backward stepwise models are reported here (Table 4.25). Ten ratios are selected by the models. A number of ratios contribute to the models substantially and to a similar extent: phalanx-metacarpal length (XPMC), metacarpal biepicondylar width (MCB), hand phalanx midshaft diameter (HPMD), hand phalanx flexor sheath ridge size (HPFS), hand power arm:load arm (XHPL), hand

phalanx arch height (HPAH), hand phalanx glenoid plate tubercle size (HPGT), and hand phalanx base width (HPBD).

Using female hand variables, the two species are discriminated with a 91% rate of correct classification (Wilks' lambda p = 0.0000) by the complete model, which is slightly better than the stepwise models. The results of the complete model are reported here (Table 4.26). The model is primarily driven by the ratios of hand phalanx arch height (HPAH) and phalanx-metacarpal length (XPMC).

Two hand variables, the phalanx-metacarpal length (XPMC) and hand phalanx arch height (HPAH) ratios, make large contributions to discriminating the species in both males and females.

Foot

Using male foot variables, the two species of *Gorilla* are discriminated with a 96% rate of correct classification (Wilks' lambda p = 0.0000) by forward and backward stepwise models. The complete model is slightly less successful. The results of the forward and backward stepwise models are reported here (Table 4.27). Six variables are selected by the models. The variables that contribute the most to the models are the ratios of foot phalanx flexor sheath ridge size (FPFS), foot phalanx arch height (FPAH), and metatarsal biepicondylar width (MTB).

Using female foot variables, the two species are discriminated with a 94% rate of correct classification (Wilks' lambda p = 0.0000) by the complete model, which is slightly better than the stepwise models. The results of the complete model are reported here (Table 4.28). The ratios that contribute the most to the model are those of foot

phalanx flexor sheath ridge size (FPFS), metatarsal arch height (MTAH), metatarsal biepicondylar width (MTB), and calcaneal tuberosity-metatarsal length (XCMT).

Two foot variables are among those that contribute most to discriminating the species in both males and females: foot phalanx flexor sheath ridge size (FPFS) and metatarsal biepicondylar width (MTB).

Summary of hand and foot

Using either hand or foot variables, *G. gorilla* and *G. beringei* are correctly discriminated from each other at a high rate in both males and females. Males are discriminated at a slightly higher rate than females. The four hand and foot variables that contribute most to discriminating the species, across both sexes, all have significantly different means between the species in both males and females. The phalanx-metacarpal length ratio (XPMC), which contributes greatly to discrimination between the *Gorilla* species in this analysis, is also one of the two hand variables that contribute the most to separation of both *Gorilla* and *Pan* species in the inter-generic analysis by species. The two foot variables that contribute most to discrimination of *Gorilla* species in this analysis, the foot phalanx flexor sheath ridge size ratio (FPFS) and the metatarsal biepicondylar width ratio (MTB), are two of the three foot variables that contribute most to discrimination of *G. beringei* from *G. gorilla* and the species of *Pan* in the inter-generic analysis by species.

**Subspecies**

Although subspecies-level analyses within a single *Gorilla* species are limited, by available samples and by current taxonomy, to analyses of the two subspecies of *G.*

*beringei*, investigation of the differences and similarities between all four currently-recognized *Gorilla* subspecies, across the two species, is necessary to address some of the questions posed by this study. Samples in this study are adequate for statistical analysis of only three *Gorilla* subspecies, *G. b. beringei, G. b. graueri,* and *G. g. gorilla*. The sample of *G. g. diehli* hand and foot bones is from one individual, which can be compared to the larger samples but cannot be statistically analyzed. In order to conduct subspecies-level analyses both within the single species *G. beringei* and also across the two species of *Gorilla*, multivariate analyses were performed both on the sample including only *G. b. beringei* and *G. b. graueri* and also on the sample including *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla*.

Multivariate analyses of *Gorilla* subspecies include both DFAs and PCAs. Discriminant function analyses are used to examine how well the subspecies can be differentiated, which variables contribute most to differentiating them and, in the analyses including subspecies across both species, whether the patterns of variation between groups reflects the current taxonomic hierarchy. Principal components analyses complement the DFAs by presenting the variation between subspecies in the context of the overall variance in the entire *Gorilla* sample. Because PCA is blind to group membership, the contribution of group differences to the overall variation in the sample can be evaluated by plotting the specimens by group on the main "axes" of variation and assessing the amount of group separation. These plots also reveal patterns of clustering among groups, indicating which groups are most similar along the main axes of overall variance. Variables that contribute most to these patterns can be compared to those that contribute most to group separation in the DFAs. Complementary PCAs were not

conducted for analyses at the levels of genera and species because differences between groups are clear based on univariate comparisons alone, but univariate differences become less clear at the subspecies level (especially in *Pan*), and differences between subspecies can be better appreciated when both kinds of multivariate analyses are considered together.

*Discriminant function analyses*

Discriminant function analyses of *Gorilla* subspecies were performed on both a within-species sample of two subspecies and a sample of three subspecies across the two species of *Gorilla*. The within-species analyses of *G. b. beringei* and *G. b. graueri* explore how well the two subspecies can be discriminated and which variables best discriminate them. The across-species analyses of *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla* look at whether, when differences between groups are maximized, the two subspecies of *G. beringei* cluster with each other to the exclusion of the representative *G. gorilla* subspecies. In other words, they look at whether hand and foot bone variation reflects the species-level structuring of the subspecies. In addition, the across-species analyses permit the single specimen of *G. g. diehli* to be classified and plotted relative to the other three subspecies.

Within-species analyses: subspecies of *G. beringei*

Hand

Using male hand variables, *G. b. beringei* and *G. b. graueri* are discriminated with an 84% rate of correct classification (Wilks' lambda p = 0.0006) by the backward stepwise model, which is more successful than the forward stepwise or complete models.

The results of the backward stepwise model are reported here (Table 4.29). Six variables are selected by the model, and all contribute substantially. They are the ratios of hand phalanx arch height (HPAH), hand phalanx flexor sheath ridge size (HPFS), metacarpal arch height (MCAH), hand phalanx midshaft diameter (HPMD), metacarpal head shape (MCHS), and metacarpal biepicondylar width (MCB).

Using female hand variables, the subspecies are discriminated with a 92% rate of correct classification (Wilks' lambda p = 0.0010) by the forward stepwise model, which is much better than the backward stepwise and complete models. The results of the forward stepwise model are reported here (Table 4.30). Two variables are selected by the model, the hand phalanx glenoid plate tubercle size ratio (HPGT) and the phalanx-metacarpal length ratio (XPMC), and both contribute substantially.

The hand variables that contribute the most to the discrimination models are completely different for males and females.

Foot

Using male foot variables, the subspecies are discriminated with a 95% rate of correct classification (Wilks' lambda p = 0.0002) by the forward and backward stepwise models, which are more successful than the complete model. The results of the stepwise models are reported here (Table 4.31). The five variables selected for the models are the ratios of calcaneal tendon facet width (CCTW), cuboid facet depth of the calcaneus (CCFD), phalanx-metatarsal length (XPMT), foot phalanx flexor sheath ridge size (FPFS), and metatarsal biepicondylar width (MTB), and all contribute substantially.

Using female foot variables, the subspecies are discriminated with a 100% rate of correct classification by forward and backward stepwise and complete models. The

results of all three models are discussed here, but only the results of the forward stepwise model are reported in Table 4.32, as this model achieves the same rate of correct classification with fewer variables. Only two variables, the ratios of foot phalanx flexor sheath ridge size (FPFS) and cuboid facet depth of the calcaneus (CCFD), are selected by the forward stepwise model (Wilks' lambda p = 0.0001). Five variables, the ratios of calcaneal tendon facet width (CCTW), cuboid facet shape of the calcaneus (CCFS), foot phalanx arch height (FPAH), cuboid facet depth of the calcaneus (CCFD), and metatarsal arch height (MTAH), are selected by the backward stepwise model (Wilks' lambda p = 0.0000). All of the selected variables contribute substantially to the models. The complete model emphasizes the same variables as the backward stepwise model.

The foot variables that are among those that contribute the most to discrimination between groups in both males and females are the ratios of calcaneal tendon facet width (CCTW), cuboid facet depth of the calcaneus (CCFD), and foot phalanx flexor sheath ridge size (FPFS).

Summary of hand and foot

Overall, the two subspecies of *G. beringei* are discriminated quite well, although the males are only discriminated moderately well by hand variables. Females are discriminated better than males by both hand and foot variables. Both sexes are discriminated better by foot variables than by hand variables.

The variables that contribute most to discrimination between the subspecies are a mix of those with significantly different means in the two subspecies and those that are not significantly different. Of the hand variables that contribute most to separation between subspecies in males, two of the five (the metacarpal head shape ratio [MCHS]

and the metacarpal biepicondylar width ratio [MCB]) have significantly different means between the subspecies. In females, one of the two most prominent variables, the hand phalanx glenoid plate tubercle size ratio (HPGT), is significantly different between the subspecies. There is no overlap between variables that make the greatest contributions to the hand ratio analysis in males and females. Of the three foot variables that contribute most to group separation in both males and females, the mean of one is significantly different between the subspecies in both sexes (the foot phalanx flexor sheath ridge size ratio [FPFS]), the mean of another is significantly different in females only (the calcaneal tendon facet width ratio [CCTW]), and the third is not significantly different in either sex.

Unlike DFAs at the genus and species levels, the within-species subspecies-level DFAs for *Gorilla* do not rely heavily on variables that are already known from the univariate analyses to differentiate the taxa. When a comparison is made of variables that contribute the most, across both sexes, to the separation of groups in the *Gorilla* species-level and subspecies-level (within-species) analyses, only the foot phalanx flexor sheath ridge size ratio (FPFS) appears on both lists.

Across-species analysis: subspecies of *Gorilla*

Hand

Using male hand variables, *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla* are discriminated with a 93% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are slightly more successful than the complete model. The results of the stepwise models are reported here (Table 4.33, Figure 4.5). Eleven variables are selected by the models.

*G. g. gorilla* and *G. b. beringei* are correctly classified at higher rates than *G. b. graueri*. All the same, all misclassified specimens of *G. b. graueri* are assigned to *G. b. beringei*, and vice versa; in other words, all *G. beringei* specimens are correctly assigned to that species, if not always to the correct subspecies. Function 1 separates *G. beringei* and *G. gorilla*. A large number of ratios are similarly weighted in this function: phalanx-metacarpal length (XPMC), hand power arm: load arm (XHPL), hand phalanx midshaft diameter (HPMD), metacarpal biepicondylar width (MCB), hand phalanx arch height (HPAH), hand phalanx base width (HPBD), hand phalanx flexor sheath ridge size (HPFS), and hand phalanx glenoid plate tubercle size (HPGT). Function 2 separates *G. b. beringei* from the other two subspecies, primarily using the ratios of hand phalanx trochlear width (HPTW), hand phalanx arch height (HPAH), metacarpal head shape (MCHS), hand phalanx base width (HPBD), and hand phalanx midshaft diameter (HPMD).

Using female hand variables, the three subspecies are discriminated with an 86% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are slightly better than the complete model. The results of the stepwise models, which select six variables, are reported here (Table 4.34, Figure 4.6).

The small sample of *G. b. graueri* is correctly classified in 100% of cases, and no cases from other subspecies are misclassified as *G. b. graueri*. Function 1 arrays the taxa along a continuum, from *G. b. graueri* to *G. b. beringei* to *G. g. gorilla*. Although the two subspecies of *G. beringei* are not clearly separated from *G. g. gorilla*, they are adjacent to one another in the continuum. Function 1 is driven by the ratios of hand phalanx arch height (HPAH), hand phalanx base width (HPBD), phalanx-metacarpal

length (XPMC), and hand phalanx flexor sheath ridge size (HPFS). Function 2 separates *G. b. beringei* from the other two subspecies, as it does in the analysis of male hand variables. Function 2 is driven by the ratios of hand phalanx glenoid plate tubercle size (HPGT), hand phalanx arch height (HPAH), and hand phalanx base width (HPBD).

In both sexes, Function 1 emphasizes differences between the two *Gorilla* species and Function 2 separates out *G. b. beringei*, but the subspecies are somewhat better-discriminated in the male sample than in the female sample. The relative success rates for discrimination of each of the subspecies are different in males and females. In the males, *G. b. graueri* is the most poorly-discriminated sample (73% rate of correct classification), while *G. b. graueri* specimens are discriminated correctly 100% of the time in the females. The four ratios that drive Function 1 in females, hand phalanx arch height (HPAH), hand phalanx base width (HPBD), phalanx-metacarpal length (XPMC), and hand phalanx flexor sheath ridge size (HPFS), are all among the eight variables that contribute substantially to Function 1 in males. Two ratios are among those that contribute most to Function 2 in both males and females: hand phalanx arch height (HPAH) and hand phalanx base width (HPBD). These two ratios are also among the four ratios that contribute the most to Function 1 in both sexes.

The single specimen of *G. g. diehli*, which is a male, was entered into the analysis of males as an ungrouped case in order to see where it falls relative to the other three subspecies. Because it was ungrouped, it was not included in the sample used to derive the functions, but it was classified according to those functions as *G. g. gorilla*. Its position on a plot of canonical scores (Figure 4.5) suggests that, according to the weighted combination of hand variables that best distinguishes the two species of

*Gorilla*, this specimen is like other *G. gorilla* specimens and unlike specimens of *G. beringei*. It also suggests that, in terms of hand morphology that separates *G. b. beringei* from *G. b. graueri* and *G. g. gorilla*, this specimen is unlike *G. b. beringei*. Although the *G. g. diehli* specimen clearly falls among the *G. g. gorilla* specimens in this plot, it must be kept in mind that it is being evaluated only on the basis of the functions that separate the other three subspecies from one another, and *G. g. diehli* may well be distinguished from the other *Gorilla* subspecies in ways that are not reflected in this analysis.

Foot

Using male foot variables, the three subspecies are discriminated with a 94% rate of correct classification by all models. The results of the forward and backward stepwise models (Wilks' lambda p = 0.0000) are reported here (Table 4.35, Figure 4.7), and seven variables are selected.

*G. g. gorilla* specimens are correctly classified 97% of the time, while success rates for classification of *G. beringei* subspecies are not as high. Function 1 discriminates the two species of *Gorilla*, mostly on the basis of the ratios of foot phalanx flexor sheath ridge size (FPFS) and foot phalanx arch height (FPAH). Function 2 separates *G. b. beringei* from the other two subspecies. Function 2 emphasizes the ratios of foot phalanx flexor sheath ridge size (FPFS), foot phalanx arch height (FPAH), calcaneal tendon facet width (CCTW), cuboid facet depth of the calcaneus (CCFD), and metatarsal biepicondylar width (MTB).

Using female foot variables, the three subspecies are discriminated with a 97% rate of correct classification by the forward and backward stepwise models (Wilks' lambda p = 0.0000), which are slightly more successful than the complete model. The

results of the stepwise models are reported here (Table 4.36, Figure 4.8), and seven variables are selected.

All three taxa are well-discriminated. Function 1 arrays the subspecies from *G. b. graueri* to *G. g. beringei* to *G. g. gorilla*, with greater distance between *G. b. beringei* and *G. g. gorilla* than between the two subspecies of *G. beringei*. Function 1 is dominated by the foot phalanx flexor sheath ridge size ratio (FPFS). Function 2 separates *G. b. beringei* from the other two subspecies, primarily on the basis of the metatarsal biepicondylar width (MTB) and foot phalanx flexor sheath ridge size (FPFS) ratios.

In both sexes, Function 1 emphasizes species-level differences, while Function 2 separates *G. b. beringei* from the other two subspecies. The subspecies with the lowest rate of correct classification is *G. b. graueri* in both males and females. The foot phalanx flexor sheath ridge size ratio (FPFS) contributes the most to Function 1 in both sexes. Both the metatarsal biepicondylar width (MTB) and foot phalanx flexor sheath ridge size (FPFS) ratios are among the variables that contribute the most to Function 2 in both males and females.

The specimen of *G. g. diehli* was entered into the analysis of males as an ungrouped case and was classified as *G. g. gorilla*, as it was on the basis of hand variables. Its position on a canonical scores plot (Figure 4.7) shows that, on the basis of the two functions that separate the other three subspecies, it groups clearly with *G. g. gorilla*. See the "Hands" section above for further discussion of this procedure and interpretation of these results.

Summary of hand and foot

Analysis of both hand and foot variables shows that variation among the three analyzed subspecies of *Gorilla* is structured in agreement with current species-level taxonomy. Function 1 reflects species-level differences in all four analyses, although the pattern of variation is not the same in males in females. In males, Function 1 clearly separates *G. g. gorilla* from *G. b. beringei* and *G. b. graueri*, using either hand or foot variables. In females, Function 1 arrays the three subspecies on a continuum, from *G. b. graueri* to *G. b. beringei* to *G. g. gorilla*, whether hand or foot variables are used. Although the two species are not as clearly separated by Function 1 in the analyses of the female sample, the subspecies of *G. beringei* are adjacent to one another in the three-subspecies continuum in both hand and foot analyses.

Function 2 separates *G. b. beringei* from the other two subspecies in all four analyses. It is also interesting that there is great overlap between the variables that contribute most to Function 2 and those that contribute most to Function 1. In both sexes, the ratios of foot phalanx flexor sheath ridge size (FPFS), hand phalanx arch height (HPAH), and hand phalanx base width (HPBD) all make large contributions to separating groups on both Functions 1 and 2. One of the two hand variables that contribute most to Function 2 in both males and females, the hand phalanx arch height ratio (HPAH), is also the hand variable that contributes the most in males to separating the two subspecies in the within-species analysis of *G. beringei* subspecies. One of the two foot variables that contribute most to Function 2 in both males and females, the foot phalanx flexor sheath ridge size ratio (FPFS), is also one of the foot variables that contributes most to separating the two subspecies in the within-species analysis of subspecies.

The single ungrouped specimen of *G. g. diehli* is classified as *G. g. gorilla* on the basis of both hand and foot variables. When its canonical scores are plotted onto a graph of Functions 1 and 2, for either hand or foot variables, it falls easily within the cluster of *G. g. gorilla* specimens, to the exclusion of the other subspecies clusters. This result is consistent with inclusion of *G. g. diehli* in the same species as *G. g. gorilla*, to the exclusion of the *G. beringei* subspecies, although *G. g. diehli* may differ from all three other subspecies in ways not detected by the analysis.

*Principal components analyses*

Principal components analyses of *Gorilla* subspecies were performed as a complement to the discriminant function analyses. As with the discriminant function analyses, they included within-species analyses of *G. b. beringei* and *G. b. graueri* and across-species analyses of *G. b. beringei*, *G. b. graueri*, and *G. g. gorilla*. The single specimen of *G. g. diehli* is included in the across-species analysis.

Within-species analyses: subspecies of *G. beringei*

Hand

Analysis of the male hand variables separates the two *G. beringei* subspecies on the first component (Figure 4.9), which explains 23.88% of the total variance. The variables with the highest loadings on Component 1 are the ratios of phalanx-metacarpal length (XPMC), metacarpal biepicondylar width (MCB), hand phalanx midshaft diameter (HPMD), metacarpal head shape (MCHS), hand phalanx trochlear width (HPTW), and hand phalanx flexor sheath ridge size (HPFS).

Analysis of the female hand variables separates the subspecies on the first component, as well (Figure 4.10). This component explains 27.10% of the total variance. The ratios with the highest loadings on Component 1 are those of hand phalanx glenoid plate tubercle size (HPGT), hand phalanx flexor sheath ridge size (HPFS), phalanx-metacarpal length (XPMC), hand phalanx midshaft diameter (HPMD), hand phalanx trochlear width (HPTW), hand power arm:load arm (XHPL), and metacarpal head shape (MCHS). Only twelve female hand variables were analyzed, so the number of variables would be smaller than the total number of cases; otherwise, probabilities could not be generated. The analysis was first run with all thirteen hand variables, and the hand phalanx arch height ratio (HPAH) was found to have the lowest loading on the first component; HPAH was then removed and the analysis re-run without it.

Although the distributions of the two subspecies on Component 1 are clearly different in both sexes, they have moderate overlap in males, while they do not overlap at all in females. This component explains slightly more of the total variance in females than in males. Five ratios are among those with the highest loadings in both males and females: phalanx-metacarpal length (XPMC), hand phalanx midshaft diameter (HPMD), metacarpal head shape (MCHS), hand phalanx trochlear width (HPTW), and hand phalanx flexor sheath ridge size (HPFS).

Foot

Analysis of the male foot variables separates the two subspecies on the first component (Figure 4.11), which explains 22.69% of the total variance. The ratios with the highest loadings on Component 1 are those of foot phalanx arch height (FPAH), calcaneal tendon facet width (CCTW), metatarsal biepicondylar width (MTB), phalanx-

metatarsal length (XPMT), and metatarsal arch height (MTAH). The first component is plotted against the third component in Figure 4.11, because the third component provides more separation between the subspecies than the second component.

Analysis of the female foot variables separates the two subspecies on the first component (Figure 4.12), which explains 36.55% of the total variance. The ratios with the highest loadings on Component 1 are metatarsal biepicondylar width (MTB), foot phalanx flexor sheath ridge size (FPFS), cuboid facet shape of the calcaneus (CCFS), cuboid facet depth of the calcaneus (CCFD), metatarsal arch height (MTAH), and calcaneal tendon facet width (CCTW).

In both sexes, there is no overlap between the two subspecies on the first component, but this component accounts for much more of the total variance in females. Three ratios are among those with the highest loadings in both males and females: calcaneal tendon facet width (CCTW), metatarsal biepicondylar width (MTB), and metatarsal arch height (MTAH).

Summary of hand and foot

In both hands and feet, and in both males and females, the first component of the analysis separates the two subspecies of *G. beringei*. Differences between the two subspecies evidently constitute a large part of the total variance in the sample. The DFAs already demonstrate that the two subspecies can be differentiated from one another, generally quite well, but the PCAs demonstrate that a large portion of the overall variation seen in a single-sex sample of *G. beringei* (including both subspecies) is variation between the subspecies. Additionally, the observation from the DFAs that the subspecies can be better-discriminated in females is supported by the observation from

the PCAs that the first component, reflecting separation between the subspecies, explains more of the total variance in females.

Correspondences between the variables that are heavily loaded in both males and females in the principal components analyses and those that contribute the most to the separation of groups in both males and females in the discriminant function analyses indicate that some of the same variables have a large influence on results from both types of analyses. Unfortunately, in the discriminant function analyses of hands, there is no overlap between the variables that contribute most to group separation in males and in females. In the principal components analyses, there are five hand ratios with high loadings in both males and females, and four of them (phalanx-metacarpal length [XPMC], hand phalanx midshaft diameter [HPMD], metacarpal head shape [MCHS], and hand phalanx flexor sheath ridge size [HPFS]) are among the eight variables that contribute the most to separating the subspecies using discriminant function analysis in *either* males or females. One of the three foot variables with the highest loadings in both males and females, the calcaneal tendon facet width ratio (CCTW), is also one of the variables that contribute the most to separation of subspecies in both males and females in the discriminant function analyses.

Across-species analysis: subspecies of *Gorilla*

Hand

Analysis of the male hand variables in three subspecies of *Gorilla*, across both species, separates the two species on the first component and separates the two subspecies of *G. beringei* on the second component (Figure 4.13). Overlaps are substantial, but the distributions are clearly different. Component 1 explains 18.81% of

the total variance, and Component 2 explains 16.01% of the total variance. The ratios with the highest loadings on Component 1 are hand phalanx arch height (HPAH), hand phalanx midshaft diameter (HPMD), hand phalanx trochlear width (HPTW), metacarpal biepicondylar width (MCB), and metacarpal dorsal ridge height (MCDR). The ratios with the highest loadings on Component 2 are phalanx-metacarpal length (XPMC), hand phalanx base width (HPBD), hand phalanx midshaft diameter (HPMD), hand phalanx flexor sheath ridge size (HPFS), metacarpal head shape (MCHS), metacarpal arch height (MCAH), and hand phalanx glenoid plate tubercle size (HPGT). The single specimen of *G. g. diehli* falls among the *G. g. gorilla* specimens but at the edge of the confidence ellipse (set at 68.27%) for *G. b. beringei*, which overlaps that for *G. g. gorilla*.

Analysis of the female hand variables separates the two species on both the first and second components and separates the *G. beringei* subspecies on both the first and the third components (Figure 4.14), with large overlaps. Component 1 explains 21.47% of the total variance, Component 2 explains 15.57% of the total variance, and Component 3 explains 13.65% of the total variance. The ratios with the highest loadings on Component 1 are hand phalanx arch height (HPAH), hand phalanx trochlear width (HPTW), hand phalanx flexor sheath ridge size (HPFS), metacarpal biepicondylar width (MCB), metacarpal dorsal ridge height (MCDR), phalanx-metacarpal length (XPMC), and hand phalanx base width (HPBD). The ratios with the highest loadings on Component 2 are hand phalanx base width (HPBD), metacarpal arch height (MCAH), hand phalanx trochlear width (HPTW), metacarpal midshaft diameter (MCM), and hand phalanx arch height (HPAH). The variables with the highest loadings on Component 3 are hand power arm:load arm (XHPL) and metacarpal head shape (MCHS) ratios.

In both males and females, Component 1 primarily separates the two species of *Gorilla*, with overlap. The hand phalanx arch height ratio (HPAH) is the variable with the highest loading on Component 1 for both males and females. Other ratios with high loadings for both males and females are hand phalanx trochlear width (HPTW), metacarpal biepicondylar width (MCB), and metacarpal dorsal ridge height (MCDR). In the analysis of females, Component 2 also separates the two species. The two subspecies of *G. beringei* are separated on Component 2 for the males and on Components 1 and 3 for the females. Four ratios contribute to separating the two subspecies of *G. beringei* in both sexes: metacarpal head shape (MCHS), hand phalanx flexor sheath ridge size (HPFS), hand phalanx base width (HPBD), and phalanx-metacarpal length (XPMC).

Foot

Analysis of the male foot variables separates the two species on the first component and separates the two subspecies of *G. beringei* mostly on the third component, although some separation of the *G. beringei* subspecies can be seen on the first component (Figure 4.15). Component 1 explains 27.80% of the total variance. The ratios with the highest loadings on Component 1 are calcaneal tuberosity-metatarsal length (XCMT), foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), metatarsal arch height (MTAH), and phalanx-metatarsal length (XPMT). Component 3 explains 11.46% of the total variance. The variables with the highest loadings on Component 3 are the ratios of calcaneal tendon facet width (CCTW) and cuboid facet shape of the calcaneus (CCFS). The single specimen of *G. g. diehli* falls among the *G. g. gorilla* specimens and is outside of the range of *G. beringei* specimens on Component 1.

Analysis of the female foot variables separates the two species on the first component and separates the two subspecies of *G. beringei* on the second component (Figure 4.16). Component 1 explains 25.62% of the total variance. The ratios with the highest loadings on Component 1 are calcaneal tuberosity-metatarsal length (XCMT), metatarsal arch height (MTAH), foot phalanx flexor sheath ridge height (FPFS), calcaneal tendon facet width (CCTW), phalanx-metatarsal length (XPMT), foot phalanx arch height (FPAH), and metatarsal biepicondylar width (MTB). Component 2 explains 13.99% of the total variance. The variables with the highest loadings on Component 2 are calcaneal tendon facet width (CCTW), cuboid facet depth of the calcaneus (CCFD), metatarsal biepicondylar width (MTB), and phalanx-metatarsal length (XPMT).

In both males and females, Component 1 primarily separates the two species of *Gorilla*, with little overlap. The calcaneal tuberosity-metatarsal length ratio (XCMT) is the variable with the highest loading on Component 1 for both males and females. Other variables with high loadings for both males and females are the ratios of foot phalanx flexor sheath ridge size (FPFS), metatarsal biepicondylar width (MTB), metatarsal arch height (MTAH), and phalanx-metatarsal length (XPMT). The subspecies of *G. beringei* are separated mostly on Component 3 for males and Component 2 for females, and the calcaneal tendon facet width (CCTW) makes a large contribution to this separation on both components.

Summary of hand and foot

In analyses of *Gorilla* subspecies across the two species of *Gorilla*, the two species are separated by the first component in all four analyses. The two subspecies of *G. beringei* are separated by the first, second and/or third component in every analysis.

In the two analyses in which some separation of *G. beringei* subspecies is seen on the first component, this component separates species of *Gorilla* much more than it separates subspecies of *G. beringei*. The one *G. g. diehli* specimen groups with *G. g. gorilla* based on both hand and foot variables. This pattern of structuring in the ungrouped data indicates that, first, differences between species and between subspecies constitute the greatest sources of variation between specimens and, second, variation in the hand and foot ratios used in this study reflects the taxonomic structuring of gorilla subspecies according to current taxonomy.

The hand variable with the highest loading in both males and females on the first component, which primarily separates the *Gorilla* species, is the hand phalanx arch height ratio (HPAH), which is one of the two variables that make a large contribution toward discriminating the two species in the species-level discriminant function analyses of both males and females. Two of the foot variables, the foot phalanx flexor sheath ridge size (FPFS) and metatarsal biepicondylar width (MTB) ratios, that are heavily loaded in both males and females on the first component are also the two foot variables that contribute most to separation of the *Gorilla* species in both males and females in the species-level discriminant function analyses.

The variables with high loadings, in both males and females, on the components that best separate the subspecies of *G. beringei* in these analyses overlap greatly with those variables in the within-species analyses of *G. beringei* subspecies. Further, these overlapping variables also figure most prominently in the DFAs that separate the subspecies of *G. beringei*. These four variables are the ratios of phalanx-metacarpal

length (XPMC), metacarpal head shape (MCHS), hand phalanx flexor sheath ridge size (HPFS), and calcaneal tendon facet width (CCTW).

**Populations**

Analyses of population-level variation in hand and foot ratios were conducted in order to make a direct comparison between *Gorilla* and *Pan* of patterns of discrimination between populations with identical geographic boundaries. For this purpose, three populations of *G. g. gorilla* and three populations of *P. t. troglodytes* were analyzed using DFA (and also comparisons of means, presented earlier in this chapter). Small sample sizes from many localities and differences in geographic representation between the genera prevented direct comparison of patterns between more populations.

This subsection describes DFAs of three populations of *G. g. gorilla*. These west-central African populations are referred to as Coast, Cameroon Interior, and Ebolowa; further information about them can be found in Chapter 2. Results are reported in Tables 4.37 – 4.40, but no graphs are provided for several reasons. First, discrimination between the *G. g. gorilla* populations is not very great in any of the analyses, resulting in large overlaps between all the groups when canonical scores are plotted. The positions of the groups relative to one another can be understood almost as easily from the canonical scores of the group means, which can be found in the tables. Second, one analysis generated only a single function, so its results cannot be plotted on a two-axis plot, in any case. Third, discrimination between the comparable *P. t. troglodytes* populations is even poorer; therefore, not much would be gained by comparing the graphs for population-level analyses of the two genera. Complementary PCAs were not performed, as discrimination between populations based on DFAs, which maximize differences

between groups, was weak; therefore, PCA-based separation can be expected to be as weak or weaker.

Hand

Using male hand variables, the three populations of *G. g. gorilla* are discriminated with a 56% rate of correct classification (Wilks' lambda p = 0.0001) by the forward and backward stepwise models. The complete model does not yield a significant difference between groups. The results of the forward and backward stepwise models are reported here (Table 4.37). Only one variable, the phalanx-metacarpal length ratio (XPMC), is selected by the models.

Individuals from the Cameroon Interior group are correctly classified in 65% of cases, Ebolowa individuals are correctly classified in 55% of cases, and Coast group individuals are only correctly classified 33% of the time. In all three groups, misclassified specimens are assigned to both of the other groups. Only one function is generated, because only one variable is selected for the model. Canonical scores array the groups from Ebolowa to Coast to Cameroon Interior, with Cameroon Interior slightly more distant from Coast than Coast is from Ebolowa.

Using female hand variables, the populations are discriminated with a 61% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, compared to a 54% rate for the complete model. The results of the forward and backward stepwise models are reported here (Table 4.38). Four ratios are selected for the models: hand phalanx trochlear width (HPTW), metacarpal head shape (MCHS), hand phalanx midshaft diameter (HPMD), and phalanx-metacarpal length (XPMC).

Ebolowa individuals are correctly classified in 85% of cases, Cameroon Interior individuals are correctly classified in 53% of cases, and Coast individuals are correctly classified only 44% of the time. Misclassified specimens in all three groups are distributed nearly evenly between the other two groups. Function 1 arrays the groups from Ebolowa to Coast to Cameroon Interior, with substantial contributions from all four variables (making an exception to include the phalanx-metacarpal length ratio (XPMC), the coefficient of which is below the usual arbitrary cut-off used in this study by a miniscule amount). The Ebolowa mean is more distant from the Coast mean than the Coast mean is from the Cameroon Interior mean, but the plotted specimens of the three groups overlap greatly. Function 2 distances the Coast group from the other two groups, mostly using the metacarpal head shape ratio (MCHS), but overlap between clusters of plotted specimens is great, once again.

Foot

Analysis of male foot variables discriminates the populations with a 45% rate of correct classification (Wilks' lambda $p = 0.0006$) using the forward and backward stepwise models, which is slightly better than the success rate of the complete model. Results of the forward and backward stepwise models are reported here (Table 4.39). Three ratios are selected by the models: metatarsal biepicondylar width (MTB), phalanx-metatarsal length (XPMT), and foot phalanx arch height (FPAH).

Only Ebolowa specimens are assigned to the correct group more than half of the time, with a success rate of 58%. The rate for the Cameroon Interior group is 48%, and the rate for the Coast group is only 19%. Misclassified specimens in all three groups are assigned to both of the other two groups. Function 1 arrays the groups from Cameroon

Interior to Coast to Ebolowa, with substantial contributions from all three variables. Function 2, representing a very small proportion of the total dispersion, very slightly distances the Coast group from the other two groups by emphasizing the foot phalanx arch height ratio (FPAH).

Using female foot variables, the populations are discriminated with a 54% rate of correct classification (Wilks' lambda $p = 0.0036$) by the forward and backward stepwise models, while the complete model has a success rate of only 44%. Results of the forward and backward stepwise models are reported here (Table 4.40). Four ratios are selected by the models: foot phalanx arch height (FPAH), calcaneal tendon facet width (CCTW), phalanx-metatarsal length (XPMT), and calcaneal tuberosity-metatarsal length (XCMT).

The Coast group has the highest rate of correct classification, at 70%. The Ebolowa specimens are assigned to the correct group 58% of the time, and the Cameroon Interior specimens are assigned to the correct group 48% of the time. Most misclassified specimens from Ebolowa are assigned to the Coast group, but misclassified specimens from the Coast and Cameroon Interior groups are nearly evenly split between the other two groups. Function 1 arrays the means from Ebolowa to Cameroon Interior to Coast, based mostly on the ratios of foot phalanx arch height (FPAH), calcaneal tendon facet width (CCTW), and phalanx-metatarsal length (XPMT), but the scatters of specimens overlap extensively. Function 2 arrays the means from Cameroon Interior to Ebolowa to Coast, emphasizing the ratios of calcaneal tuberosity-metatarsal length (XCMT), phalanx-metatarsal length (XPMT), and calcaneal tendon facet width (CCTW). Once again, overlap between plots is extensive.

Summary of hand and foot

The populations of *G. g. gorilla* are better-discriminated by the hand variables than they are by the foot variables, for both males and females. They are also better-discriminated in females than in males, for both hands and feet.

Two other patterns are evident. One is the relationship between populations in multivariate space, as assessed by their canonical scores for Function 1 in each analysis. In all four analyses, the canonical score of the Ebolowa group mean is at one end of the three-group array of scores, although its geographically intermediate location would predict it to have an intermediate score. Additionally, in three of the four analyses, the Coast group is intermediate, falling between the Ebolowa and Cameroon Interior groups, and is the most poorly-discriminated group. Only in the analysis of female foot variables does the Coast group have a higher rate of correct classification than the other groups and does the Coast group have a canonical score at one end of the array of group scores. The Cameroon Interior population is at the opposite end of the array from Ebolowa in three of the four analyses. The other pattern is the selection of an inter-element length ratio, either the phalanx-metacarpal length ratio (XPMC) or the phalanx-metatarsal length ratio (XPMT), as one of the variables in each of the analyses, none of which selects more than four variables. As these are homologous variables for the hand and foot, measuring length of the proximal phalanx relative to length of the metacarpal or metatarsal, this seems to indicate an important morphological difference.

These results are consistent with some of the findings of the comparisons of means for these populations. First, the comparisons of means found that most significant differences involved the Cameroon Interior population, and the Cameroon Interior population appeared to be more different from the Ebolowa population than from the

Coast population. This is consistent with the observation that the Cameroon Interior and Ebolowa populations are at the two ends of the array of discriminant scores in three out of four DFAs. Second, the phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT) are two of the seven variables that produce significant differences between population means, and one of these two homologous inter-element ratios is selected for each of the four DFAs, depending on whether hand or foot ratios are being analyzed.

### *Pan*

As with the genus *Gorilla*, DFAs and PCAs are used to reveal patterns of geographic variation within the genus *Pan*. Variation at the levels of species, subspecies, and population is evaluated using DFA. Principal components analysis is used to complement the subspecies-level DFAs.

#### Species

Discriminant function analysis is used to examine how well the two species of *Pan*, *P. troglodytes* and *P. paniscus*, can be differentiated and which variables contribute most to differentiating them. These species-level analyses consider the multiple subspecies of *P. troglodytes* as a single group. In the "Subspecies" section below, subspecies-level analyses are described that examine discrimination between the two species when the subspecies of *P. troglodytes* are considered as separate groups.

##### Hand

Male hand variables discriminate the two species of *Pan* with a 95% rate of correct classification (Wilks' lambda $p = 0.0000$) using the backward stepwise model,

which is slightly better than the forward stepwise and complete models. The results of the backward stepwise model are reported here (Table 4.41). The four variables selected by this model, all of which contribute substantially, are the ratios of hand phalanx flexor sheath ridge size (HPFS), phalanx-metacarpal length (XPMC), metacarpal head shape (MCHS), and hand phalanx base width (HPBD).

Female hand variables discriminate the two species with a 93% rate of correct classification (Wilks' lambda p = 0.0000) using the backward stepwise model, which is slightly more successful than the forward stepwise and complete models. The results of the backward stepwise model are reported here (Table 4.42). Four ratios are selected, and the phalanx-metacarpal length ratio (XPMC) and the hand phalanx glenoid plate tubercle ratio (HPGT) contribute most to the discriminant function.

One hand variable, the phalanx-metacarpal length ratio (XPMC), makes large contributions to discriminating the species in both males and females.

Foot

Using male foot variables, the two species are discriminated with a 91% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are identical and are slightly better than the complete model. The results of the forward and backward stepwise models are reported here (Table 4.43). Five ratios are selected by the models, and those of phalanx-metatarsal length (XPMT), metatarsal arch height (MTAH), calcaneal tuberosity-metatarsal length (XCMT), and foot phalanx arch height (FPAH) contribute substantially.

Using female foot variables, the two species are discriminated with an 87% rate of correct classification (Wilks' lambda p = 0.0000) by the complete model, which is

slightly more successful than the stepwise models. The results of the complete model are reported here (Table 4.44). The ratios that contribute most to the model are phalanx-metatarsal length (XPMT) and metatarsal arch height (MTAH).

Two foot variables, the phalanx-metatarsal length ratio (XPMT) and the metatarsal arch height ratio (MTAH), make large contributions to discriminating the species in both males and females.

Summary of hand and foot

Using either hand or foot variables, the two species of *Pan* are correctly discriminated from each other at a moderately high rate in both males and females. Discrimination is somewhat better using hand variables, and males are discriminated slightly better than females.

The three variables that make the largest contributions toward discriminating the species of *Pan*, across both sexes, all have significantly different means between the species in one or both sexes. The phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT) are significantly different in both sexes, and the metatarsal arch height (MTAH) is significantly different in females (with a low uncorrected p-value in males).

The one hand variable that makes a large contribution to discriminating the two species in both males and females in this analysis, the phalanx-metacarpal length ratio (XPMC), is also one of the two hand variables that contribute the most to separation of both *Gorilla* and *Pan* species in the analyses of the two genera by species. This ratio also plays a large part in discriminating the species of *Gorilla* in analyses of the *Gorilla* sample alone. Comparison with the analyses of the two genera is more difficult for foot

variables, because only the inter-generic analysis of males identifies a function that primarily separated the two species of *Pan*, and the separation is not great. All the same, the phalanx-metatarsal length ratio (XPMT), one of the two foot variables that make a large contribution to discriminating the species in both males and females in the *Pan*-only analysis, is one of the two variables that contribute the most to discriminating *P. paniscus* from the other three African ape species in the inter-generic analysis by species for males.

**Subspecies**

As no subspecies of *P. paniscus* have been identified, only subspecies of *P. troglodytes* are analyzed here. Of the four subspecies of *P. troglodytes* generally recognized, there are only three that have samples for both males and females in this study's dataset: *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*. The sample includes only six female *P. t. vellerosus* specimens and no males of this subspecies. Because the approach used here is to compare results of analyses of both males and females for all taxa, single-sex analyses of one taxon would not fit into the study's comparative framework. For this reason, evaluation of the *P. t. vellerosus* specimens is limited to analyses in which they can be viewed in the context of differences between other subspecies while having little or no effect on the results for the other subspecies. Details are given in the appropriate sections below.

Multivariate analyses of *P. troglodytes* subspecies include both DFAs and PCAs. The two types of analysis complement one another in addressing this study's questions regarding variation among subspecies. The contributions of each kind of analysis to

addressing these questions are discussed in more detail in the "*Gorilla*" section of this chapter, under the heading "Subspecies".

*Discriminant function analyses*

Discriminant function analyses of *P. troglodytes* subspecies was based on the three subspecies for which samples of both males and females were available: *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*. Two sets of subspecies-level analyses were performed. One set included only these three subspecies. Its purpose was to explore how well the subspecies can be discriminated and which variables best discriminate them. The six female specimens of *P. t. vellerosus*, which is not represented by any males in this study's sample, were classified and plotted relative to the other subspecies. The other set of analyses included the three subspecies that have samples of both sexes and also the sample of *P. paniscus*, in order to examine whether species-level structuring is evident between *P. paniscus* and the subspecies of *P. troglodytes*.

<u>*Pan troglodytes* subspecies only</u>

Hand

Using male hand variables, *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus* are discriminated with a 65% rate of correct classification (Wilks' lambda p = 0.0002) by the backward stepwise model, which is more successful than the forward stepwise or complete models. The results of the backward stepwise model are reported here (Table 4.45, Figure 4.17). Five variables are selected by the model.

The small sample of *P. t. verus* has an 80% rate of correct classification, with one of the five individuals misclassified as *P. t. schweinfurthii*. The rate of correct

classification for *P. t. troglodytes* is 71%, with misclassified cases assigned to both of the other taxa. The *P. t. schweinfurthii* success rate is low, at 39%, with its cases distributed among the three taxa. As the classification matrix makes clear, the two functions leave large overlaps between the groups. Function 1 arrays them from *P. t. verus* to *P. t. schweinfurthii* to *P. t. troglodytes* and is predominantly driven by the ratios of hand phalanx base width (HPBD), hand phalanx midshaft diameter (HPMD), hand phalanx trochlear width (HPTW), and metacarpal biepicondylar width (MCB). Function 2 arrays them from *P. t. verus* to *P. t. troglodytes* to *P. t. schweinfurthii*, with larger contributions from the metacarpal midshaft diameter ratio (MCM) and the hand phalanx base width ratio (HPBD).

Using female hand variables, the subspecies are discriminated with a 61% rate of correct classification (Wilks' lambda p = 0.0009) by the forward stepwise model. The backward stepwise and complete models are less successful. The results of the forward stepwise model are reported here (Table 4.46, Figure 4.18). Three variables are selected by the model.

As with the male sample, the rate of correct classification is lowest for *P. t. schweinfurthii*, at 22%. Fewer cases of this subspecies are correctly classified than are assigned to either of the other two taxa. The rate of correct classification is 65% for *P. t. troglodytes* and 60% for *P. t. verus*. Misclassified cases from *P. t. troglodytes* are assigned to both of the other taxa, but the four misclassified cases out of the sample of ten *P. t. verus* are all assigned to *P. t. schweinfurthii*. Function 1 arrays the subspecies from *P. t. troglodytes* to *P. t. schweinfurthii* to *P. t. verus*. All three variables, the hand phalanx midshaft diameter (HPMD), hand phalanx flexor sheath ridge size (HPFS), and

phalanx-metacarpal length (XPMC) ratios, make large contributions to this function. Function 2 arrays the subspecies from *P. t. verus* to *P. t. troglodytes* to *P. t. schweinfurthii*, emphasizing the phalanx-metacarpal length ratio (XPMC) and the hand phalanx flexor sheath ridge size ratio (HPFS).

In both sexes, the rate of correct classification is much lower for *P. t. schweinfurthii* than for the other two subspecies. Function 1, in both males and females, differentiates *P. t. troglodytes* and *P. t. verus*, with *P. t. schweinfurthii* between them. Function 2 retains *P. t. verus* at one end of the continuum and moves *P. t. schweinfurthii* to the other end. One variable, the hand phalanx midshaft diameter ratio (HPMD), is among those that contribute the most to Function 1 in both males and females. There is no overlap between the variables that contribute the most to Function 2 in males and females.

The six specimens of *P. t. vellerosus*, all of which are female, were entered into the analysis of females as ungrouped cases in order to classify and plot them relative to the other three subspecies, without including them in the statistical procedures used to derive the functions. Three of the *P. t. vellerosus* specimens are classified as *P. t. troglodytes*, two are classified as *P. t. schweinfurthii*, and one is classified as *P. t. verus*. A plot of canonical scores (Figure 4.18) illustrates this overlap with the other taxa, but it also shows that one *P. t. vellerosus* specimen has a higher score for Function 2 than any other specimen in the entire sample. As with the single *G. g. diehli* sample, which was also classified and plotted relative to other subspecies, it must be kept in mind that these results for *P. t. vellerosus* only reflect its position relative to the functions that separate the other three subspecies. It is possible that a subspecies analysis that included a sample

of *P. t. vellerosus* as a group to be discriminated would find it to be distinguished from the others in ways not reflected in this analysis.

Foot

Using male foot variables, the subspecies are discriminated with a 65% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models. The rate of correct classification is lower for the complete model. The results of the forward and backward stepwise models are reported here (Table 4.47, Figure 4.19). Five variables are selected by the models.

The rate of correct classification is greatest for *P. t. verus*, at 83%. The single misclassified *P. t. verus* specimen, out of a small sample of six, is assigned to *P. t. schweinfurthii*. The rate of correct classification is 66% for *P. t. troglodytes* and 56% for *P. t. schweinfurthii*. Most misclassified specimens of *P. t. troglodytes* are assigned to *P. t. schweinfurthii*, although several are assigned to *P. t. verus*. Most misclassified specimens of *P. t. schweinfurthii* are assigned to *P. t. troglodytes*, but one is assigned to *P. t. verus*. Function 1 separates *P. t. verus* from the other two taxa. Of the other two, *P. t. schweinfurthii* is nearer to *P. t. verus*. The ratios that contribute most to Function 1 are those of foot phalanx flexor sheath ridge size (FPFS), cuboid facet shape of the calcaneus (CCFS), and metatarsal biepicondylar width (MTB). Function 2 arrays the subspecies from *P. t. schweinfurthii* to *P. t. troglodytes* to *P. t. verus*. The variables that contribute most to Function 2 are the calcaneal tendon facet width ratio (CCTW) and the foot phalanx arch height ratio (FPAH).

Using female foot variables, the subspecies are discriminated with a 66% rate of correct classification (Wilks' lambda p = 0.0008) by the forward and backward stepwise

models, which are slightly better than the complete model. The results of the forward and backward stepwise models are reported here (Table 4.48, Figure 4.20). Three variables are selected by the models.

*P. t. troglodytes* has a 69% rate of correct classification, greater than *P. t. verus* (57%) or *P. t. schweinfurthii* (38%). The misclassified specimens of *P. t. troglodytes* are assigned to both of the other taxa in similar numbers. Of the seven *P. t. verus* specimens, two are misclassified as *P. t. troglodytes* and one is misclassified as *P. t. schweinfurthii*. The eight specimens of *P. t. schweinfurthii* are distributed almost evenly among the three subspecies. Function 1 arrays the taxa from *P. t. verus* to *P. t. schweinfurthii* to *P. t. troglodytes*, with substantial contributions from the phalanx-metatarsal length (XPMT), foot phalanx arch height (FPAH), and calcaneal tuberosity-metatarsal length (XCMT) ratios. Function 2 arrays them from *P. t. schweinfurthii* to *P. t. troglodytes* to *P. t. verus*, emphasizing the calcaneal tuberosity-metatarsal length ratio (XCMT) and the phalanx-metatarsal length ratio (XPMT) over the foot phalanx arch height ratio (FPAH).

In both males and females, *P. t. schweinfurthii* has the lowest rate of correct classification. Functions 1 and 2 both place *P. t. verus* at one end of the variation continuum, in both sexes, as seen in the analyses of hand variables. The *P. t. schweinfurthii* sample is in the middle of the distribution on Function 1 and is at the opposite end of the distribution on Function 2, which is also the pattern seen in the analyses of hand variables. The variables that contribute the most to the functions are quite different between males and females. Those that contribute most to Function 1 do not overlap between the sexes, and only one variable, the foot phalanx arch height ratio (FPAH), makes a substantial contribution to Function 2 in both sexes.

The six specimens of *P. t. vellerosus* were entered into the analysis of females as ungrouped cases. Four of them were classified as *P. t. troglodytes*, and two were classified as *P. t. schweinfurthii*. In a plot of canonical scores (Figure 4.20), the scatter of *P. t. vellerosus* specimens can be seen to be more constrained than the distributions of the other subspecies, although their scatter lies entirely within that of *P. t. troglodytes* and almost entirely within that of *P. t. schweinfurthii*. See the discussion of the *P. t. vellerosus* hands sample, above, for more information on this procedure and the interpretation of results.

Summary of hand and foot

On the basis of either hands or feet, *P. t. schweinfurthii* is poorly discriminated relative to *P. t. troglodytes* and *P. t. verus*. In males, the best-discriminated subspecies is *P. t. verus*, with only one specimen of its small sample misclassified in each analysis for both hands and feet. In females, for both hands and feet, *P. t. troglodytes* is better-discriminated than *P. t. verus*. The sample of *P. t. verus* has a much higher rate of correct classification in males, using either hand or foot variables, than it does in females. Overall discrimination of the three subspecies is roughly similar in hands or feet and in males or females, although rates of correct classification are a bit lower for females hands.

For both hands and feet, Functions 1 and 2 both array the subspecies with *P. t. verus* at one end of the distribution. Although there is little overlap between males and females in which variables contribute most to the functions, the same pattern of relationships between the subspecies in multivariate space is found in both males and females for analyses of both hands and feet. Function 1 arrays the subspecies from *P. t.*

*troglodytes* to *P. t. schweinfurthii* to *P. t. verus* (or the reverse), and Function 2 arrays the subspecies from *P. t. schweinfurthii* to *P. t. troglodytes* to *P. t. verus* (or the reverse). The one variable that makes a large contribution to Function 1 in both males and females is the hand phalanx midshaft diameter ratio (HPMD), which has a significantly smaller mean in *P. t. troglodytes* males than in males of either *P. t. schweinfurthii* or *P. t. verus*.

The six specimens of *P. t. vellerosus*, entered into the analyses as ungrouped cases, are mostly classified as *P. t. troglodytes*. Pooling the results from hand and foot analyses, which increases the sample size to twelve, 58% (7 of 12) of *P. t. vellerosus* cases are classified as *P. t. troglodytes*, 33% (4 of 12) as *P. t. schweinfurthii*, and 8% (1 of 12) as *P. t. verus*.

*Pan troglodytes* subspecies plus *Pan paniscus*

Hand

Using male hand variables, the four groups are discriminated with a 67% rate of correct classification (Wilks' lambda p = 0.0000) by the backward stepwise model. This success rate is better than those of the forward stepwise and complete models. The results of the backward stepwise model are reported here (Table 4.49, Figure 4.21). Seven variables are selected by the model.

*Pan paniscus* has the greatest rate of correct classification, at 86%. Six out of 7 *P. paniscus* specimens are assigned to the correct group, and the remaining one is misclassified as *P. t. schweinfurthii*. Specimens of *P. t. troglodytes* are classified with a 75% success rate. Eight *P. t. troglodytes* specimens are assigned to *P. t. schweinfurthii* and six are assigned to *P. t. verus*, but only two are assigned to *P. paniscus*. Of the five *P. t. verus* specimens, three are correctly classified and two are classified as *P. t.*

*schweinfurthii*, resulting in a 60% success rate. Specimens of *P. t. schweinfurthii* are only correctly classified in 33% of cases, with 7 specimens assigned to *P. t. troglodytes*, 4 assigned to *P. t. verus*, and only one assigned to *P. paniscus*. Function 1 distinguishes *P. paniscus* from the *P. troglodytes* subspecies, driven predominantly by the hand phalanx trochlear width (HPTW), hand phalanx flexor sheath ridge size (HPFS), and phalanx-metacarpal length (XPMC) ratios. The score nearest *P. paniscus* is that of *P. t. verus*. Functions 2 and 3 both array the taxa with *P. t. verus* at one extreme of variation. Function 2 emphasizes the contributions of the ratios of hand phalanx base width (HPBD), metacarpal head shape (MCHS), hand phalanx midshaft diameter (HPMD), hand phalanx trochlear width (HPTW), and metacarpal biepicondylar width (MCB). Function 3 emphasizes the ratios of hand phalanx base width (HPBD), metacarpal biepicondylar width (MCB), hand phalanx flexor sheath ridge size (HPFS), and hand phalanx midshaft diameter (HPMD).

Using female hand variables, the four groups are discriminated with a 64% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are more successful than the complete model. The results of the forward and backward stepwise models, which are the same, are reported here (Table 4.50, Figure 4.22). Four variables are selected by the models.

*Pan paniscus* has the greatest rate of correct classification, as it does with the male sample. Eleven of twelve *P. paniscus* specimens (92%) are classified correctly, while one is assigned to *P. t. schweinfurthii*. *P. t. troglodytes* has a 63% rate of correct classification, with 17 specimens assigned to *P. t. schweinfurthii*, 11 to *P. t. verus*, and only two to *P. paniscus*. *P. t. verus* has a 60% success rate, with two of its ten cases

assigned to *P. t. schweinfurthii* and two assigned to *P. paniscus*. *P. t. schweinfurthii* specimens are correctly classified only 44% of the time, with three of nine specimens assigned to *P. t. troglodytes* and two assigned to *P. t. verus*. Function 1 separates *P. paniscus* from the *P. troglodytes* subspecies, primarily on the basis of the phalanx-metacarpal length ratio (XPMC) and the hand phalanx glenoid plate tubercle size ratio (HPGT). The score nearest *P. paniscus* is that of *P. t. verus*. Functions 2 and 3 both array the taxa with *P. t. verus* at one extreme of variation, as with the male sample. Function 2 emphasizes the ratios of hand phalanx flexor sheath ridge size (HPFS), hand phalanx midshaft diameter (HPMD), and hand phalanx glenoid plate tubercle size (HPGT). Function 3 emphasizes the hand phalanx glenoid plate tubercle size ratio (HPGT) and the phalanx-metacarpal length ratio (XPMC).

In both males and females, the rate of correct classification is highest in *P. paniscus*, and Function 1 separates *P. paniscus* from the subspecies of *P. troglodytes*. In both sexes, the single misclassified specimen of *P. paniscus* is assigned to *P. t. schweinfurthii*. One variable, the phalanx-metacarpal length ratio (XPMC), is among those that contribute most greatly to Function 1 in both males and females. The *P. troglodytes* subspecies with a canonical score closest to that of *P. paniscus* on Function 1 is *P. t. verus*, in both sexes, and Functions 2 and 3 both place the *P. t. verus* score at one extreme of variation. Two variables, the hand phalanx flexor sheath ridge size (HPFS) and hand phalanx midshaft diameter (HPMD) ratios, are among those that contribute most to Functions 2 and 3 in both males and females.

Foot

Using male foot variables, the four groups are discriminated with a 57% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are slightly better than the complete model. The results of the forward and backward stepwise models, which are identical, are reported here (Table 4.51, Figure 4.23). Eight variables are selected by the models.

The greatest rate of correct classification is that of *P. t. verus*. Five of six *P. t. verus* specimens (83%) are assigned to that taxon by the model, while one is assigned to *P. t. schweinfurthii*. Specimens of *P. t. troglodytes* are correctly classified 58% of the time, with most misclassified specimens assigned to *P. t. schweinfurthii* and smaller numbers to the other two groups. *Pan paniscus* specimens are classified to the correct taxon in 50% of cases (four of eight), with the four misclassified specimens distributed among the other three groups. Only 44% of *P. t. schweinfurthii* specimens are correctly classified. Seven of the sixteen cases are classified correctly, and seven are classified as *P. t. troglodytes*, while one specimen is assigned to each of the other groups. Function 1 separates *P. paniscus* and *P. t. verus* from the other two groups, with the *P. paniscus* score at the extreme of the distribution. The ratios that contribute most to this function are those of foot phalanx flexor sheath ridge size (FPFS), phalanx-metatarsal length (XPMT), calcaneal tuberosity-metatarsal length (XCMT), and metatarsal biepicondylar width (MTB). Function 2 separates *P. paniscus* and *P. t. verus* from one another and from the other two taxa, leaving the other two taxa in the middle of the distribution. It is driven by the ratios of metatarsal arch height (MTAH), foot phalanx arch height (FPAH), foot phalanx flexor sheath ridge size (FPFS), and cuboid facet shape of the calcaneus (CCFS). Function 3 arrays the taxa with *P. t. verus* and *P. t. schweinfurthii* at the ends of

the continuum, based predominantly on the calcaneal tendon facet width ratio (CCTW) and the cuboid facet shape ratio of the calcaneus (CCFS).

Using female foot variables, the four groups are discriminated with a 62% rate of correct classification (Wilks' lambda p = 0.0000) by the forward and backward stepwise models, which are slightly better than the complete model. The results of the forward and backward stepwise models, which are the same, are reported here (Table 4.52, Figure 4.24). Four variables are selected by the models.

*Pan paniscus* has the greatest rate of correct classification (73%). Eight *P. paniscus* specimens are classified correctly, while one is assigned to each of the other three groups. The rate of correct classification for *P. t. troglodytes* is 64%, with twelve cases misclassified as *P. t. verus*, nine as *P. t. schweinfurthii*, and eight as *P. paniscus*. The success rate for *P. t. verus* specimens is 57%, with two of seven cases assigned to *P. t. troglodytes* and one assigned to *P. t. schweinfurthii*. The success rate for *P. t. schweinfurthii* is very low, at 25%, with misclassified specimens distributed among the other three groups. Function 1 arrays the taxa from *P. paniscus* at one end to *P. troglodytes* at the other end. The nearest score to *P. paniscus* is that of *P. t. verus*. Function 1 is weighted by the ratios of phalanx-metatarsal length (XPMT), calcaneal tuberosity-metatarsal length (XCMT), and metatarsal arch height (MTAH). Function 2 separates *P. t. verus* and *P. paniscus* from each other, with the other groups in the middle, using primarily the metatarsal arch height (MTAH) and foot phalanx arch height (FPAH) ratios. Function 3 slightly separates the *P. t. schweinfurthii* mean from those of the other groups, based mostly on the ratios of calcaneal tuberosity-metatarsal length (XCMT), phalanx-metatarsal length (XPMT), and foot phalanx arch height (FPAH).

Results from both males and females emphasize the distinctiveness of both *P. paniscus* and *P. t. verus* from the other groups, but in slightly different ways. In males, the rate of correct classification is rather low for *P. paniscus*, but Function 1 separates both *P. paniscus* and *P. t. verus* from the other groups, with *P. paniscus* farthest from the others. The rate of correct classification is highest for *P. t. verus*. In females, *P. paniscus* has the highest rate of correct classification, and Function 1 places *P. paniscus* at one end of variation. The rate of correct classification for *P. t. verus* is not high, but it is nearest to *P. paniscus* on Function 1, as in males. Two ratios, those of phalanx-metatarsal length (XPMT) and calcaneal tuberosity-metatarsal length (XCMT), are among those that contribute most to Function 1 in both sexes. Function 2 separates *P. paniscus* and *P. t. verus* from each other, leaving the other two subspecies in between them, in both sexes. The two variables that drive this function in females, the ratios of metatarsal arch height (MTAH) and foot phalanx arch height (FPAH), are the variables with the largest coefficients on this function in males.

Summary of hand and foot

Results from both the hand and foot support the distinctiveness of *P. paniscus*, in relation to the subspecies of *P. troglodytes*, but results from analyses of hand variables better reflect the generally accepted taxonomic structuring of the groups. While analyses of hand variables find the rate of correct classification to be higher for *P. paniscus* than for *P. t. troglodytes*, *P. t. schweinfurthii*, or *P. t. verus*, in both males and females, analyses of foot variables find this to be the case for females only. In addition, analyses of hand variables distinctly separate *P. paniscus* from the subspecies of *P. troglodytes* on

Function 1, while analyses of foot variables array the taxa with *P. paniscus* at one end of the distribution without clearly separating it from the other groups.

Function 1 is strongly influenced by the inter-element length ratios of the hand and foot. The phalanx-metacarpal length ratio (XPMC), the phalanx-metatarsal length ratio (XPMT), and the calcaneal tuberosity-metatarsal length ratio (XCMT) all contribute greatly to this function in both males and females. In addition to being the same type of variable (inter-element length ratio), two of these variables are homologous variables of the hand and foot; the phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT) both measure the length of the third proximal phalanx relative to either the metacarpal or the metatarsal. The phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT) have significantly different means in the two species of *Pan* in both sexes, and they also are both among variables that contribute most to discriminating the species in both sexes in the species-level DFAs. The calcaneal tuberosity-metatarsal length ratio (XCMT) has significantly different means in males only (but a low uncorrected p-value in females).

Analyses of both hand and foot variables also emphasize the distinctiveness of *P. t. verus*. Function 1 reveals similarities between *P. paniscus* and *P. t. verus*, in relation to *P. t. troglodytes* and *P. t. schweinfurthii*. The group with a canonical score closest to that of *P. paniscus* on Function 1 is *P. t. verus* in all four analyses. Further, all four analyses place *P. paniscus* and *P. t. verus* at opposite extremes on Function 2.

Two of the variables that contribute most to Function 2 in both males and females are also among the variables that contribute most, in both males and females, to functions that place *P. t. verus* at the end of the array of scores in the DFAs of *P. troglodytes*

subspecies alone; these variables are the hand phalanx midshaft diameter ratio (HPMD) and the foot phalanx arch height ratio (FPAH). The mean of the hand phalanx midshaft diameter ratio (HPMD) is significantly different between *P. t. verus* and *P. t. troglodytes* males, but not females, but no significant differences in means are found between *P. t. verus* and the other subspecies for the foot phalanx arch height ratio (FPAH).

*Principal components analysis*

Principal components analyses of *P. troglodytes* subspecies were performed as a complement to the DFAs. As with the DFAs, they included a set based on *P. troglodytes* subspecies only and a set based on *P. troglodytes* subspecies and *P. paniscus*. The six specimens of *P. t. vellerosus*, all female, are included in the analyses of *P. troglodytes* subspecies only.

<u>*Pan troglodytes* subspecies only</u>

Hand

Analysis of the male hand variables provides little basis for distinguishing the subspecies. Components 1 and 2, which explain 22.17% and 15.23% of the total variance, respectively, appear to have little relationship to subspecies membership. A plot of Components 4 and 5, which explain 8.99% and 7.99% of the total variance, respectively, appears to somewhat tightly define *P. t. verus* with respect to the other subspecies, but the *P. t. verus* cases fall entirely within the cloud of cases from the other subspecies (Figure 4.25). The variables with the highest loadings on Component 4 are the metacarpal midshaft diameter ratio (MCM) and the phalanx-metacarpal length ratio

(XPMC). The variables with the highest loadings on Component 5 are the hand phalanx glenoid plate tubercle size ratio (HPGT) and the metacarpal head shape ratio (MCHS).

Analysis of the female hand variables again provides little with which to distinguish the subspecies, although the *P. t. verus* cases are tightly clustered on most components. Component 1, which explains 23.38% of the total variance, appears to have little relationship to subspecies membership. The subspecies are best separated by a plot of Components 2 and 4, which account for 13.81% and 9.80% of the total variance, respectively (Figure 4.26). The *P. t. verus* and *P. t. vellerosus* cases are clustered at one side of the Component 2 distribution, while still being overlapped by the other two subspecies samples, and the *P. t. verus* and *P. t. vellerosus* cases are pulled apart from each other by Component 4. The variables with the highest loadings on Component 2 are the ratios of hand power arm: load arm (XHPL), metacarpal arch height (MCAH), hand phalanx base width (HPBD), and hand phalanx trochlear width (HPTW). The variable with the highest loading on Component 4 is the metacarpal biepicondylar width ratio (MCB).

In both males and females, Component 1 primarily captures differences between specimens that are unrelated to subspecies membership. On most components, in both males and females, the *P. t. verus* sample is more clearly defined than the other subspecies, but the subspecies are poorly defined in general. The variables that best define *P. t. verus* are different in males and females.

Foot

Analysis of male foot variables distinguishes *P. t. verus* from the other subspecies on several major components, while *P. t. troglodytes* and *P. t. schweinfurthii* are very

poorly distinguished from one another. The best separation of *P. t. verus* from the other subspecies is achieved by plotting Components 1 and 4, which explain 16.96% and 11.16% of the total variance, respectively (Figure 4.27). The ratios with the highest loadings on Component 1 are those of phalanx-metatarsal length (XPMT), foot phalanx arch height (FPAH), metatarsal arch height (MTAH), calcaneal tuberosity-metatarsal length (XCMT), foot phalanx flexor sheath ridge size (FPFS), and cuboid facet depth of the calcaneus (CCFD). The variables with the highest loadings on Component 4 are the calcaneal tendon facet width ratio (CCTW) and the foot phalanx arch height ratio (FPAH).

Analysis of female foot variables reveals appreciable differences between subspecies samples in all three of the major components, although the greater parts of both *P. t. troglodytes* and *P. t. schweinfurthii* samples overlap each other in every plot. The subspecies with the most tightly-clustered sample is *P. t. vellerosus*, when specimens are plotted on the second and third components (Figure 4.28). Component 2 separates the *P. t. vellerosus* and *P. t. verus* samples, and Component 3 restricts the *P. t. vellerosus* sample to a small range of variation, although the *P. t. vellerosus* sample is contained entirely within the scatters for both *P. t. troglodytes* and *P. t. schweinfurthii* on all three major components. The *P. t. verus* sample is partially pulled away from the *P. t. schweinfurthii* sample on Component 1 and is partially pulled away from the *P. t. troglodytes* sample on Component 2. Component 1 explains 19.13% of the total variance, and its most heavily loaded ratios are those of metatarsal arch height (MTAH), foot phalanx flexor sheath ridge size (FPFS), foot phalanx arch height (FPAH), and cuboid facet depth of the calcaneus (CCFD). Component 2 explains 16.38% of the total

variance, and its most heavily loaded ratios are those of cuboid facet shape of the calcaneus (CCFS), calcaneal tendon facet width (CCTW), cuboid facet depth of the calcaneus (CCFD), foot phalanx arch height (FPAH), and metatarsal biepicondylar width (MTB). Component 3, which narrowly defines *P. t. vellerosus*, explains 13.70% of the total variance, and its most heavily loaded variables are the ratios of calcaneal tuberosity-metatarsal length (XCMT), metatarsal biepicondylar width (MTB), and metatarsal arch height (MTAH).

In both males and females, *P. t. verus* is much better distinguished than either *P. t. troglodytes* or *P. t. schweinfurthii*, and the first component contributes to defining it. In each sex, both of the two components which best define *P. t. verus* include the foot phalanx arch height ratio (FPAH) as a heavily loaded variable. Other heavily loaded variables that help define *P. t. verus* in both sexes are the ratios of metatarsal arch height (MTAH), foot phalanx flexor sheath ridge size (FPFS), cuboid facet depth of the calcaneus (CCFD), and calcaneal tendon facet width (CCTW).

Summary of hand and foot

Results from analyses of both hands and feet indicate that *P. t. verus* is better-differentiated than the other subspecies of *P. troglodytes*. Differences between the subspecies do not appear to constitute a large part of the overall variation between *P. troglodytes* individuals, and *P. t. troglodytes* and *P. t. schweinfurthii* typically are not well-distinguished from one another. By contrast, *P. t. verus* is well-defined on at least some components of every analysis, even if its distribution greatly overlaps the other distributions or is entirely contained within them.

Discriminant function analyses of *P. troglodytes* subspecies (without including *P. paniscus*) also find *P. t. verus* to stand apart from *P. t. troglodytes* and *P. t. schweinfurthii* in the value of its group means, even if discrimination is not always strong. Correspondences between variables in the DFAs that contribute greatly to discrimination of *P. t. verus* and variables in the PCAs that are heavily loaded on the components that best define *P. t. verus* are stronger among foot variables than among hand variables. The foot ratio of foot phalanx arch height (FPAH) contributes greatly to distinguishing *P. t. verus* in both males and females and in both kinds of analyses. Further, of the foot variables that drive the PCA components most closely associated with *P. t. verus* in both males and females, the foot phalanx flexor sheath ridge size ratio (FPFS) and calcaneal tendon facet width ratio (CCTW) are also among those that contribute the most to discriminating *P. t. verus* in the DFA of males.

Principal components analyses reveal differences between *P. t. vellerosus* and the other subspecies of *P. troglodytes* that are not apparent in the DFAs. While its distribution greatly overlaps those of the other subspecies, or is contained within them, on most components, the *P. t. vellerosus* sample has a different distribution from the others. Interestingly, *P. t. vellerosus* appears to be especially separated from *P. t. verus* by the PCAs, which echoes the result from the DFAs that *P. t. vellerosus* specimens were less frequently classified as *P. t. verus* than as *P. t. troglodytes* or *P. t. schweinfurthii*.

<u>*Pan troglodytes* subspecies plus *Pan paniscus*</u>

Hand

Analysis of male hand variables distinguishes the *P. paniscus* sample from the *P. troglodytes* subspecies samples primarily on the second, third, and fourth components.

On the first component, the *P. paniscus* cases are tightly clustered, but their distribution is well within the distributions of the three subspecies. A plot of the second and third components (Figure 4.29) illustrates the separation of *P. paniscus* from the *P. troglodytes* subspecies. Component 2 explains 15.30% and Component 3 explains 12.80% of the total variance. The heavily loaded ratios on Component 2 are those of hand power arm:load arm (XHPL), metacarpal head shape (MCHS), metacarpal midshaft diameter (MCM), metacarpal dorsal ridge height (MCDR), and metacarpal arch height (MCAH). The heavily loaded ratios on Component 3 are those of hand phalanx flexor sheath ridge size (HPFS), metacarpal biepicondylar width (MCB), phalanx-metacarpal length (XPMC), and hand phalanx glenoid plate tubercle size (HPGT).

Analysis of female hand variables distinguishes the *P. paniscus* sample from the *P. troglodytes* subspecies samples on the first, second, and third components. A plot of the first and second components (Figure 4.30) demonstrates that the *P. paniscus* sample is distinct from the three subspecies, although its distribution falls within the distributions of all three of them. Component 1 explains 23.26% of the total variance, and its heavily loaded variables are the ratios of hand phalanx base width (HPBD), hand phalanx flexor sheath ridge size (HPFS), hand phalanx trochlear width (HPTW), hand phalanx arch height (HPAH), hand power arm:load arm (XHPL), phalanx-metacarpal length (XPMC), and hand phalanx midshaft diameter (HPMD). Component 2 explains 13.83% of the total variance, and its heavily loaded variables are the ratios of hand power arm:load arm (XHPL), hand phalanx base width (HPBD), hand phalanx trochlear width (HPTW), metacarpal head shape (MCHS), metacarpal arch height (MCAH), and phalanx-metacarpal length (XPMC). Component 3 also separates *P. paniscus*, and it explains

almost as much of the total variance as Component 2. When the variables that are heavily loaded on Component 3 are added to the list, there are only two variables left (the metacarpal biepicondylar width ratio [MCB] and the metacarpal midshaft diameter ratio [MCM]) that do not contribute substantially to separating *P. paniscus* from the three subspecies.

In both males and females, hand variables differentiate *P. paniscus* from the subspecies of *P. troglodytes*. The *P. paniscus* sample is more distinct in males than in females. Between the two or three components that differentiate *P. paniscus* in each sex and the large number of variables that are heavily loaded on each component, most variables of the hand appear to contribute to separation of *P. paniscus*. All the same, there may be some significance to the fact that the hand power arm:load arm ratio (XHPL) is the most heavily loaded variable on Component 2 for both males and females. Additionally, the hand phalanx flexor sheath ridge size ratio (HPFS) is the most heavily-loaded variable on Component 3 in males, and it is the second most heavily-loaded variable on Component 1 in females.

Foot

Analysis of male foot variables separates *P. paniscus* and *P. t. verus* from the other two subspecies on the second and third components (Figure 4.31). Component 2 explains 15.18% of the total variance, based mostly on the ratios of phalanx-metatarsal length (XPMT), cuboid facet shape of the calcaneus (CCFS), and calcaneal tuberosity-metatarsal length (XCMT). Component 3 explains 12.97% of the total variance, based mostly on the metatarsal biepicondylar width ratio (MTB) and the cuboid facet depth ratio of the calcaneus (CCFD).

Analysis of female foot variables differentiates the *P. paniscus* sample from the three subspecies mostly on the fourth component (Figure 4.32). Component 4 explains 12.45% of the total variance, relying most heavily on the ratios of phalanx-metatarsal length (XPMT), calcaneal tuberosity-metatarsal length (XCMT), and metatarsal biepicondylar width (MTB).

In both male and female samples, foot variables clearly differentiate *P. paniscus* from *P. t. troglodytes* and *P. t. schweinfurthii*. In females, *P. paniscus* is also distinct from *P. t. verus*, but the male samples of these two taxa vary together in relation to the other two subspecies. The three variables that are responsible for separating *P. paniscus* from the subspecies in females, the ratios of phalanx-metatarsal length (XPMT), calcaneal tuberosity-metatarsal length (XCMT), and metatarsal biepicondylar width (MTB), are among the five variables that separate *P. paniscus* and *P. t. verus* from the other two subspecies in males.

Summary of hand and foot

Both hand variables and foot variables differentiate *P. paniscus* from the subspecies of *P. troglodytes* in both males and females. In no analysis does any one subspecies separate from the other subspecies more than *P. paniscus* separates from the three subspecies; this clustering pattern reflects the hierarchy of current taxonomy. At the same time, the first component only shows strong separation of *P. paniscus* in one analysis, that for female hands, indicating that there are other factors that influence variation in these hand and foot variables more than species membership. For all components of all analyses, *P. t. troglodytes* and *P. t. schweinfurthii* greatly overlap each other. On components that separate *P. paniscus* from the *P. troglodytes* subspecies, *P. t.*

*verus* usually clusters with the other subspecies, although the shape or extent of its distribution is frequently quite different. The exception is the analysis of male foot variables, in which the *P. paniscus* and *P. t. verus* samples vary similarly in relation to the other subspecies.

In the DFAs of *Pan* species, the phalanx-metatarsal length ratio (XPMT) is one of the two foot variables that contribute most to discriminating the species in both males and females, and it is also the most heavily loaded variable on components that distinguish the species, in both sexes, in the PCAs. In the DFAs, one hand variable, the phalanx-metacarpal length ratio (XPMC), makes large contributions in both males and females to discriminating *P. troglodytes* and *P. paniscus*. This variable is also among those that have high loadings on the components that separate the species in the PCAs. The two hand variables that appear to have the greatest roles in the PCAs, across both sexes, in distinguishing the two species are the hand power arm:load arm ratio (XHPL) and hand phalanx flexor sheath ridge size ratio (HPFS); HPFS is selected by the DFA model for both sexes but contributes substantially to the discriminant function in males only, and XHPL is not among the variables selected by analyses of either sex.

**Populations**

Analyses of variation in hand and foot ratios among *Pan* populations were conducted in order to directly compare patterns of population-level discrimination in *Gorilla* and *Pan*. Discriminant function analyses (and also comparisons of means, presented earlier in this chapter) were used to examine the amount of differentiation between three populations of *P. t. troglodytes* and to compare results with the amount of differentiation between three populations of *G. g. gorilla* from the same geographical

regions as the three *P. t. troglodytes* populations. Small sample sizes from many localities and differences in geographic representation between the genera prevented direct comparison of patterns between more populations.

This subsection describes DFAs of the three populations of *P. t. troglodytes*. As with the geographically comparable populations of *G. g. gorilla*, these west-central African populations are referred to as Coast, Cameroon Interior, and Ebolowa; further information about them can be found in Chapter 2. Results are reported in Tables 4.53 – 4.55, but no graphs are provided. The first reason no graphs are provided is that discrimination between the *P. t. troglodytes* populations is poor in all of the analyses, resulting in large overlaps between all the groups when canonical scores are plotted. The positions of the groups relative to one another can be understood almost as easily from the canonical scores of the group means, which can be found in the tables. The second reason is that multivariate measures of differences between groups were not significant for one analysis. The third reason is that discrimination between the comparable *G. g. gorilla* populations is also not great, and visual assessment would not add much to the observation of poor population-level discrimination in both genera. Complementary PCAs were not performed, as discrimination between populations based on DFAs, which maximize differences between groups, was weak; therefore, PCA-based separation can be expected to be as weak or weaker.

Hand

Analysis of the three populations using male hand variables yields a 47% rate of correct classification (Wilks' lambda $p = 0.0226$) using the forward and backward stepwise models. The complete model does not find significant differences between

groups. Results are reported for the forward and backward stepwise models (Table 4.53). Three ratios are selected by the models: metacarpal dorsal ridge height (MCDR), hand phalanx base width (HPBD), and hand phalanx flexor sheath ridge size (HPFS).

Only the Ebolowa specimens, with a correct classification rate of 55%, are assigned to the correct group more than half of the time. The Cameroon Interior group has a 47% rate of correct classification, and the Coast group is correctly classified 38% of the time. In all three groups, misclassified specimens are assigned to the other two groups with equal or nearly equal frequency. Function 1 slightly separates the Ebolowa group from the Coast and Cameroon Interior groups, based mostly on the hand phalanx base width ratio (HPBD) and the hand phalanx flexor sheath ridge size ratio (HPFS). Function 2 arrays the groups from Cameroon Interior to Ebolowa to Coast, based primarily on the metacarpal dorsal ridge height ratio (MCDR).

Using the female hand variables, the populations are discriminated with a 49% rate of correct classification (Wilks' lambda $p = 0.0040$) by the forward and backward stepwise models. The complete model does not find significant differences between groups. Results are reported for the forward and backward stepwise models (Table 4.54). Three ratios are selected by the models: metacarpal head shape (MCHS), hand phalanx base width (HPBD), and hand phalanx flexor sheath ridge size (HPFS).

Individuals from the Ebolowa group are correctly classified 56% of the time, and individuals from the Cameroon Interior group are correctly classified 55% of the time, while the Coast group has a low 21% rate of correct classification. In each group, misclassified specimens are assigned to both of the other groups. Function 1 arrays the groups from Ebolowa to Coast to Cameroon Interior, with all three variables contributing

substantially. Function 2 emphasizes the difference between the Coast group and the others, based mostly on the metacarpal head shape ratio (MCHS) and the hand phalanx base width ratio (HPBD). Overlap between plots is extensive.

Overall rates of correct classification are below 50% for both males and females, with rates of correct classification for individual populations never rising far above 50% and sometimes falling much lower. In both males and females, the Ebolowa and Cameroon Interior populations are better discriminated than the Coast population. The hand phalanx base width ratio (HPBD) and the hand phalanx flexor sheath ridge size ratio (HPFS) make large contributions toward separating the Ebolowa and Cameroon Interior populations in both sexes.

Foot

Using male foot variables, the populations are discriminated with a 47% rate of correct classification (Wilks' lambda $p = 0.0186$) by the forward and backward stepwise models. The complete model does not find significant differences between groups. Results are reported for the forward and backward stepwise models (Table 4.55). Two ratios are selected by the models: foot phalanx arch height (FPAH) and cuboid facet depth of the calcaneus (CCFD).

Only individuals of the Cameroon Interior group are correctly classified more than half of the time, with a success rate of 60%. Five of six misclassified Cameroon Interior specimens are assigned to the Ebolowa group. The rate of correct classification for the Coast group is 47% and for the Ebolowa group is 38%. Neither of these two groups shows a clear bias in the group assignment of misclassified specimens. Function 1 separates the Cameroon Interior group from the others, with both variables weighted

heavily, but there is great overlap between the group plots. Function 2 barely separates the groups.

The analysis of female foot variables finds no significant differences between groups.

Summary of hand and foot

The three analyses that find significant differences between *P. t. troglodytes* populations all have similar rates of correct classification. There is no clear explanation for why the analysis of female foot variables should have been so much less successful at discriminating groups than any other population-level analysis, including those for *G. g. gorilla*, other than the generally low rates of correct classification for all of the population-level discriminant function analyses,

The analyses of hand variables for the male and female samples show a shared pattern in the relative position of the groups in multivariate space and the contributions of variables to discrimination between groups. Based on canonical scores of group means for Function 1, the Coast group is intermediate for both males and females. The Coast group also has the lowest rate of correct classification of the three populations for both males and females. The two variables that contribute the most to the discrimination of groups in both males and females are the hand phalanx base width ratio (HPBD) and the hand phalanx flexor sheath ridge size ratio (HPFS), in that order. The hand phalanx base width ratio (HPBD) is the only variable of the hand or foot that has a significantly different mean between any of these three populations; this difference is between females from the Cameroon Interior and Ebolowa groups.

Unfortunately, having only one significant set of results for the foot variables, it is not possible to look for patterns in the analyses of foot variables. The results of the analysis of male foot variables are not the same as the analyses of hand variables in the relative positions of groups or the relative rates of correct classification, although the Cameroon Interior group is always at one end of the array of canonical scores on Function 1 and never has the lowest rate of correct classification. As for the contributions of variables, there are no homologues among the ratios that contribute most to the hand and foot analyses.

## Patterns and comparisons

This section is made up of four main subsections that attempt to synthesize the preceding analyses of hand and foot ratios in order to identify patterns within each genus and compare patterns between *Gorilla* and *Pan*. First, patterns of variation at the subspecies level are further explored by considering whether, and to what extent, differences in body size between taxa are likely to account for the morphological differences found between them. Second, patterns of group discrimination are assessed within each genus and compared between the genera. Third, patterns are sought in which variables, and which types of variables, best differentiate groups within each genus and across the two genera. Finally, the potential functional significance of the selected hand and foot ratios is considered.

### Body size proxy correlations

The purpose of this section is to investigate the possibility of a relationship between body size and geographic variation in hand and foot bone morphology and

proportions at the subspecies level, using Pearson correlation analysis. Because direct measurements of body size are not available for the vast majority of specimens, a geometric mean of a set of measurements from the forelimb and hindlimb is used as a body size proxy. The *Gorilla* analysis includes *G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*. Two sets of *Pan* analyses are reported, one including three subspecies of *P. troglodytes*, *P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*, and the other including *P. paniscus*, as well.

The geometric mean that is used here as a body size proxy is calculated from all measurements listed in Table 2.4. This set of measurements is the same as the set of "all variables" defined for the principal components analyses in Chapter 3. It includes measurements from both the forelimb and the hindlimb skeletons, more specifically from the humerus, radius, third metacarpal, third proximal hand phalanx, femur, tibia, first metatarsal, third metatarsal, third proximal foot phalanx, and calcaneus.

First, ANOVAs were used to look for significant differences between subspecies in the body size proxy (geometric mean for combined limb skeletons). Males and females were analyzed separately. Then, Pearson correlation coefficients were generated for the association between canonical scores of the DFAs and the body size proxy. Males and females were analyzed separately, and hands and feet were analyzed separately. Pearson correlations were considered significant at $p \leq 0.05$. The Pearson correlation coefficients were considered to indicate a strong relationship between the variables at $r > 0.7$ (absolute value), with the justification that a correlation coefficient with a smaller absolute value indicates that the body size proxy accounts for less than half of the variance of the DFA score, because in that case $r^2 < 0.49$.

*Gorilla*

Based on ANOVAs of the body size proxy, significant differences exist between *Gorilla* subspecies only when comparisons are made across the species *G. gorilla* and *G. beringei* (Table 4.56). In males, the geometric mean of combined limb skeletons is significantly greater in *G. g. gorilla* than in *G. b. beringei* and *G. b. graueri*. In females, it is significantly greater in *G. g. gorilla* than in *G. b. graueri*. As a side note, these size differences between the species are largely attributable to size differences in the hand and foot, as illustrated by the comparisons of means in Table 3.1. This was verified by ANOVAs of geometric means based on measurements of long bones only (not including hands and feet), which find no significant differences between any of these three subspecies.

Pearson correlation analysis demonstrates significant correlations between canonical scores and the body size proxy only for scores on Function 1, which discriminates *G. gorilla* from *G. beringei* (Table 4.57). Canonical scores from Function 1 are significantly correlated with the body size proxy in male hands and feet and in female feet. No canonical scores from Function 2, which discriminates the two subspecies of *G. beringei*, are significantly correlated with the body size proxy.

The significant correlation coefficients from the analyses of Function 1 scores all have absolute values of no greater than 0.42, which is much lower than the cutoff point of 0.7 for a correlation to be considered strong. These results indicate that, even between the species of *Gorilla*, with significantly different body size proxies, the association between the two variables is weak. There is no association between the body size proxy and canonical scores on the function that discriminates the two subspecies of *G. beringei*.

*Pan*

Based on ANOVAs of the body size proxy, there are significant differences between species of *Pan* but not between subspecies of *P. troglodytes* (Table 4.56). In the set of analyses including *P. paniscus* in addition to three subspecies of *P. troglodytes*, the geometric mean of combined limb skeletons is significantly smaller in *P. paniscus* than in each of the three *P. troglodytes* subspecies in males, and it is significantly smaller in *P. paniscus* than in *P. t. troglodytes* in females. No significant differences between *P. troglodytes* subspecies are found in the set of analyses including the subspecies only.

Pearson correlation analyses were conducted using canonical scores of Function 1 from the DFA including *P. paniscus* and the *P. troglodytes* subspecies and canonical scores of Function 1 from the DFA including only subspecies of *P. troglodytes* (Table 4.57). Function 1 of the DFAs including *P. paniscus*, in addition to the *P. troglodytes* subspecies, always distinguishes *P. paniscus* from *P. troglodytes*, although the DFAs of hand variables better separate the two species, while the DFAs of foot variables array the taxa with *P. paniscus* at one end of the distribution. Function 1 of the DFAs including only *P. troglodytes* subspecies arrays the subspecies from *P. t. troglodytes* to *P. t. schweinfurthii* to *P. t. verus* (or the reverse), in hands and feet of both sexes.

Canonical scores from Function 1 of the DFAs including *P. paniscus* and subspecies of *P. troglodytes* are significantly correlated with the body size proxy in analyses of both hands and feet in both males and females. Although they are all significant, the correlation coefficients have absolute values of no greater than 0.52, falling short of the 0.7 cutoff point for a correlation to be considered strong. Canonical scores from Function 1 of the DFAs including only *P. troglodytes* subspecies are

significantly correlated with the body size proxy only in the analysis of male hands, which has a low correlation coefficient of 0.27. In sum, the association between the body size proxy and canonical scores is moderately weak when the two species of *Pan* are compared, despite the significant differences in body size proxy between *P. paniscus* and the subspecies of *P. troglodytes*, and relationships between the two variables are very weak to absent when the subspecies of *P. troglodytes* are compared to one another.

*Summary of Gorilla and Pan*

Results from both *Gorilla* and *Pan* support the conclusion that there is very little relationship between body size and subspecies-level discrimination based on hand and foot bone morphology and proportions. Subspecies-level discrimination within *G. beringei* appears to be entirely unrelated to body size. Among subspecies of *P. troglodytes*, only discrimination based on male hands has a significant relationship to the body size proxy, and this relationship is very weak. Even the canonical scores that discriminate species of *Gorilla* and *Pan* are only weakly correlated with the body size proxy, although the body size proxy is significantly different between them.

## Group discrimination: Patterns and comparisons

Within-genus patterns

The purpose of this section is to look for patterns within each genus in the relative magnitudes of rates of correct classification in various discriminant function analyses. Patterns of differences between analyses are sought on the basis of taxonomic level of analysis, anatomical region (hand vs. foot), and sex.

Taxonomy

*Gorilla*

The hierarchical structuring of current *Gorilla* taxonomy is partially reflected in the rates of discrimination between groups at the different taxonomic levels of analysis (Table 4.58). The genus-level analyses comparing *Gorilla* and *Pan* all achieve a 100% rate of correct classification. The species-level analyses all show high rates of discrimination between *G. gorilla* and *G. beringei*, but the rates of correct classification at this level are all lower than the 100% rates of the genus-level analyses. This relationship between the rates of discrimination achieved at the genus and species levels reflects the hierarchical relationship between these taxonomic levels.

The subspecies-level analyses, however, also show some very high rates of correct classification. The two-way analyses, comparing the two subspecies of *G. beringei*, show that discrimination of these subspecies based on female hands or female feet is actually better than the discrimination achieved by the species-level analyses of female hands or female feet. Further, the *G. beringei* subspecies have a 100% rate of correct classification based on female feet, which is equal to the genus-level discrimination rate. Based on male feet, the discrimination rate of the two *G. beringei* subspecies is almost as great as that of the two *Gorilla* species. Only the analyses based on male hands show the discrimination rate of *G. beringei* subspecies to be much lower than that of *Gorilla* species.

The three-way analyses of *Gorilla* subspecies, which include the two subspecies of *G. beringei* and also one subspecies of *G. gorilla*, show a lower rate of correct classification than the corresponding analyses of *Gorilla* species, based on male hands and feet and female hands; however, based on female feet, discrimination of *Gorilla*

subspecies was greater than discrimination of *Gorilla* species. There are two potentially confounding factors when comparing the two-way and three-way subspecies-level analyses of *Gorilla*. One factor is the number of groups. All else being equal, one would expect to get a lower overall rate of correct classification in an analysis including three groups than in an analysis including only two groups. This also applies to comparing the three-way subspecies-level analysis with the species-level analysis, which only includes two groups. The other factor is that the three-way analysis includes subspecies from two different species. All else being equal, one would expect the subspecies from different species to discriminate at a higher rate than the subspecies from the same species, which would predispose the three-way analysis to a higher overall rate of correct classification. These two confounding factors appear to have cancelled each other out, more or less, as results from the two subspecies-level analyses are similar.

On balance, it appears that the two-way and three-way subspecies analyses both send the same signal. They both suggest that, based on morphology of the hands and feet, the subspecies of *Gorilla* can be discriminated nearly as well and sometimes better than the species of *Gorilla*. This relationship between the rates of discrimination achieved at the species and subspecies levels is not reflective of the hierarchical relationship between these taxonomic levels.

All of the population-level analyses, which include three populations within *G. g. gorilla*, show much lower rates of correct classification than any of the analyses at the levels of species or subspecies. As these populations are all within the same subspecies, one would expect them to discriminate poorly in relation to observed subspecies-level discrimination, and they do.

*Pan*

The hierarchical structuring of *Pan* taxonomy is well-reflected in the rates of discrimination between groups at different taxonomic levels of analysis (Table 4.59). The species-level analyses all show high rates of discrimination between *P. troglodytes* and *P. paniscus*, but the rates of correct classification at this level do not reach the 100% discrimination rates achieved by the genus-level analyses. This relationship between the rates of discrimination at the genus and species levels reflects the hierarchical relationship between these taxonomic levels.

The subspecies-level analyses all result in rates of correct classification which are much lower than any of the species-level rates, and the population-level analyses all result in rates of correct classification which are much lower than any of the subspecies-level rates. One set of subspecies-level analyses includes three subspecies of *P. troglodytes* and the other adds *P. paniscus* to the three subspecies. The population-level analyses include three populations within *P. t. troglodytes*. The relative magnitudes of discrimination rates between the species, subspecies, and population levels consistently reflect the hierarchical relationships between the taxonomic levels.

Anatomical region: hand vs. foot

*Gorilla*

No broad pattern in whether hands or feet better discriminate groups is detected in *Gorilla* (Table 4.58). Averaged across males and females, discrimination rates at the species level are about the same for both anatomical regions; male hands are better-discriminated than male feet, but female hands are less well-discriminated than female

feet. At the subspecies level, both within species and across species, rates are higher for feet both when averaged across the sexes and when the sexes are considered separately. At the population level, rates are higher for hands, both when the sexes are averaged and when they are considered separately.

*Pan*

In *Pan*, as well, no broad pattern is apparent in whether hands or feet better discriminate groups (Table 4.59). At the species level, the discrimination rate for hands is higher than that for feet, when the sexes are averaged or considered separately. The same pattern is seen in the subspecies-level analyses which include *P. paniscus*, but not in the within-species subspecies-level analyses, suggesting that the better discrimination seen in the hands for the species-level analyses is responsible for the better discrimination seen in the hands for the subspecies-level analyses which include *P. paniscus*. The within-species subspecies-level analyses and the population-level analyses do not show strong differences between the discrimination rates of the hands and feet. For the within-species subspecies-level analysis, the discrimination rates are the same in male hands and feet but higher in female feet than in female hands. For the population level analyses, the discrimination rates are the same in male hands and feet, while discrimination is better in female hands than in female feet, as results for the analysis of female feet are not significant.

Sex

*Gorilla*

No broad pattern in which sex provides better discrimination is detected in *Gorilla* (Table 4.60). At the species and subspecies (three-way, across-species) levels, the male samples have a higher rate of correct classification than that of the females when results from hands and feet are averaged. The male samples also have a higher discrimination rate at both of these levels when hand and foot analyses are considered separately, with one exception: female feet discriminate better than male feet at the subspecies (three-way, across-species) level. Meanwhile, at the subspecies (two-way, within-species) and population levels, the female samples have a higher rate of correct classification when results from the hand and feet are averaged or considered separately.

*Pan*

No broad pattern of sex differences in discrimination rates is revealed by the *Pan* analyses, either (Table 4.61). At the species and subspecies (three-way, within-species) levels, the male rate of correct classification is a little bit higher than the female rate when results from the hands and feet are averaged. This is also true when hands and feet are considered separately, with one exception: female feet discriminate slightly better than male feet at the subspecies (three-way, within-species) level. At the subspecies (four-way, *P. paniscus* included) and population levels, discrimination rates of the female samples are slightly higher than those for the male samples, when results from hands and feet are averaged. When hands and feet are considered separately at the subspecies (four-way, *P. paniscus* included) level, female feet are better-discriminated than male feet, but female hands are less-well-discriminated than male hands. At the population level, female hands are better-discriminated than male hands, but the female foot analysis results are not significant.

Comparisons of patterns in *Gorilla* and *Pan*

The purpose of this section is to look for similarities and differences between *Gorilla* and *Pan* in the within-genus patterns of group discrimination. Comparisons are made between patterns of group discrimination based on taxonomic level of analysis, anatomical region (hand vs. foot), and sex.

Taxonomy

The relative discrimination rates at the different taxonomic levels of analysis in *Pan* consistently reflect the hierarchical relationships of the taxonomic levels, from the lowest rates at the population level to the highest rates at the genus level. In *Gorilla*, the only exception to this pattern is that the subspecies-level analyses show discrimination rates nearly as high as or higher than those for the species-level analyses.

If the discrimination rates at each taxonomic level of analysis are compared between *Gorilla* and *Pan*, a general difference is evident. Analyses of *Gorilla* groups usually have higher rates of correct classification than the corresponding analyses of *Pan* groups. This is true, but not dramatic, at the levels of species and population. At the subspecies level, whether the analysis compares only subspecies within a species or compares groups across two species, the difference is dramatic; every subspecies-level analysis of *Gorilla* has a much higher discrimination rate than every subspecies-level analysis of *Pan*.

This comparison may be refined by conducting separate DFAs for each pair of *P. troglodytes* subspecies, in order to provide results that are more directly comparable to the results of DFAs for the single pair of *G. beringei* subspecies. Tables 4.62 and 4.63

illustrate that, even when *P. troglodytes* subspecies-level DFAs are restricted to two groups per analysis, the two *G. beringei* subspecies are still discriminated at higher rates than any pair of *P. troglodytes* subspecies. The greatest contrast is evident when rates of correct classification in the analyses of *G. beringei* subspecies are compared to rates of correct classification in the analyses of *P. t. schweinfurthii* and *P. t. troglodytes*. It is also remarkable to note that the two neighboring subspecies of *G. beringei* are discriminated at higher rates than are the two most geographically distant subspecies of *P. troglodytes*, *P. t. schweinfurthii* and *P. t. verus*.

Anatomical region: hand vs. foot

Neither *Gorilla* nor *Pan* shows a general pattern of differences between hands and feet in which anatomical region better discriminates groups. In addition, there is no strong evidence for a pattern across the genera in which anatomical region better discriminates groups at any one taxonomic level.

Sex

No general pattern of sex differences in rates of correct classification is found in either *Gorilla* or *Pan*. The best candidate for a sex-based difference seen across genera is at the species level, where the male sample has a higher rate of correct classification for both hands and feet in both *Gorilla* and *Pan*.

**Differentiating variables: Patterns and comparisons**

Within-genus patterns

The purpose of this section is to look at whether there are patterns within each genus in terms of which variables best differentiate groups and which *types* of variables

best differentiate groups, using both univariate and discriminant function analyses. For the purpose of this discussion, the variables included in the study are sorted into five types of variables: length proportions (phalanx-metacarpal length ratio [XPMC], phalanx-metatarsal length ratio [XPMT], and calcaneal tuberosity-metatarsal length ratio [XCMT]), midshaft diameters (metacarpal midshaft diameter ratio [MCM], hand phalanx midshaft diameter ratio [HPMD]), arch heights (metacarpal arch height ratio [MCAH], hand phalanx arch height ratio [HPAH], metatarsal arch height ratio [MTAH], and foot phalanx arch height ratio [FPAH]), shapes of articular surfaces (metacarpal head shape ratio [MCHS], hand phalanx base width ratio [HPBD], hand phalanx trochlear width ratio [HPTW], hand power arm:load arm ratio [XHPL], cuboid facet shape ratio of the calcaneus [CCFS], and cuboid facet depth ratio of the calcaneus [CCFD]) and measurements of tendon/ligament attachment sites (hand phalanx flexor sheath ridge size ratio [HPFS], metacarpal dorsal ridge height ratio [MCDR], metacarpal biepicondylar width ratio [MCB], hand phalanx glenoid plate tubercle size ratio [HPGT], foot phalanx flexor sheath ridge size ratio [FPFS], metatarsal biepicondylar width ratio [MTB], and calcaneal tendon facet width ratio [CCTW]). This discussion concentrates on the results of analyses at the species and subspecies levels (Tables 4.64 – 4.67), but results of analyses at the population level are also addressed.

The variables that best differentiate groups within a genus, at a given level of analysis, are considered to be those that are "differentiating variables" in both males and females. "Differentiating variables" are defined as those that are either significantly different based on univariate analyses or among the variables that contribute most to discriminating groups in DFAs or both.

*Gorilla*

There are nine variables that best differentiate the two species of *Gorilla* (Tables 4.64 and 4.65), by distinguishing them from one another in *both* sexes using either univariate analysis or DFA. Two are length proportions: the phalanx-metacarpal length ratio (XPMC) and the calcaneal tuberosity-metatarsal length ratio (XCMT). Two are arch heights: the hand phalanx arch height ratio (HPAH) and the metatarsal arch height ratio (MTAH). Two are shapes of articular surfaces: the hand phalanx base width ratio (HPBD) and the cuboid facet depth ratio of the calcaneus (CCFD). Three are measurements of tendon/ligament attachment sites: the metacarpal biepicondylar width ratio (MCB), the foot phalanx flexor sheath ridge size ratio (FPFS), and the metatarsal biepicondylar width ratio (MTB).

There are five variables that best differentiate the two subspecies of *G. beringei* (Tables 4.66 and 4.67). One is a length proportion: the phalanx-metacarpal length ratio (XPMC). One is a shape of an articular surface: the cuboid facet depth ratio of the calcaneus (CCFD). Three are measurements of tendon/ligament attachment sites: the foot phalanx flexor sheath ridge size ratio (FPFS), the metatarsal biepicondylar width ratio (MTB), and the calcaneal tendon facet width ratio (CCTW). Four of these five variables, the ratios of phalanx-metacarpal length (XPMC), cuboid facet depth of the calcaneus (CCFD), foot phalanx flexor sheath ridge size (FPFS), and metatarsal biepicondylar width (MTB), are also among those that best differentiate the two species of *Gorilla*.

Across the species and subspecies levels, length proportions and measurements of tendon/ligament attachments appear to be most useful in differentiating groups of

*Gorilla*, taking into consideration the total number of each type of variable included in the study. This pattern is reinforced by the results for the population-level univariate analyses (including three populations within *G. g. gorilla*). Of the seven variables that are significantly different between populations, in at least *one* sex (note, not necessarily different in both sexes), all three length proportions in the study are included (the phalanx-metacarpal length ratio [XPMC], the phalanx-metatarsal length ratio [XPMT], and the calcaneal tuberosity-metatarsal length ratio [XCMT]), and two of the other four variables are measurements of tendon/ligament attachments (the metacarpal biepicondylar width ratio [MCB] and the metatarsal biepicondylar width ratio [MTB]). Because populations are only weakly separated by population-level DFAs, the variables that contribute most to the functions are not considered in this discussion.

*Pan*

There are five variables that best differentiate the two species of *Pan* (Tables 4.64 and 4.65). Two are length proportions: the phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT). One is an arch height: the metatarsal arch height ratio (MTAH). Two are measurements of tendon/ligament attachment sites: the hand phalanx flexor sheath ridge size ratio (HPFS) and the hand phalanx glenoid plate tubercle size ratio (HPGT).

There are only two variables that best differentiate the three subspecies of *P. troglodytes* (Tables 4.66 and 4.67), neither of which is among the variables that best differentiate the two species of *Pan*. One is a midshaft diameter: the hand phalanx midshaft diameter ratio (HPMD). One is an arch height: the foot phalanx arch height ratio (FPAH).

There is no strong indication of a pattern, across the species and subspecies levels, in which variables, or which types of variables, are most useful in differentiating groups of *Pan*. No pattern is suggested by the population-level univariate analyses (three populations within *P. t. troglodytes*), either. Only one variable, the hand phalanx base width ratio (HPBD), is significantly different between populations, and neither this variable nor its variable type (shapes of articular surfaces) are represented on the lists of variables that best differentiate groups at the species or subspecies levels. Because populations are very weakly separated by population-level DFAs, the variables that contribute most to the functions are not considered in this discussion.

Comparisons of within-genus patterns in *Gorilla* and *Pan*

The genus *Gorilla* shows patterns in terms of which variables, and which types of variables, best differentiate groups (i.e., are differentiating variables in both sexes) at the species and subspecies levels. Length proportions and measurements of tendon/ligament attachment sites appear to be particularly prominent among them, and there is a good deal of overlap between these variables at the two levels. Results from population-level comparisons support the observed patterns. By contrast, no patterns are observed in which variables best differentiate groups of *Pan*, using the same criteria.

Despite the absence of a pattern within *Pan*, some correspondence between differentiating variables is seen between the genera. Every variable among those that best differentiate groups in *Pan*, at either the species or subspecies level, is also a differentiating variable in at least one sex at the same level in *Gorilla*, but the reverse is not the case. In other words, the variables that best differentiate groups in *Pan* are a

subset of variables that differentiate *Gorilla* groups in at least one sex, but the variables that best differentiate groups in *Gorilla* are not always differentiating variables in *Pan*.

Patterns across the genera

The purpose of this section is to look at whether there are patterns across the two genera in terms of which variables, and which types of variables, differentiate groups based on univariate analyses and DFAs. This discussion concentrates on the results of analyses at the species and subspecies levels (Tables 4.64 – 4.67), although results from the genus level are also addressed. Including across-genus results from the population level would not be useful, because population-level differences are so small in *Pan*.

Table 4.68 summarizes across-genus patterns in which variables, and which types of variables, differentiate groups. Table 4.68 includes only variables that are differentiating variables in at least one sex of each genus at the species level, at the subspecies level, or at both the species and subspecies levels. As a reminder, differentiating variables are those that are either significantly different based on univariate analyses or among the variables that contribute most to discriminating groups in DFAs or both.

Types of variables

For each variable in Table 4.68, its type of variable is indicated. At the top of each column, below the type of variable, is the number of this type included in the complete list of variables used in the study. By counting the number of X's in the column and comparing it to the number at the top of the column, one can appreciate how

important each type of variable is in differentiating groups of both *Gorilla* and *Pan* at the species and/or subspecies levels.

Length proportions are clearly important. All three length proportions included in the study are listed in Table 4.68. In addition, two of them (the phalanx-metacarpal length ratio [XPMC] and the phalanx-metatarsal length ratio [XPMT]) are among the four variables that differentiate *Gorilla* and *Pan* groups at *both* the species and subspecies levels.

Measurements of tendon and ligament attachment sites are also clearly important. Six of seven such variables are included in Table 4.68. One is among the four variables that differentiate groups at both the species and subspecies levels. This type of variable appears to be particularly important for differentiating groups at the subspecies level. Five of the seven measurements of tendon and ligament attachment sites are differentiating variables in both genera at the subspecies level (including four at the subspecies level only and one at both species and subspecies levels). Looking at it another way, half (five of ten) of the differentiating variables at the subspecies level are of this type, when this type represents less than a third of the variables included in the study.

Arch heights may be important. Two of four arch height measurements are included in Table 4.68, and one is among the four variables that differentiate groups at both the species and subspecies levels. Midshaft diameters do not appear to be very useful, as only one appears in Table 4.68 and it is only listed at the subspecies level, but there are only two such variables in the study. Shapes of articular surfaces are clearly less useful than length proportions and measurements of tendon/ligament attachment

sites, as only two of six such variables appear in Table 4.68, and none of them is among the four that differentiate groups at both the species and subspecies levels.

There is little correspondence between variables that differentiate the genera from one another and those that differentiate groups of both genera at the species and subspecies levels. Most variables in the study are significantly different between genera, in at least one sex, but three variables are not significantly different in either sex: the metacarpal arch height ratio (MCAH), the foot phalanx flexor sheath ridge size ratio (FPFS), and the calcaneal tendon facet width ratio (CCTW). Of these three variables, the foot phalanx flexor sheath ridge size ratio (FPFS) and the calcaneal tendon facet width ratio (CCTW) are both included in Table 4.68 at the subspecies level, and FPFS also differentiates *Gorilla* species (but not *Pan* species) in both sexes based on either univariate analyses or DFAs. In the genus-level DFAs, there are four variables that contribute the most to discriminating genera in both sexes: the hand phalanx midshaft diameter ratio (HPMD), the hand power arm:load arm ratio (XHPL), the metacarpal head shape ratio (MCHS), and the calcaneal tuberosity-metatarsal length ratio (XCMT). Two of these four variables are shapes of articular surfaces, which are a less-useful type of variable for discriminating groups at the species and subspecies levels, and neither variable is included in Table 4.68. The other two variables appear in Table 4.68 but are each only listed for one level of analysis. One of the two, the calcaneal tuberosity-metatarsal length ratio (XCMT), is a length proportion, which is an important type of variable for differentiating groups at the species and subspecies levels, but none of the four variables is a measurement of a tendon/ligament attachment.

Other potential patterns

One might wonder whether there is any difference between the variables of the hand and the foot in their importance for differentiating groups. From a functional perspective, this is an interesting question, as the hands and feet are used differently during locomotor behaviors. As it turns out, however, Table 4.68 shows a good balance between hand and foot variables.

Similarly, it makes sense to look for potential sex-related patterns across genera in the importance of different variables. Males tend to be heavier (much heavier in *Gorilla*) than females, and males and females tend to exhibit different patterns of locomotor behavior; therefore, differences in morphological patterns would be predicted. Tables 4.64 – 4.67 may be inspected for such potential patterns. At the species level, one variable (the foot phalanx arch height ratio [FPAH]) is a differentiating variable in both genera in males only, but it differentiates both sexes of *Pan* at the subspecies level. At the subspecies level, one variable (the metacarpal biepicondylar width ratio [MCB]) is a differentiating variable in both genera in males only, but it differentiates both sexes of *Gorilla* at the species level. No variable is a differentiating variable in only one sex of both genera at both the species and subspecies levels. No sex-related pattern across genera is apparent.

**Functional interpretations**

The hand and foot ratios in this study were originally selected because they were thought likely to reflect the relative frequency of positional behaviors that are either characteristically arboreal (climbing and suspension) or characteristically terrestrial (knuckle-walking). Regardless of their functional significance, analyses of these ratios

contribute to an understanding of geographic variation in African ape hand and foot morphology; however, they also offered the possibility of putting the observed geographic variation in the context of variation in habitat and positional behavior.

Comparisons of means make it clear that many, if not all, of these variables do not reflect differences in positional behavior between groups. If each variable did, in fact, reflect relative amounts of either arboreal or terrestrial positional behaviors, one would expect to see consistent results within each category, arboreal and terrestrial, in the directions of variation for variables that are significantly different between groups. In other words, when comparing a particular pair of taxa, one would expect the same taxon to have the greater mean for every significantly different variable in each category, arboreal or terrestrial. It would be possible for the same taxon to have the greater mean for all significantly different variables in *both* the arboreal and the terrestrial categories, because the frequencies of arboreal positional behaviors and terrestrial positional behaviors are here considered on two separate continua and are not two ends of the same continuum (as many researchers have considered them to be); however, within each category, the same taxon should always register either a greater or a lesser frequency of the characteristic positional behaviors. In fact, comparisons between genera, species, and subspecies make it clear that this is not the case. The most telling comparison is probably that of the two genera, which have the greatest number of significant differences between groups and also might be expected to show the greatest contrast in degree of arboreality and degree of terrestriality. Out of eight "arboreal variables" with significant differences between the genera, *Pan* has the greater mean in five, and *Gorilla* has the greater mean in three. Eleven "terrestrial variables" are significantly different between the genera, and

*Pan* has the greater mean in five, while *Gorilla* has the greater mean in six. The purported functional signals are completely inconsistent.

Of course, the best way to test the functional significance of these variables would be to correlate differences in frequencies of positional behaviors (or maybe even differences in habitat) with directions of variation in the means for the variables. Unfortunately, details of positional behavior and habitat are not known for most of the populations sampled in this study, but contrasts between *Gorilla* and *Pan* and between *G. b. beringei* and *G. g. gorilla* can be employed to examine whether variation in the hand and foot ratios in this study is consistent with known variation in frequencies of arboreal and terrestrial positional behaviors.

In order to assess whether the variables in this study reflect relative frequencies of arboreal or terrestrial positional behaviors in the two pairs of taxa in which contrasts in positional behaviors are reasonably well-established, directions of variation for each variable were compiled from the comparisons of means for *Gorilla* vs. *Pan* and for *G. b. beringei* vs. *G. g. gorilla* (summarized in Tables 4.69 and 4.70, full details in Tables 4.1, 4.2, 4.7 and 4.8). As *Pan* is known to spend more time in the trees and to travel further on the ground than *Gorilla*, in general, and as *G. g. gorilla* is known to spend more time in the trees and to travel further on the ground than *G. b. beringei* (e.g., Yamagiwa and Mwanza, 1994; Doran, 1996; Tutin, 1996; Herbinger et al., 2001), the mean for each variable, whether an "arboreal" or a "terrestrial" variable, would be expected to be greater in *Pan* and in *G. g. gorilla* if the variable were, in fact, reflecting relative frequencies of substrate/superstrate-characteristic positional behaviors. For each variable and each pairwise comparison of taxa, Table 4.69 (for hand variables) or Table 4.70 (for foot

variables) indicates whether the mean is greater (whether significantly or not), in *both* males and females, in the expected taxon.

Of the twenty-two ratios of the hand and foot skeleton included in this study, only four vary in the direction predicted, if they were to reflect frequencies of arboreal and terrestrial positional behaviors, in both pairwise comparisons and in both sexes. These four potentially function-associated variables are the metacarpal biepicondylar width ratio (MCB) and the hand phalanx base width ratio (HPBD) from the hand and the cuboid facet depth ratio of the calcaneus (CCFD) and calcaneal tendon facet width ratio (CCTW) from the foot. As further support for the potential functional relevance of this short list of variables, three of the four variables (the ratios of metacarpal biepicondylar width [MCB], cuboid facet depth of the calcaneus [CCFD], and calcaneal tendon facet width [CCTW]) have greater means in *G. b. graueri* than in *G. b. beringei* in both sexes; *G. b. graueri* appears to engage in both more climbing and more walking than *G. b. beringei* from the Virungas (Yamagiwa and Mwanza, 1994), although *G. b. graueri* habitats vary greatly and few populations have been studied. At the same time, the observation that one of the four variables does not vary in the expected direction when the two eastern gorilla subspecies are compared underscores that most of these variables appear unreliable as universal indicators of frequencies of arboreal and terrestrial positional behaviors among African apes.

To what extent do the four potentially function-associated variables identified above contribute to differentiating groups within the two genera? Reference to Table 4.68 answers this question at a glance. Not one of these four variables is among the four variables that differentiate both species and subspecies within both *Gorilla* and *Pan*. The

hand phalanx base width ratio (HPBD) differentiates species in both genera, and the metacarpal biepicondylar width ratio (MCB) and the calcaneal tendon facet width ratio (CCTW) differentiate subspecies in both genera, but the cuboid facet depth ratio of the calcaneus (CCFD) does not appear in the table at all. If these four variables do, in fact, reflect frequencies of arboreal and terrestrial positional behaviors in African ape groups, one must conclude that, overall, taxonomic divisions within African ape genera do not closely correspond to differences in positional behavior (and perhaps, by extension, habitat).

This assessment of potential relationships between variables and function would be incomplete without exploring one wrinkle in the analysis. Some of the "terrestrial" variables used in this study are based on features that have been interpreted in the literature (e.g., Susman, 1979) as adaptations for terrestrial walking in part because they have greater expression in *Gorilla* than in *Pan*, on the assumption that the taxon that spends more time on the ground (*Gorilla*) is also the taxon with a higher frequency of terrestrial walking. Although this assumption is incorrect (see Chapter 1), one could argue that the features with greater expression in *Gorilla* are, in fact, correlated with greater "terrestriality" in the sense of spending more time on the ground. For example, it is conceivable that some of these features could reflect lesser mechanical loading of *Gorilla* hands due to greater amounts of time spent sitting or standing rather than walking and some of these features could reflect mechanical loading of *Gorilla* feet specific to squatting, which is a common terrestrial posture.

To explore the possibility that features with greater expression in *Gorilla* than in *Pan* are correlated with greater amounts of terrestriality, simply meaning time spent on

the ground, directions of variation for each terrestrial variable were summarized as in Tables 4.69 and 4.70, except the predicted directions were *Gorilla* > *Pan* and *G. b. beringei* > *G. g. gorilla*. Out of 12 "terrestrial" variables of the hand and foot, only three varied in the predicted direction in both pairwise comparisons and in both sexes. These three variables are the metacarpal head shape ratio (MCHS), the hand power arm:load arm ratio (XHPL), and the calcaneal tuberosity-metatarsal length ratio (XCMT). Perhaps greater values for the metacarpal head shape ratio (MCHS) in *Gorilla* and *G. b. beringei* reflect smaller values for the denominator of this ratio rather than larger values for the numerator. The denominator is metacarpal head height, which could potentially be more reduced than metacarpal head width, the numerator, in the presence of lower frequencies of terrestrial locomotion. At the same time, metacarpal head height is the numerator of the hand power arm:load arm ratio (XHPL); therefore, if metacarpal head height is reduced in *Gorilla* and *G. b. beringei*, the explanation for greater values for XHPL in these taxa must lie in the denominator. The hand power arm:load arm ratio (XHPL) and the calcaneal tuberosity-metatarsal length ratio (XCMT) both have ray bone lengths as their denominators. Perhaps greater values for these ratios in *Gorilla* and *G. b. beringei* reflect shorter ray bones in these taxa, which seems more likely to relate to lesser arboreality (and colder habitats in the case of *G. b. beringei*) than to non-locomotor behaviors on the ground. It is also conceivable that the results for the calcaneal tuberosity-metatarsal length ratio (XCMT) reflect, to some extent, an effect on calcaneal tuberosity length in *Gorilla* and *G. b. beringei* from tension on the calcaneal tendon due to greater amounts of time spent squatting on the ground.

In any case, not one of these three variables is among the four variables that differentiate both species and subspecies within both *Gorilla* and *Pan* (see Table 4.68). Among the variables that differentiate either species or subspecies of both genera, only the calcaneal tuberosity-metatarsal length ratio (XCMT), which differentiates species of both genera, is on the list (see Table 4.68). In addition to the other conclusions above regarding functional interpretations, it must be concluded that the "terrestrial" variables in this study are not reliable as universal indicators of relative terrestriality (meaning simply spending more time on the ground) among African apes and, if these three terrestriality-associated variables do, in fact, reflect terrestriality, taxonomic divisions within African ape genera do not correspond to differences in terrestriality.

Table 4.1. *Gorilla* vs. *Pan*: Results of comparisons of means and two-sample t-tests[1,2] for hand ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MCAH | Gorilla | 0.0841 | 1.0000 | Gorilla | 0.2826 | 1.0000 |
| HPFS | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| HPAH | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |
| XPMC | Pan | 0.0000 | **0.0001** | Pan | 0.0000 | **0.0000** |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MCM | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |
| MCDR | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0097 | 0.1267 |
| MCHS | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |
| MCB | Pan | 0.0000 | **0.0000** | Pan | 0.0006 | **0.0080** |
| HPMD | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| HPBD | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| HPTW | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| HPGT | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| XHPL | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.2. *Gorilla* vs. *Pan*: Results of comparisons of means and two-sample t-tests[1,2] for foot ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MTAH | Pan | 0.0349 | 0.3143 | Pan | 0.0000 | **0.0000** |
| FPFS | Gorilla | 0.1725 | 1.0000 | Gorilla | 0.0335 | 0.3012 |
| FPAH | Gorilla | 0.0298 | 0.2681 | Gorilla | 0.0017 | **0.0150** |
| CCFS | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |
| CCFD | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| XPMT | Pan | 0.0000 | **0.0000** | Pan | 0.0000 | **0.0000** |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MTB | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |
| CCTW | Pan | 0.9973 | 1.0000 | Pan | 0.5188 | 1.0000 |
| XCMT | Gorilla | 0.0000 | **0.0000** | Gorilla | 0.0000 | **0.0000** |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.3. *Gorilla* species (*G. gorilla* vs. *G. beringei*): Results of comparisons of means and two-sample t-tests[1,2] for hand ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MCAH | gorilla | 0.6458 | 1.0000 | gorilla | 0.0485 | 0.6301 |
| HPFS | beringei | 0.0000 | **0.0000** | beringei | 0.0118 | 0.1538 |
| HPAH | gorilla | 0.0000 | **0.0000** | gorilla | 0.0000 | **0.0000** |
| XPMC | beringei | 0.0000 | **0.0001** | beringei | 0.0000 | **0.0005** |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MCM | gorilla | 0.2952 | 1.0000 | beringei | 0.6712 | 1.0000 |
| MCDR | gorilla | 0.0339 | 0.4407 | gorilla | 0.0061 | 0.0790 |
| MCHS | gorilla | 0.0171 | 0.2221 | gorilla | 0.0861 | 1.0000 |
| MCB | gorilla | 0.0000 | **0.0000** | gorilla | 0.0001 | **0.0018** |
| HPMD | gorilla | 0.3380 | 1.0000 | beringei | 0.0523 | 0.6804 |
| HPBD | gorilla | 0.0021 | **0.0273** | gorilla | 0.0039 | **0.0510** |
| HPTW | beringei | 0.2872 | 1.0000 | beringei | 0.8370 | 1.0000 |
| HPGT | gorilla | 0.0000 | **0.0000** | gorilla | 0.1504 | 1.0000 |
| XHPL | beringei | 0.0296 | 0.3843 | beringei | 0.0042 | 0.0549 |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.4. *Gorilla* species (*G. gorilla* vs. *G. beringei*): Results of comparisons of means and two-sample t-tests[1,2] for foot ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MTAH | beringei | 0.0000 | **0.0000** | beringei | 0.0004 | **0.0040** |
| FPFS | beringei | 0.0000 | **0.0000** | beringei | 0.0004 | **0.0032** |
| FPAH | gorilla | 0.0079 | 0.0715 | gorilla | 0.0247 | 0.2226 |
| CCFS | gorilla | 0.0246 | 0.2217 | gorilla | 0.4337 | 1.0000 |
| CCFD | gorilla | 0.0012 | **0.0107** | gorilla | 0.0013 | **0.0120** |
| XPMT | beringei | 0.0042 | **0.0381** | beringei | 0.0726 | 0.6531 |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MTB | gorilla | 0.0000 | **0.0000** | gorilla | 0.0011 | **0.0095** |
| CCTW | gorilla | 0.0355 | 0.3199 | gorilla | 0.0180 | 0.1624 |
| XCMT | beringei | 0.0000 | **0.0000** | beringei | 0.0001 | **0.0008** |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.5. *G. b. beringei* vs. *G. b. graueri*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | graueri | 0.4911 | graueri | 1.0000 |
| HPFS | graueri | 1.0000 | graueri | 0.1901 |
| HPAH | beringei | 1.0000 | beringei | 1.0000 |
| XPMC | graueri | **0.0160** | graueri | 0.0713 |
| | | | | |
| *Terrestrial* | | | | |
| MCM | beringei | 1.0000 | beringei | 1.0000 |
| MCDR | graueri | 1.0000 | graueri | 1.0000 |
| MCHS | beringei | **0.0409** | beringei | 0.1050 |
| MCB | graueri | **0.0086** | graueri | 1.0000 |
| HPMD | beringei | 0.7049 | beringei | 0.7261 |
| HPBD | beringei | 1.0000 | graueri | 1.0000 |
| HPTW | beringei | 0.2029 | graueri | 0.8070 |
| HPGT | beringei | 1.0000 | beringei | **0.0132** |
| XHPL | beringei | 0.6363 | graueri | 1.0000 |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.6. *G. b. beringei* vs. *G. b. graueri*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | beringei | 1.0000 | beringei | 1.0000 |
| FPFS | graueri | **0.0177** | graueri | **0.0000** |
| FPAH | beringei | 0.7210 | beringei | 0.2907 |
| CCFS | beringei | 0.7357 | beringei | 0.1370 |
| CCFD | graueri | 0.1136 | graueri | 0.4300 |
| XPMT | beringei | 0.3459 | graueri | 1.0000 |
| | | | | |
| *Terrestrial* | | | | |
| MTB | graueri | 0.1189 | graueri | **0.0056** |
| CCTW | graueri | 0.0929 | graueri | **0.0105** |
| XCMT | graueri | 1.0000 | graueri | 1.0000 |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.7. *G. b. beringei* vs. *G. g. gorilla*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | gorilla | 0.5745 | gorilla | 0.0816 |
| HPFS | beringei | **0.0000** | beringei | 1.0000 |
| HPAH | gorilla | **0.0061** | gorilla | **0.0001** |
| XPMC | beringei | **0.0387** | beringei | 0.0962 |
| | | | | |
| *Terrestrial* | | | | |
| MCM | gorilla | 1.0000 | beringei | 1.0000 |
| MCDR | gorilla | 0.6916 | gorilla | 0.0906 |
| MCHS | beringei | 1.0000 | beringei | 1.0000 |
| MCB | gorilla | **0.0000** | gorilla | **0.0136** |
| HPMD | beringei | 1.0000 | beringei | 0.1736 |
| HPBD | gorilla | 0.3342 | gorilla | 0.1372 |
| HPTW | beringei | 0.1215 | gorilla | 1.0000 |
| HPGT | gorilla | **0.0111** | beringei | 1.0000 |
| XHPL | beringei | **0.0418** | beringei | 0.6506 |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.8. *G. b. beringei* vs. *G. g. gorilla*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | beringei | **0.0001** | beringei | **0.0000** |
| FPFS | beringei | **0.0036** | beringei | 0.1895 |
| FPAH | gorilla | 1.0000 | gorilla | 0.6534 |
| CCFS | gorilla | 1.0000 | beringei | 1.0000 |
| CCFD | gorilla | **0.0011** | gorilla | **0.0083** |
| XPMT | beringei | **0.0040** | beringei | 0.9574 |
| | | | | |
| *Terrestrial* | | | | |
| MTB | gorilla | **0.0000** | gorilla | **0.0000** |
| CCTW | gorilla | **0.0136** | gorilla | **0.0002** |
| XCMT | beringei | **0.0001** | beringei | **0.0005** |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.9. *G. b. graueri* vs. *G. g. gorilla*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | graueri | 1.0000 | gorilla | 0.6674 |
| HPFS | graueri | **0.0000** | graueri | **0.0125** |
| HPAH | gorilla | **0.0000** | gorilla | **0.0000** |
| XPMC | graueri | **0.0000** | graueri | **0.0000** |
| | | | | |
| *Terrestrial* | | | | |
| MCM | gorilla | 0.4210 | graueri | 1.0000 |
| MCDR | gorilla | 0.6020 | gorilla | 0.2452 |
| MCHS | gorilla | **0.0022** | gorilla | **0.0154** |
| MCB | gorilla | **0.0099** | gorilla | 0.1229 |
| HPMD | gorilla | 0.5636 | graueri | 1.0000 |
| HPBD | gorilla | **0.0033** | gorilla | 0.3703 |
| HPTW | gorilla | 1.0000 | graueri | 1.0000 |
| HPGT | gorilla | **0.0000** | gorilla | **0.0067** |
| XHPL | graueri | 0.7666 | graueri | **0.0348** |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.10. *G. b. graueri* vs. *G. g. gorilla*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | graueri | **0.0000** | graueri | **0.0003** |
| FPFS | graueri | **0.0000** | graueri | **0.0000** |
| FPAH | gorilla | **0.0264** | gorilla | **0.0022** |
| CCFS | gorilla | **0.0288** | gorilla | 0.1802 |
| CCFD | gorilla | 0.2606 | gorilla | 0.8410 |
| XPMT | graueri | 0.1315 | graueri | 0.6560 |
| | | | | |
| *Terrestrial* | | | | |
| MTB | gorilla | **0.0000** | gorilla | 0.7671 |
| CCTW | gorilla | 1.0000 | gorilla | 1.0000 |
| XCMT | graueri | **0.0000** | graueri | **0.0001** |

[1] Each ANOVA procedure included three gorilla subspecies (*G. g. gorilla*, *G. b. beringei*, and *G. b. graueri*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.11. *Pan* species (*P. troglodytes* vs. *P. paniscus*): Results of comparisons of means and two-sample t-tests[1,2] for hand ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MCAH | paniscus | 0.9203 | 1.0000 | paniscus | 0.4379 | 1.0000 |
| HPFS | trog. | 0.0019 | **0.0248** | trog. | 0.0008 | **0.0098** |
| HPAH | paniscus | 0.6669 | 1.0000 | paniscus | 0.1020 | 1.0000 |
| XPMC | trog. | 0.0002 | **0.0024** | trog. | 0.0000 | **0.0000** |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MCM | paniscus | 0.0812 | 1.0000 | paniscus | 0.8373 | 1.0000 |
| MCDR | trog. | 0.0155 | 0.2016 | trog. | 0.0045 | 0.0579 |
| MCHS | trog. | 0.1196 | 1.0000 | trog. | 0.0982 | 1.0000 |
| MCB | trog. | 0.6716 | 1.0000 | paniscus | 0.5674 | 1.0000 |
| HPMD | paniscus | 0.0526 | 0.6832 | paniscus | 0.5105 | 1.0000 |
| HPBD | paniscus | 0.2474 | 1.0000 | trog. | 0.1108 | 1.0000 |
| HPTW | paniscus | 0.0365 | 0.4742 | trog. | 0.4725 | 1.0000 |
| HPGT | trog. | 0.0015 | **0.0192** | trog. | 0.0000 | **0.0000** |
| XHPL | trog. | 0.5582 | 1.0000 | paniscus | 0.1937 | 1.0000 |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.12. *Pan* species (*P. troglodytes* vs. *P. paniscus*): Results of comparisons of means and two-sample t-tests[1,2] for foot ratios

| **Variables** | **Males** | | | **Females** | | |
|---|---|---|---|---|---|---|
| | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] | **greater mean** | **uncorrected p-value** | **corrected p-value**[3] |
| *Arboreal* | | | | | | |
| MTAH | trog. | 0.0254 | 0.2287 | trog. | 0.0007 | **0.0060** |
| FPFS | paniscus | 0.3314 | 1.0000 | trog. | 0.5677 | 1.0000 |
| FPAH | paniscus | 0.6422 | 1.0000 | paniscus | 0.3365 | 1.0000 |
| CCFS | trog. | 0.8418 | 1.0000 | paniscus | 0.3721 | 1.0000 |
| CCFD | paniscus | 0.6300 | 1.0000 | paniscus | 0.1616 | 1.0000 |
| XPMT | trog. | 0.0000 | **0.0000** | trog. | 0.0001 | **0.0010** |
| | | | | | | |
| *Terrestrial* | | | | | | |
| MTB | paniscus | 0.0448 | 0.4031 | paniscus | 0.3093 | 1.0000 |
| CCTW | paniscus | 0.7017 | 1.0000 | paniscus | 0.5755 | 1.0000 |
| XCMT | paniscus | 0.0023 | **0.0208** | paniscus | 0.0383 | 0.3447 |

[1] Separate variance

[2] P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$.

[3] Bonferroni adjustment was used. P-values less than or equal to 0.05 are in bold.

Table 4.13. *P. t. troglodytes* vs. *P. t. schweinfurthii*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HPFS | troglodytes | 1.0000 | troglodytes | 0.1384 |
| HPAH | troglodytes | 0.1243 | troglodytes | 0.8075 |
| XPMC | troglodytes | 1.0000 | troglodytes | 1.0000 |
| | | | | |
| *Terrestrial* | | | | |
| MCM | schweinfurthii | 0.6849 | troglodytes | 1.0000 |
| MCDR | schweinfurthii | 0.4305 | schweinfurthii | 0.9637 |
| MCHS | troglodytes | 1.0000 | troglodytes | 0.3910 |
| MCB | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HPMD | schweinfurthii | **0.0086** | schweinfurthii | 0.4787 |
| HPBD | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HPTW | schweinfurthii | 0.0884 | troglodytes | 1.0000 |
| HPGT | troglodytes | 0.5574 | troglodytes | 0.4922 |
| XHPL | troglodytes | 1.0000 | troglodytes | 1.0000 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.14. *P. t. troglodytes* vs. *P. t. schweinfurthii*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | troglodytes | 1.0000 | troglodytes | 0.9752 |
| FPFS | schweinfurthii | 0.0606 | troglodytes | 0.2450 |
| FPAH | schweinfurthii | 0.8519 | troglodytes | 0.5713 |
| CCFS | troglodytes | 0.1549 | troglodytes | 0.6408 |
| CCFD | schweinfurthii | 1.0000 | troglodytes | 1.0000 |
| XPMT | troglodytes | 1.0000 | troglodytes | 0.3631 |
| | | | | |
| *Terrestrial* | | | | |
| MTB | troglodytes | 1.0000 | troglodytes | 0.7468 |
| CCTW | troglodytes | 0.0685 | troglodytes | 0.5533 |
| XCMT | schweinfurthii | 1.0000 | schweinfurthii | 0.2526 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.15. *P. t. troglodytes* vs. *P. t. verus*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | verus | 1.0000 | verus | 0.7295 |
| HPFS | troglodytes | 1.0000 | troglodytes | **0.0284** |
| HPAH | troglodytes | 0.2159 | verus | 1.0000 |
| XPMC | troglodytes | 1.0000 | troglodytes | 0.0651 |
| | | | | |
| *Terrestrial* | | | | |
| MCM | troglodytes | 0.4484 | troglodytes | 1.0000 |
| MCDR | verus | 1.0000 | troglodytes | 1.0000 |
| MCHS | troglodytes | 1.0000 | verus | 1.0000 |
| MCB | verus | 0.1740 | verus | 1.0000 |
| HPMD | verus | **0.0228** | verus | 0.1178 |
| HPBD | verus | 0.9575 | troglodytes | 1.0000 |
| HPTW | verus | 0.0858 | troglodytes | 1.0000 |
| HPGT | troglodytes | 1.0000 | verus | 1.0000 |
| XHPL | troglodytes | 1.0000 | verus | 0.2384 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.16. *P. t. troglodytes* vs. *P. t. verus*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | verus | 0.5247 | verus | 0.7215 |
| FPFS | verus | **0.0000** | troglodytes | 1.0000 |
| FPAH | troglodytes | 0.4647 | troglodytes | 0.1691 |
| CCFS | troglodytes | **0.0265** | troglodytes | 0.0573 |
| CCFD | troglodytes | 1.0000 | troglodytes | 0.5696 |
| XPMT | troglodytes | 0.2178 | troglodytes | **0.0034** |
| | | | | |
| *Terrestrial* | | | | |
| MTB | verus | 0.0575 | troglodytes | 1.0000 |
| CCTW | verus | 1.0000 | verus | 1.0000 |
| XCMT | verus | 1.0000 | verus | 0.7660 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.17. *P. t. schweinfurthii* vs. *P. t. verus*:
Results of comparisons of means and ANOVAs[1] for hand ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MCAH | verus | 1.0000 | verus | 1.0000 |
| HPFS | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| HPAH | schweinfurthii | 1.0000 | verus | 1.0000 |
| XPMC | verus | 1.0000 | schweinfurthii | 0.4471 |
| | | | | |
| *Terrestrial* | | | | |
| MCM | schweinfurthii | 0.1534 | schweinfurthii | 1.0000 |
| MCDR | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| MCHS | schweinfurthii | 1.0000 | verus | 0.3358 |
| MCB | verus | 0.4552 | verus | 1.0000 |
| HPMD | verus | 1.0000 | verus | 1.0000 |
| HPBD | verus | 1.0000 | schweinfurthii | 1.0000 |
| HPTW | verus | 1.0000 | verus | 1.0000 |
| HPGT | verus | 1.0000 | verus | 0.2929 |
| XHPL | schweinfurthii | 1.0000 | verus | 0.2169 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.18. *P. t. schweinfurthii* vs. *P. t. verus*:
Results of comparisons of means and ANOVAs[1] for foot ratios

| **Variables** | **Males** | | **Females** | |
|---|---|---|---|---|
| | **greater mean** | **corrected p-value**[2] | **greater mean** | **corrected p-value**[2] |
| *Arboreal* | | | | |
| MTAH | verus | 0.4253 | verus | 0.3339 |
| FPFS | verus | **0.0031** | verus | 1.0000 |
| FPAH | schweinfurthii | 0.1774 | schweinfurthii | 1.0000 |
| CCFS | schweinfurthii | 0.6565 | schweinfurthii | 1.0000 |
| CCFD | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |
| XPMT | schweinfurthii | 0.5131 | schweinfurthii | 0.4601 |
| | | | | |
| *Terrestrial* | | | | |
| MTB | verus | 0.0653 | verus | 1.0000 |
| CCTW | verus | 0.0957 | verus | 0.3783 |
| XCMT | schweinfurthii | 1.0000 | schweinfurthii | 1.0000 |

[1] Each ANOVA procedure included three *P. troglodytes* subspecies (*P. t. troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*), but only the pairwise comparisons included in these analyses are reported here. Results for each pair of subspecies are tabulated separately. A separate ANOVA procedure was conducted for each variable.

[2] P-values, corrected with Bonferroni adjustments, were generated as part of each ANOVA procedure. P-values have been rounded to four decimal places. In any case where $p \geq 0.99995$, the p-value is rounded to $p = 1.0000$. P-values less than or equal to 0.05 are in bold.

Table 4.19. *Gorilla* and *Pan* hands by genus: Canonical discriminant functions, standardized by pooled within-group variances (forward/backward stepwise models)

| | Function 1 – Males[1] | Function 1 – Females[2] |
|---|---|---|
| MCM | 0.3029 | 0.4514 |
| MCDR | 0.2605 | --- |
| MCHS | 0.5134 | 0.7349 |
| MCB | 0.1692 | 0.3032 |
| MCAH | --- | --- |
| HPMD | -0.7757 | -0.6373 |
| HPBD | --- | --- |
| HPFS | -0.4053 | -0.2213 |
| HPTW | --- | --- |
| HPGT | -0.1813 | -0.2409 |
| HPAH | -0.4819 | -0.2772 |
| XPMC | --- | 0.1539 |
| XHPL | 0.7015 | 0.8634 |

[1]100% rate of correct classification in jackknifed matrix (Wilks' lambda p = 0.0000).
[2]100% rate of correct classification in jackknifed matrix (Wilks' lambda p = 0.0000).

Table 4.20. *Gorilla* and *Pan* feet by genus: Canonical discriminant functions, standardized by pooled within-group variances (forward/backward stepwise models)

| | Function 1 – Males[1] | Function 1 – Females[2] |
|---|---|---|
| MTB | 0.4604 | 0.2508 |
| MTAH | -0.1162 | -0.2461 |
| FPFS | --- | --- |
| FPAH | 0.1642 | --- |
| CCTW | --- | 0.1660 |
| CCFS | 0.2670 | 0.1964 |
| CCFD | -0.2781 | -0.1762 |
| XPMT | -0.3063 | -0.2233 |
| XCMT | 0.9799 | 0.9499 |

[1] 100% rate of correct classification in jackknifed matrix (Wilks' lambda p = 0.0000).
[2] 100% rate of correct classification in jackknifed matrix (Wilks' lambda p = 0.0000).

Table 4.21. Male *Gorilla* and *Pan* hands by species: Discriminant function analysis (complete model)

A. Jackknifed classification matrix

| | Gb | Gg | Pp | Pt | %correct |
|---|---|---|---|---|---|
| Gb | 24 | 1 | 0 | 0 | 96 |
| Gg | 2 | 95 | 0 | 0 | 98 |
| Pp | 0 | 0 | 7 | 0 | 100 |
| Pt | 0 | 0 | 5 | 81 | 94 |
| Total | 26 | 96 | 12 | 81 | 96 |

Gb = *G. beringei*
Gg = *G. gorilla*
Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MCM | 0.2729 | 0.2655 | 0.1298 |
| MCDR | 0.2408 | -0.0688 | 0.0524 |
| MCHS | 0.5432 | 0.1902 | -0.4343 |
| MCB | 0.1187 | 0.5374 | -0.3215 |
| MCAH | -0.0143 | 0.2723 | 0.0209 |
| HPMD | -0.7283 | 0.1818 | -0.1136 |
| HPBD | -0.0799 | 0.2709 | -0.1427 |
| HPFS | -0.2781 | -0.5493 | -0.3837 |
| HPTW | -0.0293 | -0.0415 | 0.3527 |
| HPGT | -0.1796 | 0.2432 | -0.5558 |
| HPAH | -0.4743 | 0.4197 | -0.1748 |
| XPMC | 0.1878 | -0.6228 | -0.3550 |
| XHPL | 0.7559 | -0.2629 | -0.0669 |
| | | | |
| Canonical correlations | 0.9547 | 0.7532 | 0.4617 |
| Cumulative % of total dispersion | 86.68 | 97.72 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Gb | 3.2401 | -2.6864 | 0.5028 |
| Gg | 2.6432 | 0.7853 | -0.1100 |
| Pp | -4.6287 | 2.0685 | 2.5400 |
| Pt | -3.5464 | -0.2731 | -0.2288 |

Table 4.22. Female *Gorilla* and *Pan* hands by species: Discriminant function analysis (complete model)

A. Jackknifed classification matrix

| | Gb | Gg | Pp | Pt | %correct |
|---|---|---|---|---|---|
| Gb | 11 | 2 | 0 | 0 | 85 |
| Gg | 8 | 65 | 0 | 1 | 88 |
| Pp | 0 | 0 | 12 | 0 | 100 |
| Pt | 0 | 0 | 12 | 94 | 89 |
| Total | 19 | 67 | 24 | 95 | 89 |

Gb = *G. beringei*
Gg = *G. gorilla*
Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MCM | 0.4093 | 0.1929 | 0.1004 |
| MCDR | 0.1018 | -0.0575 | 0.1612 |
| MCHS | 0.6689 | 0.1296 | 0.3541 |
| MCB | 0.2251 | 0.2885 | 0.2862 |
| MCAH | -0.0578 | 0.3275 | 0.2030 |
| HPMD | -0.6410 | 0.0894 | -0.1442 |
| HPBD | 0.0314 | 0.0851 | 0.4279 |
| HPFS | -0.1802 | -0.3016 | 0.0905 |
| HPTW | -0.0757 | 0.1878 | -0.3407 |
| HPGT | -0.2206 | -0.3382 | 0.4505 |
| HPAH | -0.3209 | 0.3988 | 0.3576 |
| XPMC | 0.1620 | -0.7182 | 0.2347 |
| XHPL | 0.8962 | -0.3922 | -0.1945 |
| | | | |
| Canonical correlations | 0.9408 | 0.6528 | 0.4620 |
| Cumulative % of total dispersion | 88.38 | 96.89 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Gb | 3.7143 | -2.1812 | -1.3060 |
| Gg | 3.1066 | 0.4407 | 0.2457 |
| Pp | -2.5504 | 2.2994 | -1.4555 |
| Pt | -2.3355 | -0.3005 | 0.1534 |

Table 4.23. Male *Gorilla* and *Pan* feet by species: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Gb | Gg | Pp | Pt | %correct |
|---|---|---|---|---|---|
| Gb | 18 | 1 | 0 | 0 | 95 |
| Gg | 4 | 87 | 0 | 0 | 96 |
| Pp | 0 | 0 | 5 | 3 | 63 |
| Pt | 0 | 0 | 8 | 76 | 90 |
| Total | 22 | 88 | 13 | 79 | 92 |

Gb = *G. beringei*
Gg = *G. gorilla*
Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MTB | 0.3422 | 0.5323 | 0.1252 |
| MTAH | -0.0844 | -0.4645 | 0.3283 |
| FPFS | 0.0487 | -0.5377 | -0.5579 |
| FPAH | 0.1265 | 0.4476 | 0.0605 |
| CCTW | --- | --- | --- |
| CCFS | 0.2172 | 0.2348 | 0.1442 |
| CCFD | -0.2741 | 0.1548 | -0.2111 |
| XPMT | -0.3727 | -0.1696 | 0.6890 |
| XCMT | 0.9363 | -0.2211 | 0.0672 |
| | | | |
| Canonical correlations | 0.9641 | 0.7538 | 0.3453 |
| Cumulative % of total dispersion | 90.07 | 99.07 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Gb | 4.0460 | -3.2605 | -0.1281 |
| Gg | 3.0981 | 0.7541 | 0.0683 |
| Pp | -2.2950 | 0.7836 | -1.7608 |
| Pt | -4.0529 | -0.1540 | 0.1226 |

Table 4.24. Female *Gorilla* and *Pan* feet by species: Discriminant function analysis (complete and forward/backward stepwise model)

A. Jackknifed classification matrix

| | Gb | Gg | Pp | Pt | %correct |
|---|---|---|---|---|---|
| Gb | 13 | 1 | 0 | 0 | 93 |
| Gg | 4 | 68 | 1 | 0 | 93 |
| Pp | 0 | 0 | 9 | 2 | 82 |
| Pt | 0 | 0 | 14 | 88 | 86 |
| Total | 17 | 69 | 24 | 90 | 89 |

Gb = *G. beringei*
Gg = *G. gorilla*
Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MTB | 0.1602 | 0.5017 | 0.3812 |
| MTAH | -0.1850 | -0.4900 | 0.0506 |
| FPFS | -0.0096 | -0.5553 | -0.2640 |
| FPAH | 0.0650 | 0.3290 | 0.1776 |
| CCTW | 0.1368 | 0.2548 | 0.1326 |
| CCFS | 0.1860 | 0.1544 | -0.0170 |
| CCFD | -0.1652 | 0.1959 | -0.3470 |
| XPMT | -0.2788 | -0.2384 | 0.8256 |
| XCMT | 0.9356 | -0.2235 | 0.0516 |
| | | | |
| Canonical correlations | 0.9548 | 0.6797 | 0.2956 |
| Cumulative % of total dispersion | 91.53 | 99.15 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Gb | 4.4629 | -2.9456 | -0.3069 |
| Gg | 3.4349 | 0.6232 | 0.1022 |
| Pp | -1.7024 | 1.1876 | -1.1950 |
| Pt | -2.8873 | -0.1698 | 0.0979 |

Table 4.25. Male *Gorilla* hands by species: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Gb | Gg | %correct |
|---|---|---|---|
| Gb | 24 | 1 | 96 |
| Gg | 2 | 95 | 98 |
| Total | 26 | 96 | 98 |

Gb = *G. beringei*
Gg = *G. gorilla*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | --- |
| MCB | 0.5238 |
| MCAH | 0.2900 |
| HPMD | 0.4810 |
| HPBD | 0.4417 |
| HPFS | -0.4668 |
| HPTW | -0.2780 |
| HPGT | 0.4474 |
| HPAH | 0.4573 |
| XPMC | -0.5566 |
| XHPL | -0.4607 |
| | |
| Canonical correlations | 0.8599 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Gb | -3.2905 |
| Gg | 0.8481 |

Table 4.26. Female *Gorilla* hands by species: Discriminant function analysis (complete model)

A. Jackknifed classification matrix

| | Gb | Gg | %correct |
|---|---|---|---|
| Gb | 11 | 2 | 85 |
| Gg | 6 | 68 | 92 |
| Total | 17 | 70 | 91 |

Gb = *G. beringei*
Gg = *G. gorilla*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | 0.2806 |
| MCDR | -0.0846 |
| MCHS | 0.2446 |
| MCB | 0.2701 |
| MCAH | 0.3242 |
| HPMD | 0.0129 |
| HPBD | 0.3945 |
| HPFS | -0.2949 |
| HPTW | 0.1445 |
| HPGT | 0.1240 |
| HPAH | 0.6076 |
| XPMC | -0.4614 |
| XHPL | -0.3008 |
| | |
| Canonical correlations | 0.7563 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Gb | -2.7259 |
| Gg | 0.4789 |

Table 4.27. Male *Gorilla* feet by species: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Gb | Gg | %correct |
|---|---|---|---|
| Gb | 18 | 1 | 95 |
| Gg | 3 | 88 | 97 |
| Total | 21 | 89 | 96 |

Gb = *G. beringei*
Gg = *G. gorilla*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | 0.4005 |
| MTAH | -0.3570 |
| FPFS | -0.6921 |
| FPAH | 0.4015 |
| CCTW | --- |
| CCFS | --- |
| CCFD | 0.2330 |
| XPMT | --- |
| XCMT | -0.3869 |
| | |
| Canonical correlations | 0.8401 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Gb | -3.3587 |
| Gg | 0.7013 |

Table 4.28. Female *Gorilla* feet by species: Discriminant function analysis (complete model)

A. Jackknifed classification matrix

| | Gb | Gg | %correct |
|---|---|---|---|
| Gb | 13 | 1 | 93 |
| Gg | 4 | 69 | 95 |
| Total | 17 | 70 | 94 |

Gb = *G. beringei*
Gg = *G. gorilla*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | 0.4490 |
| MTAH | -0.4864 |
| FPFS | -0.5794 |
| FPAH | 0.3038 |
| CCTW | 0.1286 |
| CCFS | 0.1434 |
| CCFD | 0.2897 |
| XPMT | 0.1476 |
| XCMT | -0.4180 |
| | |
| Canonical correlations | 0.8170 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Gb | -3.1981 |
| Gg | 0.6133 |

Table 4.29. Male *G. beringei* hands by subspecies: Discriminant function analysis (backward stepwise model)

A. Jackknifed classification matrix

| | beringei | graueri | %correct |
|---|---|---|---|
| beringei | 9 | 1 | 90 |
| graueri | 3 | 12 | 80 |
| Total | 12 | 13 | 84 |

beringei = *G. b. beringei*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | 0.6205 |
| MCB | -0.5881 |
| MCAH | -0.6639 |
| HPMD | 0.6321 |
| HPBD | --- |
| HPFS | 0.7432 |
| HPTW | --- |
| HPGT | --- |
| HPAH | 0.7684 |
| XPMC | --- |
| XHPL | --- |
| | |
| Canonical correlations | 0.8354 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0006

C. Canonical scores of group means

| | 1 |
|---|---|
| beringei | 1.7855 |
| graueri | -1.1903 |

Table 4.30. Female *G. beringei* hands by subspecies: Discriminant function analysis (forward stepwise model)

A. Jackknifed classification matrix

| | beringei | graueri | %correct |
|---|---|---|---|
| beringei | 5 | 1 | 83 |
| graueri | 0 | 7 | 100 |
| Total | 5 | 8 | 92 |

beringei = *G. b. beringei*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | --- |
| MCB | --- |
| MCAH | --- |
| HPMD | --- |
| HPBD | --- |
| HPFS | --- |
| HPTW | --- |
| HPGT | 0.8562 |
| HPAH | --- |
| XPMC | -0.7344 |
| XHPL | --- |
| | |
| Canonical correlations | 0.8658 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0010

C. Canonical scores of group means

| | 1 |
|---|---|
| beringei | 1.7190 |
| graueri | -1.4735 |

Table 4.31. Male *G. beringei* feet by subspecies: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | beringei | graueri | %correct |
|---|---|---|---|
| beringei | 5 | 1 | 83 |
| graueri | 0 | 13 | 100 |
| Total | 5 | 14 | 95 |

beringei = *G. b. beringei*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | 0.4756 |
| MTAH | --- |
| FPFS | 0.4904 |
| FPAH | --- |
| CCTW | 0.9434 |
| CCFS | --- |
| CCFD | 0.8998 |
| XPMT | -0.7737 |
| XCMT | --- |
| | |
| Canonical correlations | 0.9066 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0002

C. Canonical scores of group means

| | 1 |
|---|---|
| beringei | -2.9918 |
| graueri | 1.3808 |

Table 4.32. Female *G. beringei* feet by subspecies: Discriminant function analysis (forward stepwise model)

A. Jackknifed classification matrix

| | beringei | graueri | %correct |
|---|---|---|---|
| beringei | 7 | 0 | 100 |
| graueri | 0 | 7 | 100 |
| Total | 7 | 7 | 100 |

beringei = *G. b. beringei*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | --- |
| MTAH | --- |
| FPFS | 0.9766 |
| FPAH | --- |
| CCTW | --- |
| CCFS | --- |
| CCFD | 0.5431 |
| XPMT | --- |
| XCMT | --- |
| | |
| Canonical correlations | 0.9105 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0001

C. Canonical scores of group means

| | 1 |
|---|---|
| beringei | -2.0391 |
| graueri | 2.0391 |

Table 4.33. Male *Gorilla* hands by subspecies: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | beringei | gorilla | graueri | %correct |
|---|---|---|---|---|
| beringei | 9 | 0 | 1 | 90 |
| gorilla | 4 | 92 | 0 | 96 |
| graueri | 4 | 0 | 11 | 73 |
| Total | 17 | 92 | 12 | 93 |

beringei = *G. b. beringei*
gorilla = *G. g. gorilla*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | --- | --- |
| MCHS | 0.0962 | 0.6062 |
| MCB | -0.4765 | -0.3127 |
| MCAH | -0.2837 | -0.3502 |
| HPMD | -0.4810 | -0.4523 |
| HPBD | -0.4713 | -0.4988 |
| HPFS | 0.4590 | 0.1746 |
| HPTW | 0.2991 | 0.6708 |
| HPGT | -0.4499 | -0.0835 |
| HPAH | -0.4752 | 0.6643 |
| XPMC | 0.5601 | -0.2171 |
| XHPL | 0.5047 | 0.3901 |
| | | |
| Canonical correlations | 0.8611 | 0.4697 |
| Cumulative % of total dispersion | 91.02 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| beringei | 3.2361 | 1.4249 |
| gorilla | -0.8535 | -0.0025 |
| graueri | 3.3049 | -0.9342 |

Table 4.34. Female *Gorilla* hands by subspecies: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | beringei | gorilla | graueri | %correct |
|---|---|---|---|---|
| beringei | 5 | 1 | 0 | 83 |
| gorilla | 11 | 63 | 0 | 85 |
| graueri | 0 | 0 | 7 | 100 |
| Total | 16 | 64 | 7 | 86 |

beringei = *G. b. beringei*
gorilla = *G. g. gorilla*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | --- | --- |
| MCHS | 0.3153 | 0.3337 |
| MCB | --- | --- |
| MCAH | --- | --- |
| HPMD | --- | --- |
| HPBD | 0.5332 | -0.4445 |
| HPFS | -0.4033 | -0.2653 |
| HPTW | --- | --- |
| HPGT | 0.3732 | 0.7052 |
| HPAH | 0.5763 | -0.5781 |
| XPMC | -0.5288 | -0.1837 |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.7574 | 0.3951 |
| Cumulative % of total dispersion | 87.92 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| beringei | -1.4355 | 1.4586 |
| gorilla | 0.4477 | -0.0619 |
| graueri | -3.5020 | -0.5961 |

Table 4.35. Male *Gorilla* feet by subspecies: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | beringei | gorilla | graueri | %correct |
|---|---|---|---|---|
| beringei | 5 | 0 | 1 | 83 |
| gorilla | 2 | 87 | 1 | 97 |
| graueri | 2 | 1 | 10 | 77 |
| Total | 9 | 88 | 12 | 94 |

beringei = *G. b. beringei*
gorilla = *G. g. gorilla*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | 0.3562 | 0.4040 |
| MTAH | -0.3476 | -0.2477 |
| FPFS | -0.7018 | 0.6148 |
| FPAH | 0.4315 | -0.4835 |
| CCTW | 0.0480 | 0.4742 |
| CCFS | --- | --- |
| CCFD | 0.2029 | 0.4338 |
| XPMT | --- | --- |
| XCMT | -0.3835 | -0.0349 |
| | | |
| Canonical correlations | 0.8417 | 0.4576 |
| Cumulative % of total dispersion | 90.17 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| beringei | -3.0073 | -1.8536 |
| gorilla | 0.7051 | 0.0143 |
| graueri | -3.4933 | 0.7565 |

Table 4.36. Female *Gorilla* feet by subspecies: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | beringei | gorilla | graueri | %correct |
|---|---|---|---|---|
| beringei | 7 | 0 | 0 | 100 |
| gorilla | 2 | 71 | 0 | 97 |
| graueri | 1 | 0 | 6 | 86 |
| Total | 10 | 71 | 6 | 97 |

beringei = *G. b. beringei*
gorilla = *G. g. gorilla*
graueri = *G. b. graueri*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | 0.2775 | 0.6760 |
| MTAH | -0.3642 | -0.3740 |
| FPFS | -0.6896 | 0.6064 |
| FPAH | 0.3615 | -0.2394 |
| CCTW | --- | --- |
| CCFS | 0.2653 | -0.3379 |
| CCFD | 0.2559 | 0.2444 |
| XPMT | --- | --- |
| XCMT | -0.3733 | -0.3109 |
| | | |
| Canonical correlations | 0.8265 | 0.6254 |
| Cumulative % of total dispersion | 77.05 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| beringei | -2.1647 | -2.3855 |
| gorilla | 0.6069 | 0.0959 |
| graueri | -4.1644 | 1.3857 |

Table 4.37. Male *Gorilla* hands by population: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 28 | 6 | 9 | 65 |
| Coast | 7 | 6 | 5 | 33 |
| Ebolowa | 4 | 9 | 16 | 55 |
| Total | 39 | 21 | 30 | 56 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | --- |
| MCB | --- |
| MCAH | --- |
| HPMD | --- |
| HPBD | --- |
| HPFS | --- |
| HPTW | --- |
| HPGT | --- |
| HPAH | --- |
| XPMC | 1.0000 |
| XHPL | --- |
| | |
| Canonical correlations | 0.4502 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0001

C. Canonical scores of group means

| | 1 |
|---|---|
| Cam Int | 0.4974 |
| Coast | -0.2104 |
| Ebolowa | -0.6069 |

Table 4.38. Female *Gorilla* hands by population: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 23 | 10 | 10 | 53 |
| Coast | 3 | 4 | 2 | 44 |
| Ebolowa | 1 | 2 | 17 | 85 |
| Total | 27 | 16 | 29 | 61 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | --- | --- |
| MCHS | 0.6601 | 0.7737 |
| MCB | --- | --- |
| MCAH | --- | --- |
| HPMD | -0.5800 | 0.3845 |
| HPBD | --- | --- |
| HPFS | --- | --- |
| HPTW | 0.6899 | -0.2889 |
| HPGT | --- | --- |
| HPAH | --- | --- |
| XPMC | 0.3946 | -0.2920 |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.6101 | 0.3144 |
| Cumulative % of total dispersion | 84.39 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | 0.5387 | 0.1312 |
| Coast | 0.0740 | -0.8573 |
| Ebolowa | -1.1914 | 0.1036 |

Table 4.39. Male *Gorilla* feet by population: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 20 | 14 | 8 | 48 |
| Coast | 6 | 3 | 7 | 19 |
| Ebolowa | 5 | 6 | 15 | 58 |
| Total | 31 | 23 | 30 | 45 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | 0.7685 | 0.1595 |
| MTAH | --- | --- |
| FPFS | --- | --- |
| FPAH | -0.4161 | 0.8968 |
| CCTW | --- | --- |
| CCFS | --- | --- |
| CCFD | --- | --- |
| XPMT | -0.7524 | -0.3751 |
| XCMT | --- | --- |
| | | |
| Canonical correlations | 0.4921 | 0.1342 |
| Cumulative % of total dispersion | 94.57 | 100.00 |

[1] Wilks' lambda p = 0.0006

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | -0.5016 | 0.0570 |
| Coast | 0.0726 | -0.2737 |
| Ebolowa | 0.7655 | 0.0763 |

Table 4.40. Female *Gorilla* feet by population: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 20 | 11 | 11 | 48 |
| Coast | 2 | 7 | 1 | 70 |
| Ebolowa | 2 | 6 | 11 | 58 |
| Total | 24 | 24 | 23 | 54 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | --- | --- |
| MTAH | --- | --- |
| FPFS | --- | --- |
| FPAH | 0.7518 | 0.0948 |
| CCTW | -0.5307 | 0.5207 |
| CCFS | --- | --- |
| CCFD | --- | --- |
| XPMT | 0.4229 | -0.6363 |
| XCMT | 0.2271 | 0.9405 |
| | | |
| Canonical correlations | 0.4294 | 0.3614 |
| Cumulative % of total dispersion | 60.07 | 100.00 |

[1] Wilks' lambda p = 0.0036

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | 0.2204 | -0.2590 |
| Coast | 0.5053 | 0.8415 |
| Ebolowa | -0.7531 | 0.1296 |

Table 4.41. Male *Pan* hands by species: Discriminant function analysis (backward stepwise model)

A. Jackknifed classification matrix

| | Pp | Pt | %correct |
|---|---|---|---|
| Pp | 7 | 0 | 100 |
| Pt | 5 | 81 | 94 |
| Total | 12 | 81 | 95 |

Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | 0.5089 |
| MCB | --- |
| MCAH | --- |
| HPMD | --- |
| HPBD | -0.4333 |
| HPFS | 0.6959 |
| HPTW | --- |
| HPGT | --- |
| HPAH | --- |
| XPMC | 0.6936 |
| XHPL | --- |
| | |
| Canonical correlations | 0.6312 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Pp | -2.8218 |
| Pt | 0.2297 |

Table 4.42. Female *Pan* hands by species: Discriminant function analysis (backward stepwise model)

A. Jackknifed classification matrix

| | Pp | Pt | %correct |
|---|---|---|---|
| Pp | 12 | 0 | 100 |
| Pt | 8 | 98 | 92 |
| Total | 20 | 98 | 93 |

Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MCM | --- |
| MCDR | --- |
| MCHS | --- |
| MCB | --- |
| MCAH | --- |
| HPMD | --- |
| HPBD | --- |
| HPFS | 0.2960 |
| HPTW | -0.2843 |
| HPGT | 0.5239 |
| HPAH | --- |
| XPMC | 0.7810 |
| XHPL | --- |
| | |
| Canonical correlations | 0.6330 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Pp | -2.4096 |
| Pt | 0.2728 |

Table 4.43. Male *Pan* feet by species: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Pp | Pt | %correct |
|---|---|---|---|
| Pp | 8 | 0 | 100 |
| Pt | 8 | 76 | 90 |
| Total | 16 | 76 | 91 |

Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | 0.2831 |
| MTAH | -0.6081 |
| FPFS | --- |
| FPAH | 0.4423 |
| CCTW | --- |
| CCFS | --- |
| CCFD | --- |
| XPMT | -0.7430 |
| XCMT | 0.5894 |
| | |
| Canonical correlations | 0.6309 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Pp | 2.6059 |
| Pt | -0.2482 |

Table 4.44. Female *Pan* feet by species: Discriminant function analysis (complete model)

A. Jackknifed classification matrix

| | Pp | Pt | %correct |
|---|---|---|---|
| Pp | 9 | 2 | 82 |
| Pt | 13 | 89 | 87 |
| Total | 22 | 91 | 87 |

Pp = *P. paniscus*
Pt = *P. troglodytes*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 |
|---|---|
| MTB | 0.1816 |
| MTAH | -0.5431 |
| FPFS | -0.1813 |
| FPAH | 0.2066 |
| CCTW | 0.1424 |
| CCFS | 0.2336 |
| CCFD | 0.1550 |
| XPMT | -0.7920 |
| XCMT | 0.2896 |
| | |
| Canonical correlations | 0.5593 |
| Cumulative % of total dispersion | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 |
|---|---|
| Pp | 2.0361 |
| Pt | -0.2196 |

Table 4.45. Male *P. troglodytes* hands by subspecies: Discriminant function analysis (backward stepwise model)

A. Jackknifed classification matrix

| | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|
| schweinfurth | 7 | 6 | 5 | 39 |
| troglodytes | 11 | 45 | 7 | 71 |
| verus | 1 | 0 | 4 | 80 |
| Total | 19 | 51 | 16 | 65 |

schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | 0.2559 | 0.8669 |
| MCDR | --- | --- |
| MCHS | --- | --- |
| MCB | -0.4724 | -0.3031 |
| MCAH | --- | --- |
| HPMD | -0.8942 | 0.1491 |
| HPBD | 0.9597 | -0.5574 |
| HPFS | --- | --- |
| HPTW | -0.8375 | 0.2441 |
| HPGT | --- | --- |
| HPAH | --- | --- |
| XPMC | --- | --- |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.5428 | 0.2497 |
| Cumulative % of total dispersion | 86.27 | 100.00 |

[1] Wilks' lambda p = 0.0002

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| schweinfurth | -0.7621 | 0.3873 |
| troglodytes | 0.3600 | -0.0530 |
| verus | -1.7920 | -0.7270 |

Table 4.46. Female *P. troglodytes* hands by subspecies: Discriminant function analysis (forward stepwise model)

A. Jackknifed classification matrix

| | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|
| schweinfurth | 2 | 3 | 4 | 22 |
| troglodytes | 18 | 53 | 10 | 65 |
| verus | 4 | 0 | 6 | 60 |
| Total | 24 | 56 | 20 | 61 |

schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | --- | --- |
| MCHS | --- | --- |
| MCB | --- | --- |
| MCAH | --- | --- |
| HPMD | 0.7291 | 0.0969 |
| HPBD | --- | --- |
| HPFS | -0.7243 | -0.5611 |
| HPTW | --- | --- |
| HPGT | --- | --- |
| HPAH | --- | --- |
| XPMC | -0.4123 | 0.9410 |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.4464 | 0.1154 |
| Cumulative % of total dispersion | 94.86 | 100.00 |

[1] Wilks' lambda p = 0.0009

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| schweinfurth | 0.6934 | 0.3260 |
| troglodytes | -0.2308 | -0.0135 |
| verus | 1.2451 | -0.1837 |

Table 4.47. Male *P. troglodytes* feet by subspecies: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|
| schweinfurth | 9 | 6 | 1 | 56 |
| troglodytes | 18 | 41 | 3 | 66 |
| verus | 1 | 0 | 5 | 83 |
| Total | 28 | 47 | 9 | 65 |

schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | 0.4120 | 0.3476 |
| MTAH | --- | --- |
| FPFS | 0.9242 | -0.1204 |
| FPAH | -0.3660 | -0.4343 |
| CCTW | -0.0082 | 0.8196 |
| CCFS | -0.5460 | 0.3034 |
| CCFD | --- | --- |
| XPMT | --- | --- |
| XCMT | --- | --- |
| | | |
| Canonical correlations | 0.6691 | 0.3704 |
| Cumulative % of total dispersion | 0.8360 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| schweinfurth | 0.3818 | -0.7893 |
| troglodytes | -0.3888 | 0.1574 |
| verus | 2.9991 | 0.4787 |

Table 4.48. Female *P. troglodytes* feet by subspecies: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|
| schweinfurth | 3 | 3 | 2 | 38 |
| troglodytes | 14 | 56 | 11 | 69 |
| verus | 1 | 2 | 4 | 57 |
| Total | 18 | 61 | 17 | 66 |

schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | --- | --- |
| MTAH | --- | --- |
| FPFS | --- | --- |
| FPAH | 0.5606 | 0.0437 |
| CCTW | --- | --- |
| CCFS | --- | --- |
| CCFD | --- | --- |
| XPMT | 0.8183 | -0.4567 |
| XCMT | -0.4675 | -0.8432 |
| | | |
| Canonical correlations | 0.4619 | 0.1018 |
| Cumulative % of total dispersion | 96.28 | 100.00 |

[1] Wilks' lambda p = 0.0008

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| schweinfurth | -0.8379 | -0.2908 |
| troglodytes | 0.2131 | 0.0112 |
| verus | -1.5086 | 0.2029 |

Table 4.49. Male *P. troglodytes* hands by subspecies plus *P. paniscus*: Discriminant function analysis (backward stepwise model)

A. Jackknifed classification matrix

| | Pp | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|---|
| Pp | 6 | 1 | 0 | 0 | 86 |
| schweinfurth | 1 | 6 | 7 | 4 | 33 |
| troglodytes | 2 | 8 | 47 | 6 | 75 |
| verus | 0 | 2 | 0 | 3 | 60 |
| Total | 9 | 17 | 54 | 13 | 67 |

Pp = *P. paniscus*
schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MCM | --- | --- | --- |
| MCDR | --- | --- | --- |
| MCHS | 0.1765 | 0.7676 | 0.0195 |
| MCB | -0.2737 | 0.6842 | 0.7074 |
| MCAH | --- | --- | --- |
| HPMD | -0.3495 | 0.7563 | -0.5499 |
| HPBD | 0.2863 | -1.1044 | 0.7229 |
| HPFS | 0.6711 | 0.3374 | -0.6545 |
| HPTW | -0.7153 | 0.7325 | 0.0046 |
| HPGT | --- | --- | --- |
| HPAH | --- | --- | --- |
| XPMC | 0.6220 | 0.2513 | 0.3090 |
| XHPL | --- | --- | --- |
| | | | |
| Canonical correlations | 0.6902 | 0.4924 | 0.1572 |
| Cumulative % of total dispersion | 72.48 | 97.98 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Pp | -2.7605 | -1.0380 | -0.0182 |
| schweinfurth | -0.4213 | 0.7401 | -0.2297 |
| troglodytes | 0.5225 | -0.2000 | 0.0279 |
| verus | -1.2020 | 1.3084 | 0.5011 |

Table 4.50. Female *P. troglodytes* hands by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Pp | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|---|
| Pp | 11 | 1 | 0 | 0 | 92 |
| schweinfurth | 0 | 4 | 3 | 2 | 44 |
| troglodytes | 2 | 17 | 51 | 11 | 63 |
| verus | 2 | 2 | 0 | 6 | 60 |
| Total | 15 | 24 | 54 | 19 | 64 |

Pp = *P. paniscus*
schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MCM | --- | --- | --- |
| MCDR | --- | --- | --- |
| MCHS | --- | --- | --- |
| MCB | --- | --- | --- |
| MCAH | --- | --- | --- |
| HPMD | 0.3804 | 0.6062 | 0.1855 |
| HPBD | --- | --- | --- |
| HPFS | -0.3255 | -0.6557 | -0.3787 |
| HPTW | --- | --- | --- |
| HPGT | -0.4352 | 0.5768 | -0.6816 |
| HPAH | --- | --- | --- |
| XPMC | -0.7958 | 0.1630 | 0.6212 |
| XHPL | --- | --- | --- |
| | | | |
| Canonical correlations | 0.6852 | 0.3253 | 0.1926 |
| Cumulative % of total dispersion | 84.94 | 96.30 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Pp | 2.4682 | -0.3630 | -0.0388 |
| schweinfurth | 0.2746 | 0.3620 | 0.6158 |
| troglodytes | -0.4719 | -0.1045 | -0.0312 |
| verus | 0.6134 | 0.9559 | -0.2552 |

Table 4.51. Male *P. troglodytes* feet by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Pp | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|---|
| Pp | 4 | 1 | 2 | 1 | 50 |
| schweinfurth | 1 | 7 | 7 | 1 | 44 |
| troglodytes | 5 | 19 | 36 | 2 | 58 |
| verus | 0 | 1 | 0 | 5 | 83 |
| Total | 10 | 28 | 45 | 9 | 57 |

Pp = *P. paniscus*
schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MTB | 0.4143 | 0.0875 | 0.2922 |
| MTAH | -0.2247 | 0.7647 | 0.0828 |
| FPFS | 0.7217 | 0.4873 | -0.1832 |
| FPAH | -0.0356 | -0.6937 | -0.3737 |
| CCTW | 0.0984 | -0.0787 | 0.7925 |
| CCFS | -0.3073 | -0.4370 | 0.4020 |
| CCFD | --- | --- | --- |
| XPMT | -0.6296 | 0.3745 | -0.1954 |
| XCMT | 0.4659 | -0.3626 | -0.1712 |
| | | | |
| Canonical correlations | 0.7160 | 0.5775 | 0.3686 |
| Cumulative % of total dispersion | 61.54 | 90.80 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Pp | 2.3502 | -1.5183 | 0.1711 |
| schweinfurth | 0.1533 | 0.1268 | -0.8401 |
| troglodytes | -0.5552 | -0.0353 | 0.1622 |
| verus | 2.1950 | 2.0515 | 0.3362 |

Table 4.52. Female *P. troglodytes* feet by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models)

A. Jackknifed classification matrix

| | Pp | schweinfu | troglodyt | verus | %correct |
|---|---|---|---|---|---|
| Pp | 8 | 1 | 1 | 1 | 73 |
| schweinfurth | 1 | 2 | 3 | 2 | 25 |
| troglodytes | 8 | 9 | 52 | 12 | 64 |
| verus | 0 | 1 | 2 | 4 | 57 |
| Total | 17 | 13 | 58 | 19 | 62 |

Pp = *P. paniscus*
schweinfurth = *P. t. schweinfurthii*
troglodytes = *P. t. troglodytes*
verus = *P. t. verus*

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| MTB | --- | --- | --- |
| MTAH | 0.4144 | 0.7737 | 0.3856 |
| FPFS | --- | --- | --- |
| FPAH | 0.0244 | -0.7955 | 0.4423 |
| CCTW | --- | --- | --- |
| CCFS | --- | --- | --- |
| CCFD | --- | --- | --- |
| XPMT | 0.8548 | -0.2923 | -0.4424 |
| XCMT | -0.4703 | 0.0842 | -0.6038 |
| | | | |
| Canonical correlations | 0.5946 | 0.3726 | 0.1455 |
| Cumulative % of total dispersion | 74.94 | 97.04 | 100.00 |

[1] Wilks' lambda p = 0.0000

C. Canonical scores of group means

| | 1 | 2 | 3 |
|---|---|---|---|
| Pp | -1.8410 | -0.5362 | 0.0951 |
| schweinfurth | -0.6016 | 0.2579 | -0.4841 |
| troglodytes | 0.3788 | -0.0683 | 0.0195 |
| verus | -0.8031 | 1.3379 | 0.1781 |

Table 4.53. Male *Pan* hands by population: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 7 | 4 | 4 | 47 |
| Coast | 4 | 6 | 6 | 38 |
| Ebolowa | 5 | 4 | 11 | 55 |
| Total | 16 | 14 | 21 | 47 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | 0.1150 | 0.9455 |
| MCHS | --- | --- |
| MCB | --- | --- |
| MCAH | --- | --- |
| HPMD | --- | --- |
| HPBD | 1.1413 | 0.0810 |
| HPFS | -0.8030 | 0.3165 |
| HPTW | --- | --- |
| HPGT | --- | --- |
| HPAH | --- | --- |
| XPMC | --- | --- |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.4307 | 0.3199 |
| Cumulative % of total dispersion | 66.64 | 100.00 |

[1] Wilks' lambda p = 0.0226

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | 0.4864 | -0.3729 |
| Coast | 0.2501 | 0.4510 |
| Ebolowa | -0.5649 | -0.0811 |

Table 4.54. Female *Pan* hands by population: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 23 | 11 | 8 | 55 |
| Coast | 5 | 3 | 6 | 21 |
| Ebolowa | 3 | 4 | 9 | 56 |
| Total | 31 | 18 | 23 | 49 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MCM | --- | --- |
| MCDR | --- | --- |
| MCHS | 0.5957 | 0.8413 |
| MCB | --- | --- |
| MCAH | --- | --- |
| HPMD | --- | --- |
| HPBD | 1.1941 | -0.5185 |
| HPFS | -0.7215 | 0.2660 |
| HPTW | --- | --- |
| HPGT | --- | --- |
| HPAH | --- | --- |
| XPMC | --- | --- |
| XHPL | --- | --- |
| | | |
| Canonical correlations | 0.4561 | 0.2149 |
| Cumulative % of total dispersion | 84.44 | 100.00 |

[1] Wilks' lambda p = 0.0040

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | 0.3928 | 0.0686 |
| Coast | -0.2366 | -0.4265 |
| Ebolowa | -0.8241 | 0.1930 |

Table 4.55. Male *Pan* feet by population: Discriminant function analysis (forward/backward stepwise model)

A. Jackknifed classification matrix

| | Cam Int | Coast | Ebolowa | %correct |
|---|---|---|---|---|
| Cam Int | 9 | 1 | 5 | 60 |
| Coast | 5 | 8 | 4 | 47 |
| Ebolowa | 5 | 8 | 8 | 38 |
| Total | 19 | 17 | 17 | 47 |

Cam Int = Cameroon Interior

B. Canonical discriminant functions[1], standardized by pooled within-group variances

| | Function 1 | Function 2 |
|---|---|---|
| MTB | --- | --- |
| MTAH | --- | --- |
| FPFS | --- | --- |
| FPAH | 0.7621 | 0.6783 |
| CCTW | --- | --- |
| CCFS | --- | --- |
| CCFD | 0.8159 | -0.6125 |
| XPMT | --- | --- |
| XCMT | --- | --- |
| | | |
| Canonical correlations | 0.4394 | 0.1563 |
| Cumulative % of total dispersion | 90.53 | 100.00 |

[1] Wilks' lambda p = 0.0186

C. Canonical scores of group means

| | 1 | 2 |
|---|---|---|
| Cam Int | -0.7547 | -0.0151 |
| Coast | 0.3363 | -0.1954 |
| Ebolowa | 0.2668 | 0.1689 |

Table 4.56. Subspecies-level ANOVAs of body size proxies[1] in *Gorilla* and *Pan*: Summary of significant pairwise differences based on Bonferroni post-hoc tests

| | Males | Females |
|---|---|---|
| *Gorilla* subspecies[2] | Ggg>Gbb<br>Ggg>Gbg | Ggg>Gbg |
| *P. paniscus* vs. *P. troglodytes* subspecies[3] | Pts>Pp<br>Ptt>Pp<br>Ptv>Pp | Ptt>Pp |
| *P. troglodytes* subspecies[4] | none | none |

[1] The body size proxy is a geometric mean based on the set of "all variables", as defined for the principal components analyses in Chapter 3. This set of variables includes measurements from the humerus, radius, third metacarpal, third proximal hand phalanx, femur, tibia, first metatarsal, third metatarsal, third proximal foot phalanx, and calcaneus.
[2] *G. gorilla gorilla* (Ggg), *G. beringei beringei* (Gbb), and *G. b. graueri* (Gbg)
[3] *P. paniscus* (Pp), *P. troglodytes troglodytes* (Ptt), *P. t. schweinfurthii* (Pts), and *P. t. verus* (Ptv)
[4] *P. troglodytes troglodytes*, *P. t. schweinfurthii*, and *P. t. verus*

Table 4.57. Pearson correlation coefficients for associations between body size proxies[1] and canonical scores from subspecies-level DFAs of hand and foot ratios[2]

| | | | Function 1:<br>*G. gorilla* vs. *G. beringei* | Function 2:<br>*G. beringei* subspecies |
|---|---|---|---|---|
| *Gorilla* | M | Hands | **-0.3347**** | 0.0533 |
| | | Feet | **0.4223***** | 0.1196 |
| | F | Hands | 0.2515 | -0.0670 |
| | | Feet | **0.3698**** | 0.1384 |
| | | | | |
| | | | Function 1:<br>*P. troglodytes* subspecies<br>+ *P. paniscus* | Function 1:<br>*P. troglodytes* subspecies<br>only |
| *Pan* | M | Hands | **0.5230***** | **0.2654*** |
| | | Feet | **-0.4410***** | -0.2413 |
| | F | Hands | **-0.4280***** | -0.1897 |
| | | Feet | **0.3558**** | 0.0449 |

[1] The body size proxy is a geometric mean based on the set of "all variables", as defined for the principal components analyses in Chapter 3. This set of variables includes measurements from the humerus, radius, third metacarpal, third proximal hand phalanx, femur, tibia, first metatarsal, third metatarsal, third proximal foot phalanx, and calcaneus.
[2] Significant correlation coefficients are in bold.
* $p \leq 0.05$
** $p \leq 0.01$
*** $p \leq 0.001$

Table 4.58. Total rates (%) of correct classification for *Gorilla* DFAs (jackknifed matrices): hands and feet compared[1]

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | hands | feet | mean | hands | feet | mean |
| Species | **98** | 96 | 97 | 91 | **94** | 92.5 |
| Subspecies (2-way, *G. beringei*) | 84 | **95** | 89.5 | 92 | **100** | 96 |
| Subspecies (3-way, cross-species) | 93 | **94** | 93.5 | 86 | **97** | 91.5 |
| Population | **56** | 45 | 50.5 | **61** | 54 | 57.5 |

[1] Value for anatomical region with higher rate of correct classification for each level of analysis is in bold.

Table 4.59. Total rates (%) of correct classification for *Pan* DFAs (jackknifed matrices): hands and feet compared[1]

| | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | hands | feet | mean | hands | feet | mean |
| Species | **95** | 91 | 93 | **93** | 87 | 90 |
| Subspecies (3-way, *P. troglodytes*) | 65 | 65 | 65 | 61 | **66** | 63.5 |
| Subspecies + *P. paniscus* (4-way) | **67** | 57 | 62 | **64** | 62 | 63 |
| Population | 47 | 47 | 47 | **49** | NS[2] | 49 |

[1] Value for anatomical region with higher rate of correct classification for each level of analysis is in bold.
[2] NS = not significant

Table 4.60. Total rates (%) of correct classification for *Gorilla* DFAs (jackknifed matrices): males and females compared[1]

| | Hands | | | Feet | | |
|---|---|---|---|---|---|---|
| | M | F | mean | M | F | mean |
| Species | **98** | 91 | 94.5 | **96** | 94 | 95 |
| Subspecies (2-way, *G. beringei*) | 84 | **92** | 88 | 95 | **100** | 97.5 |
| Subspecies (3-way, cross-species) | **93** | 86 | 89.5 | 94 | **97** | 95.5 |
| Population | 56 | **61** | 58.5 | 45 | **54** | 49.5 |

[1] Value for sex with higher rate of correct classification for each level of analysis is in bold.

Table 4.61. Total rates (%) of correct classification for *Pan* DFAs (jackknifed matrices): males and females compared[1]

| | Hands | | | Feet | | |
|---|---|---|---|---|---|---|
| | M | F | mean | M | F | mean |
| Species | **95** | 93 | 94 | **91** | 87 | 89 |
| Subspecies (3-way, *P. troglodytes*) | **65** | 61 | 63 | 65 | **66** | 65.5 |
| Subspecies + *P. paniscus* (4-way) | **67** | 64 | 65.5 | 57 | **62** | 59.5 |
| Population | 47 | **49** | 48 | **47** | NA | 47 |

[1] Value for sex with higher rate of correct classification for each level of analysis is in bold.

Table 4.62. Total rates (%) of correct classification for DFAs of *Gorilla* and *Pan* males (jackknifed matrices): comparison of within-genus patterns using pairwise analyses of *P. troglodytes* subspecies[1]

| | *Gorilla* | | *Pan* | | |
|---|---|---|---|---|---|
| | hands | feet | hands | feet | |
| species | 98 | 96 | 95 | 91 | species |
| subspecies[2] | 84 | 95 | 78 | 91 | Pts vs. Ptv |
| | | | 87 | 94 | Ptt vs. Ptv |
| | | | 77 | 65 | Pts vs. Ptt |
| population | 56 | 45 | 47 | 47 | population |

[1] Pts = *P. t. schweinfurthii*, Ptv = *P. t. verus*, Ptt = *P. t. troglodytes*
[2] *G. beringei beringei* and *G. b. graueri*

Table 4.63. Total rates (%) of correct classification for DFAs of *Gorilla* and *Pan* females (jackknifed matrices): comparison of within-genus patterns using pairwise analyses of *P. troglodytes* subspecies[1]

| | *Gorilla* | | *Pan* | | |
|---|---|---|---|---|---|
| | hands | feet | hands | feet | |
| species | 91 | 94 | 93 | 87 | species |
| subspecies[2] | 92 | 100 | 84 | 87 | Pts vs. Ptv |
| | | | 82 | 82 | Ptt vs. Ptv |
| | | | 67 | 64 | Pts vs. Ptt |
| population | 61 | 54 | 49 | not sig. | population |

[1] Pts = *P. t. schweinfurthii*, Ptv = *P. t. verus*, Ptt = *P. t. troglodytes*
[2] *G. beringei beringei* and *G. b. graueri*

Table 4.64. Hand variables that differentiate species in univariate and discriminant function analyses[1]

| **Variables**[2] | ***Gorilla*** | | | | ***Pan*** | | | |
|---|---|---|---|---|---|---|---|---|
| | **M** | | **F** | | **M** | | **F** | |
| | **uni** | **DFA** | **uni** | **DFA** | **uni** | **DFA** | **uni** | **DFA** |
| *Arboreal* | | | | | | | | |
| MCAH | | | | | | | | |
| **HPFS** | x | x | | | x | x | x | |
| HPAH | x | x | x | x | | | | |
| **XPMC** | x | x | x | x | x | x | x | x |
| | | | | | | | | |
| *Terrestrial* | | | | | | | | |
| MCM | | | | | | | | |
| MCDR | | | | | | | | |
| MCHS | | | | | | x | | |
| MCB | x | x | x | | | | | |
| HPMD | | x | | | | | | |
| **HPBD** | x | x | x | | | x | | |
| HPTW | | | | | | | | |
| **HPGT** | x | x | | | x | | x | x |
| XHPL | | x | | | | | | |

[1] For each univariate analysis (uni), variables that are significantly different between species are indicated. For each discriminant function analysis (DFA), variables that contribute most to discriminating species (i.e., have coefficients of 0.40 or greater) are indicated.

[2] Variables in bold differentiate species in at least one sex of each genus.

Table 4.65. Foot variables that differentiate species in univariate and discriminant function analyses[1]

| **Variables**[2] | ***Gorilla*** | | | | ***Pan*** | | | |
|---|---|---|---|---|---|---|---|---|
| | **M** | | **F** | | **M** | | **F** | |
| | **uni** | **DFA** | **uni** | **DFA** | **uni** | **DFA** | **uni** | **DFA** |
| *Arboreal* | | | | | | | | |
| **MTAH** | x | | x | x | | x | x | x |
| FPFS | x | x | x | x | | | | |
| **FPAH** | | x | | | | x | | |
| CCFS | | | | | | | | |
| CCFD | x | | x | | | | | |
| **XPMT** | x | | | | x | x | x | x |
| | | | | | | | | |
| *Terrestrial* | | | | | | | | |
| MTB | x | x | x | x | | | | |
| CCTW | | | | | | | | |
| **XCMT** | x | | x | x | x | x | | |

[1] For each univariate analysis (uni), variables that are significantly different between species are indicated. For each discriminant function analysis (DFA), variables that contribute most to discriminating species (i.e., have coefficients of 0.40 or greater) are indicated.

[2] Variables in bold differentiate species in at least one sex of each genus.

Table 4.66. Hand variables that differentiate subspecies (within-species analyses) in univariate and discriminant function analyses[1]

| **Variables**[2] | ***Gorilla*** (within *G. beringei*) | | | | ***Pan*** (within *P. troglodytes*) | | | |
|---|---|---|---|---|---|---|---|---|
| | **M** | | **F** | | **M** | | **F** | |
| | **uni** | **DFA** | **uni** | **DFA** | **uni** | **DFA**[3] | **uni** | **DFA**[3] |
| *Arboreal* | | | | | | | | |
| MCAH | | x | | | | | | |
| **HPFS** | | x | | | | | x | x |
| HPAH | | x | | | | | | |
| **XPMC** | x | | | x | | | | x |
| | | | | | | | | |
| *Terrestrial* | | | | | | | | |
| MCM | | | | | | x | | |
| MCDR | | | | | | | | |
| MCHS | x | x | | | | | | |
| **MCB** | x | x | | | | x | | |
| **HPMD** | | x | | | x | x | | x |
| HPBD | | | | | | x | | |
| HPTW | | | | | | x | | |
| HPGT | | | x | x | | | | |
| XHPL | | | | | | | | |

[1] For each univariate analysis (uni), variables that are significantly different between subspecies are indicated. For each discriminant function analysis (DFA), variables that contribute most to discriminating subspecies (i.e., have coefficients of 0.40 or greater) are indicated.

[2] Variables in bold differentiate subspecies in at least one sex of each genus.

[3] Variables listed include both those that contribute most to Function 1 and those that contribute most to Function 2.

Table 4.67. Foot variables that differentiate subspecies (within-species analyses) in univariate and discriminant function analyses[1]

| **Variables**[2] | ***Gorilla*** (within *G. beringei*) | | | | ***Pan*** (within *P. troglodytes*) | | | |
|---|---|---|---|---|---|---|---|---|
| | **M** | | **F** | | **M** | | **F** | |
| | **uni** | **DFA** | **uni** | **DFA**[3] | **uni** | **DFA**[4] | **uni** | **DFA**[4] |
| *Arboreal* | | | | | | | | |
| MTAH | | | | x | | | | |
| **FPFS** | x | x | x | x | x | x | | |
| **FPAH** | | | | x | | x | | x |
| **CCFS** | | | | x | x | x | | |
| CCFD | | x | | x | | | | |
| **XPMT** | | x | | | | | x | x |
| | | | | | | | | |
| *Terrestrial* | | | | | | | | |
| **MTB** | | x | x | | | x | | |
| **CCTW** | | x | x | x | | x | | |
| XCMT | | | | | | | | x |

[1] For each univariate analysis (uni), variables that are significantly different between subspecies are indicated. For each discriminant function analysis (DFA), variables that contribute most to discriminating subspecies (i.e., have coefficients of 0.40 or greater) are indicated.

[2] Variables in bold differentiate subspecies in at least one sex of each genus.

[3] Both forward and backward stepwise models result in 100% discrimination; variables listed include those that contribute most to each of the two models.

[4] Variables listed include both those that contribute most to Function 1 and those that contribute most to Function 2.

Table 4.68. Hand and foot variables that differentiate groups in both *Gorilla* and *Pan*, at species and subspecies levels, with type of variable indicated

| Variable[1] | Type of variable[2] | | | | |
|---|---|---|---|---|---|
| | length proportions (3) | midshaft diameters (2) | arch heights (4) | shapes of artic surfaces (6) | tendon/ligament attachments (7) |
| *Species/subspecies* | | | | | |
| HPFS | | | | | X |
| XPMC | X | | | | |
| FPAH | | | X | | |
| XPMT | X | | | | |
| *Species only* | | | | | |
| MTAH | | | X | | |
| HPBD | | | | X | |
| HPGT | | | | | X |
| XCMT | X | | | | |
| *Subspecies only* | | | | | |
| FPFS | | | | | X |
| CCFS | | | | X | |
| MCB | | | | | X |
| HPMD | | X | | | |
| MTB | | | | | X |
| CCTW | | | | | X |

[1] Includes only variables that are "differentiating variables" in at least one sex of *each genus* at the species level, at the subspecies level, or at both the species and subspecies levels. "Differentiating variables" are those that are either significantly different based on univariate analyses or among the variables that contribute most to discriminating groups in DFAs or both.

[2] Number in parentheses after each type of variable is the number of variables of this type included in the study.

Table 4.69. Hand variables and direction of variation[1]

| **Variables** | **Comparisons of means:** "Yes" if true in both sexes | |
|---|---|---|
| | ***Pan* > *Gorilla* ?** | ***G. g. gorilla* > *G. b. beringei* ?** |
| *Arboreal* | | |
| MCAH | No | Yes |
| HPFS | Yes | No |
| HPAH | No | Yes |
| XPMC | Yes | No |
| | | |
| *Terrestrial* | | |
| MCM | No | No |
| MCDR | No | Yes |
| MCHS | No | No |
| **MCB** | **Yes** | **Yes** |
| HPMD | Yes | No |
| **HPBD** | **Yes** | **Yes** |
| HPTW | Yes | No |
| HPGT | Yes | No |
| XHPL | No | No |

[1] Entire row is in bold text if entry is "Yes" in both columns of Comparisons of Means.

Table 4.70. Foot variables and direction of variation[1]

| **Variables** | **Comparisons of means:** "Yes" if true in both sexes | |
|---|---|---|
| | ***Pan* > *Gorilla* ?** | ***G. g. gorilla* > *G. b. beringei* ?** |
| *Arboreal* | | |
| MTAH | Yes | No |
| FPFS | No | No |
| FPAH | No | Yes |
| CCFS | No | No |
| **CCFD** | **Yes** | **Yes** |
| XPMT | Yes | No |
| | | |
| *Terrestrial* | | |
| MTB | No | Yes |
| **CCTW** | **Yes** | **Yes** |
| XCMT | No | No |

[1] Entire row is in bold text if entry is "Yes" in both columns of Comparisons of Means.

Figure 4.1. Male *Gorilla* and *Pan* hands by species: Discriminant function analysis (complete model). The confidence ellipses for the samples are set at 68.27%.

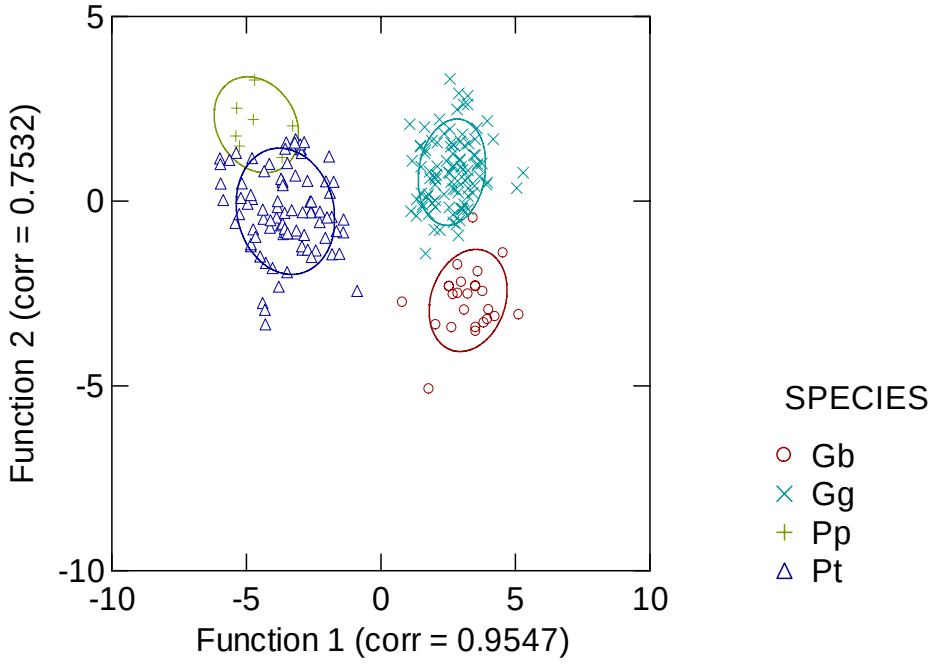


Figure 4.2. Female *Gorilla* and *Pan* hands by species: Discriminant function analysis (complete model). The confidence ellipses for the samples are set at 68.27%.

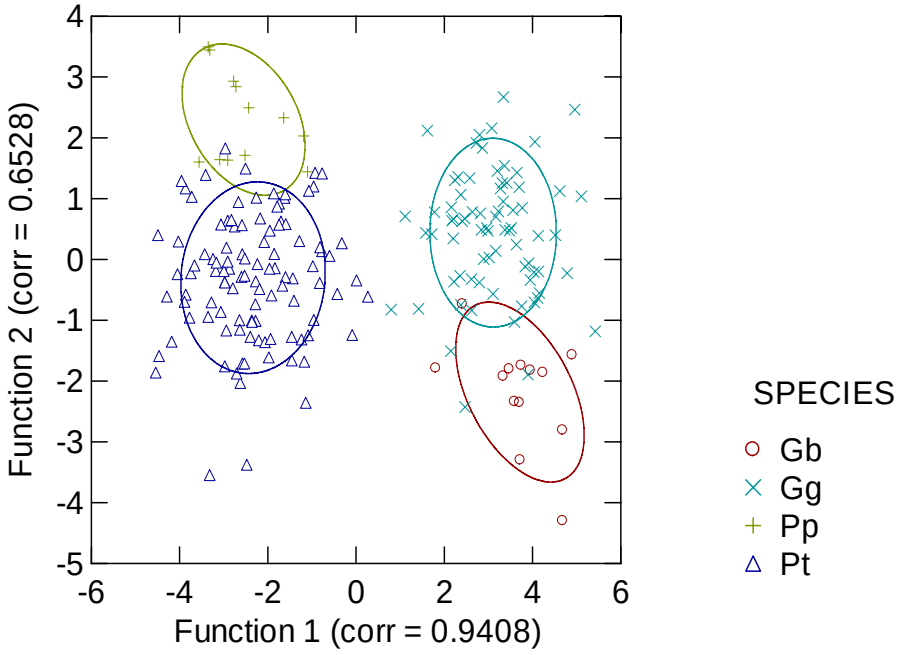


Figure 4.3. Male *Gorilla* and *Pan* feet by species: Discriminant function analysis (forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

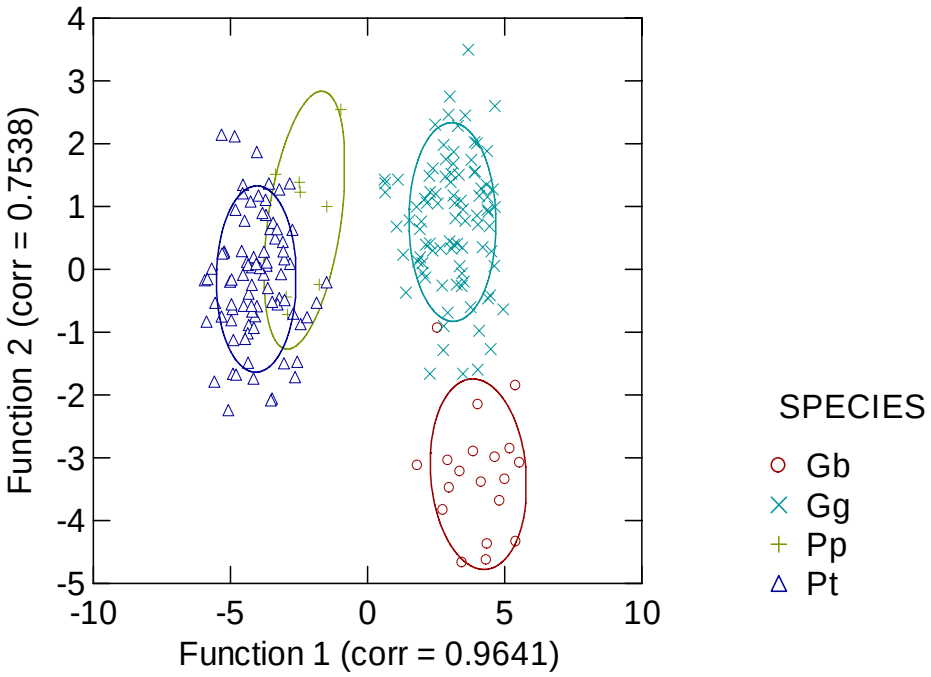


Figure 4.4. Female *Gorilla* and *Pan* feet by species: Discriminant function analysis (complete and forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

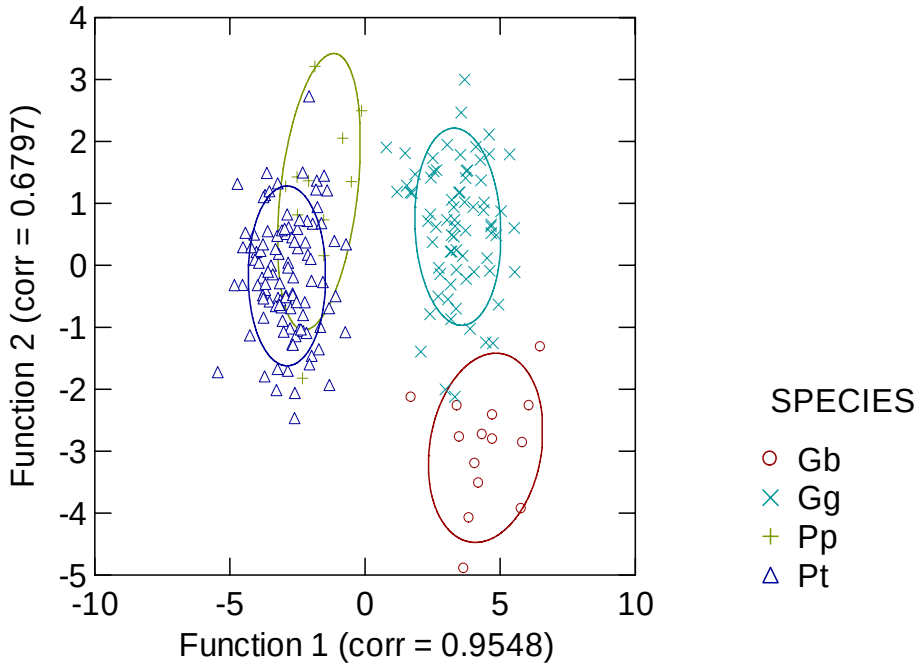


Figure 4.5. Male *Gorilla* hands by subspecies: Discriminant function analysis (forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

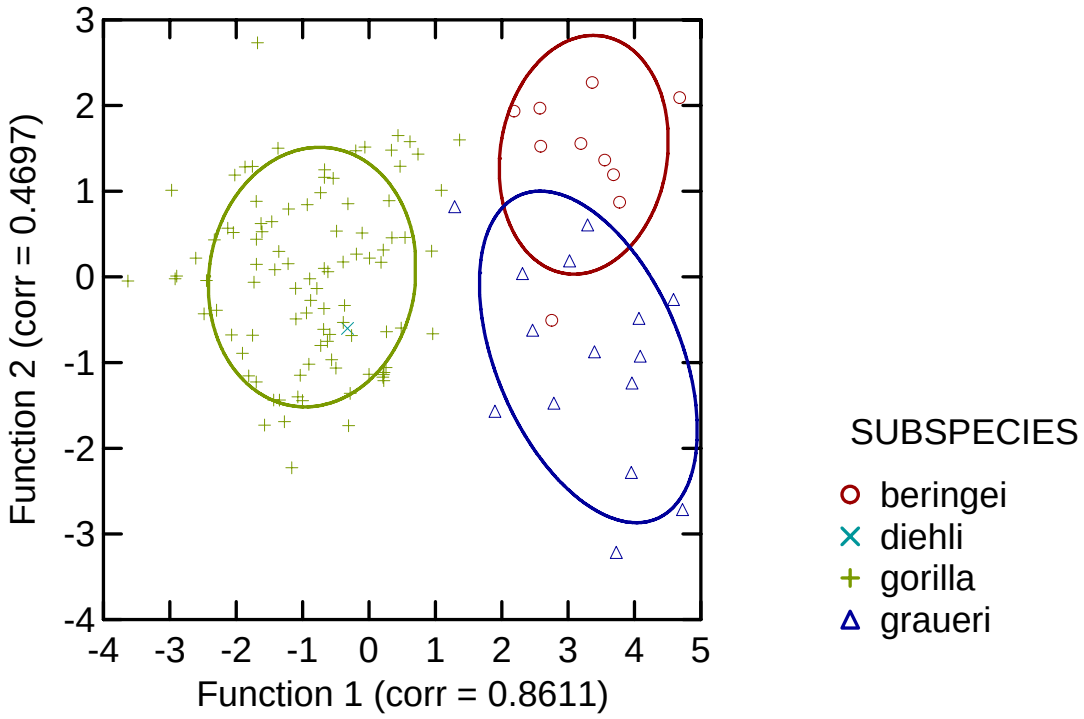


Figure 4.6. Female *Gorilla* hands by subspecies: Discriminant function analysis (forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

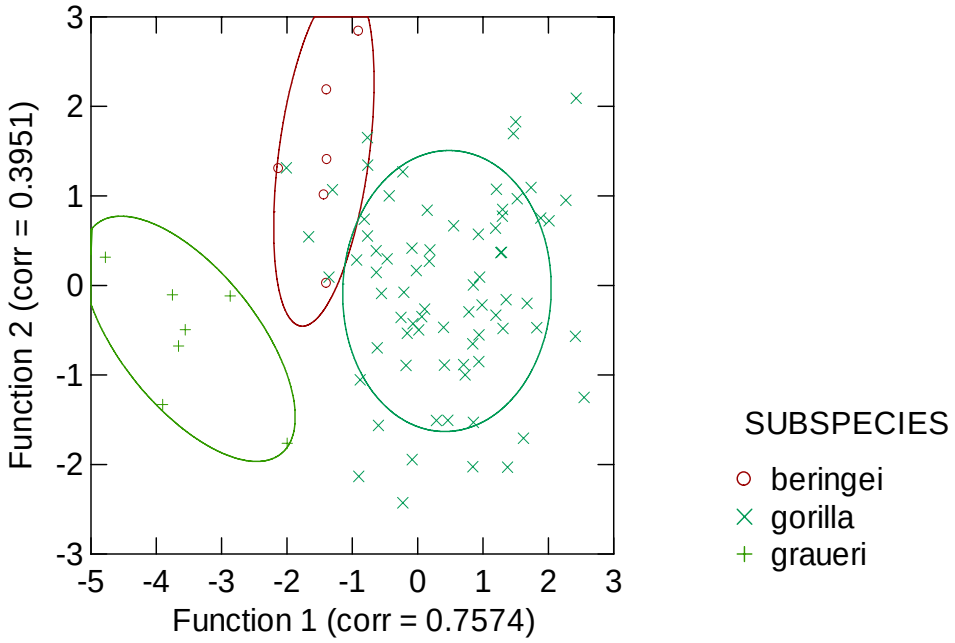


Figure 4.7. Male *Gorilla* feet by subspecies: Discriminant function analysis (forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

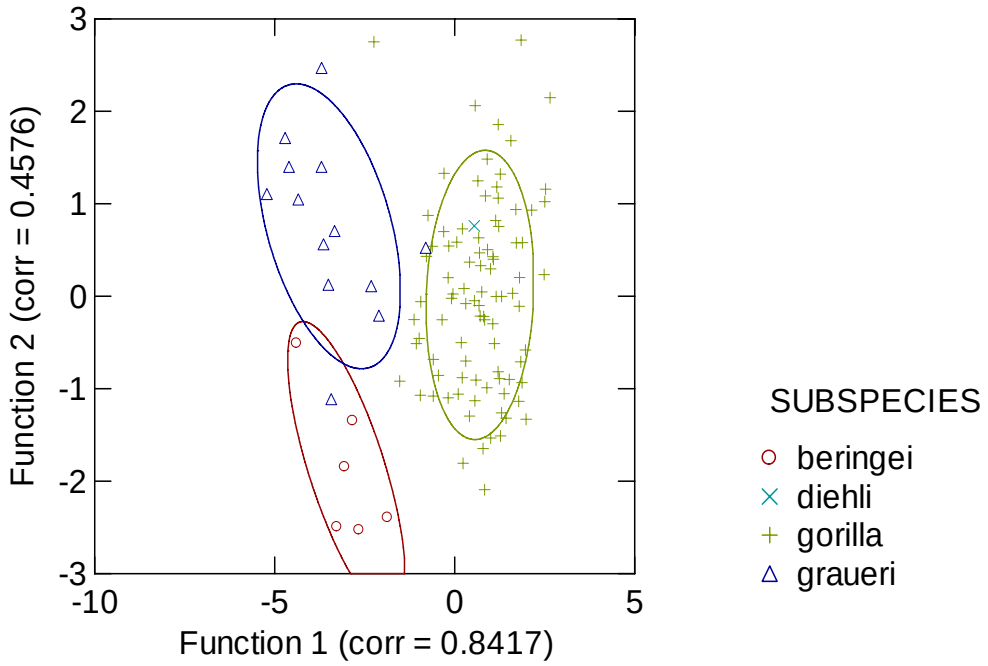


Figure 4.8. Female *Gorilla* feet by subspecies: Discriminant function analysis (forward/backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

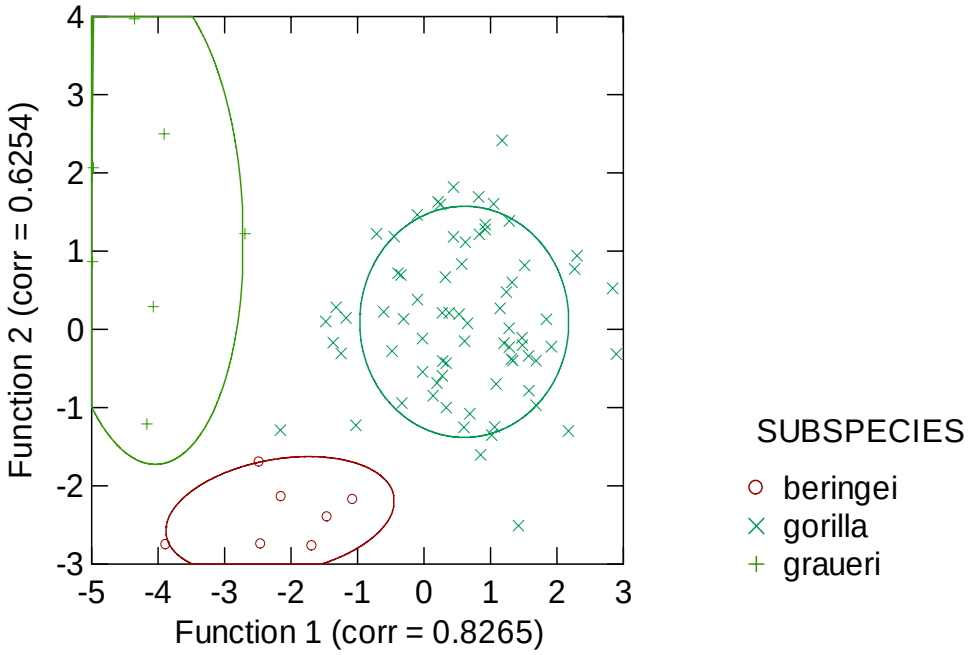
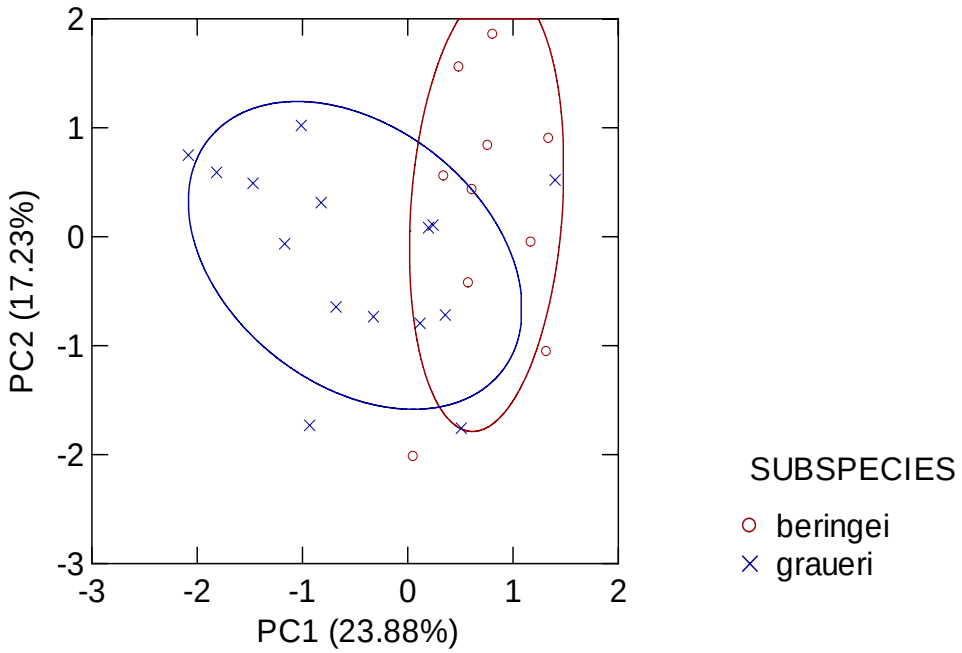


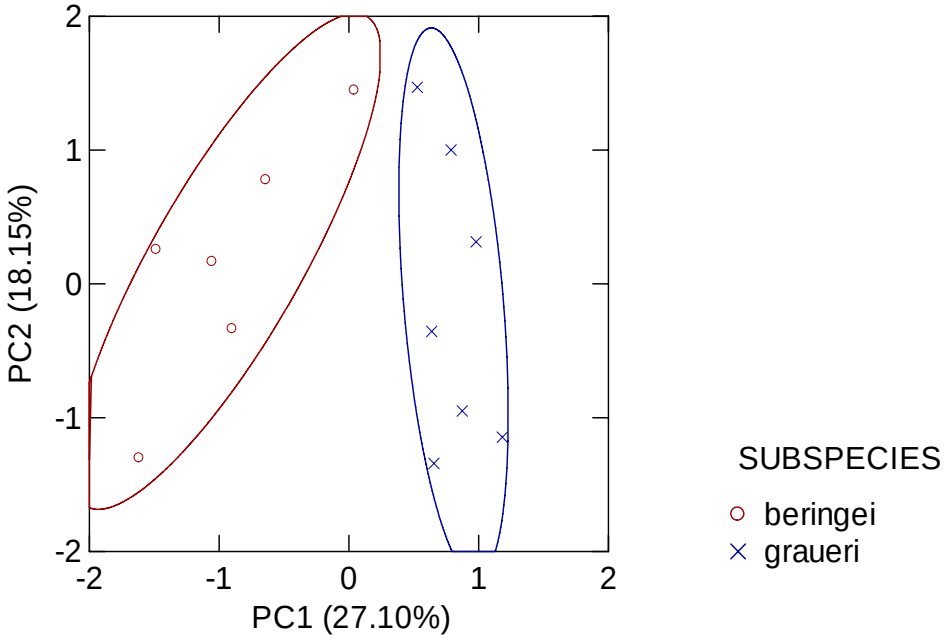
Figure 4.9. Male *G. beringei* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component Loadings

| | 1 | 2 |
|---|---|---|
| XPMC | -0.7965 | 0.1013 |
| MCB | -0.7624 | -0.1162 |
| HPMD | 0.6974 | -0.2538 |
| MCHS | 0.6815 | 0.1014 |
| HPTW | 0.6160 | 0.5459 |
| HPBD | 0.3159 | 0.7042 |
| HPFS | -0.4397 | 0.6055 |
| MCAH | -0.3798 | 0.5942 |
| HPAH | -0.0702 | 0.5704 |
| XHPL | 0.1272 | 0.5103 |
| MCDR | 0.1184 | 0.1116 |
| MCM | 0.2444 | -0.1080 |
| HPGT | 0.1611 | 0.1335 |

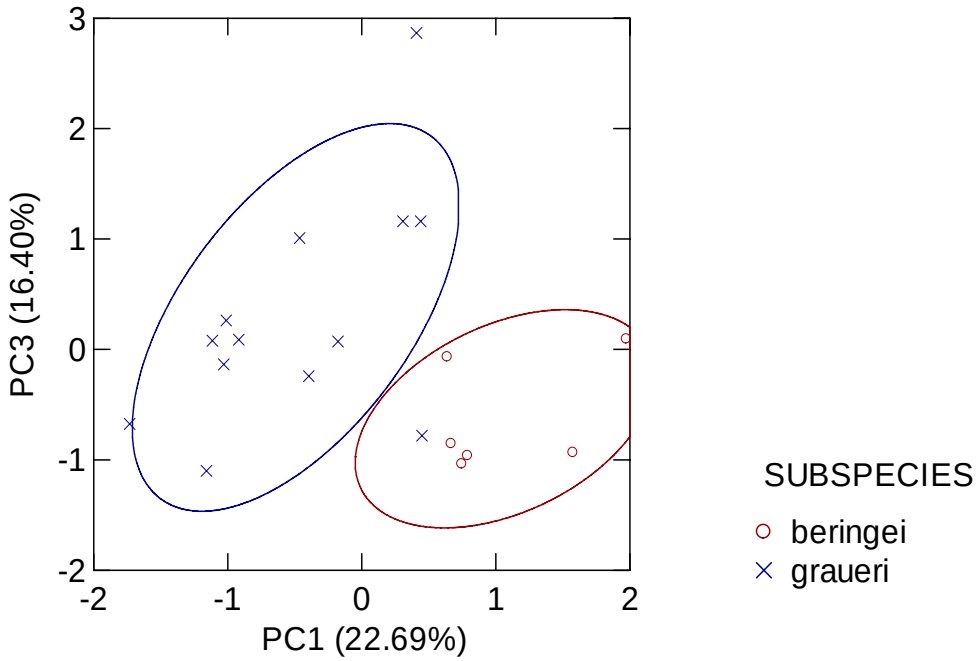
Figure 4.10. Female *G. beringei* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component Loadings

| | 1 | 2 |
|---|---|---|
| HPGT | -0.8590 | 0.1401 |
| HPFS | 0.7609 | 0.2560 |
| XPMC | 0.6935 | 0.1845 |
| HPMD | -0.6064 | -0.3328 |
| HPTW | 0.5734 | 0.0817 |
| XHPL | 0.5166 | -0.3664 |
| MCHS | -0.4763 | 0.8106 |
| MCB | 0.2109 | -0.8059 |
| MCAH | 0.3490 | 0.5762 |
| HPBD | 0.1378 | -0.0760 |
| MCM | -0.1453 | -0.3299 |
| MCDR | 0.2392 | 0.2329 |

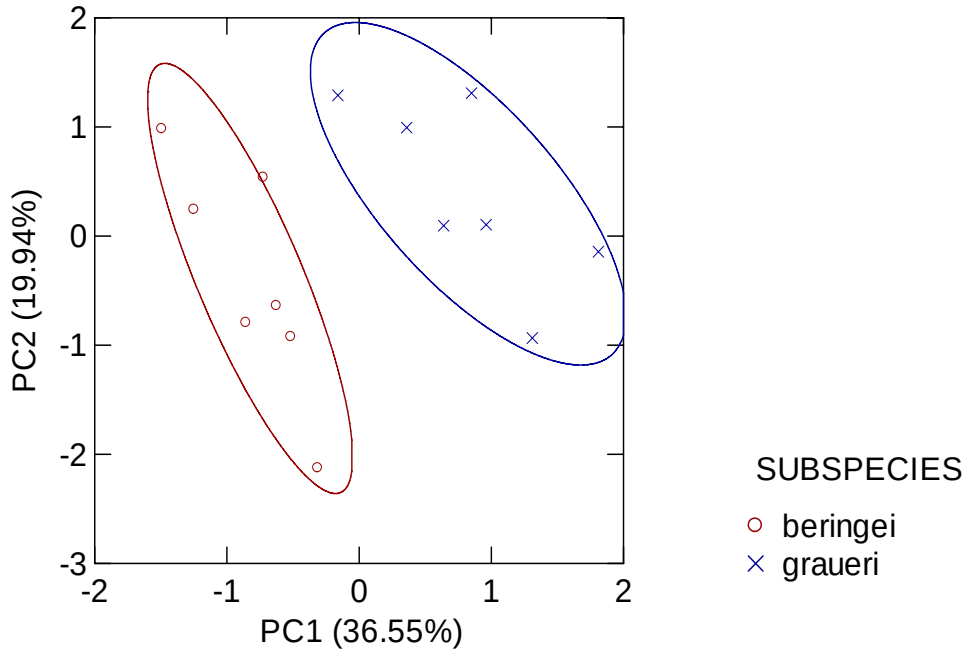
Figure 4.11. Male *G. beringei* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component Loadings

| | 1 | 3 |
|---|---|---|
| FPAH | 0.7479 | 0.3509 |
| CCTW | -0.6766 | 0.4843 |
| MTB | -0.5637 | 0.1355 |
| XPMT | 0.5539 | 0.5175 |
| MTAH | 0.4793 | -0.0945 |
| CCFS | 0.2534 | -0.0800 |
| FPFS | -0.1323 | 0.5896 |
| CCFD | -0.2098 | 0.4904 |
| XCMT | 0.2124 | 0.4781 |

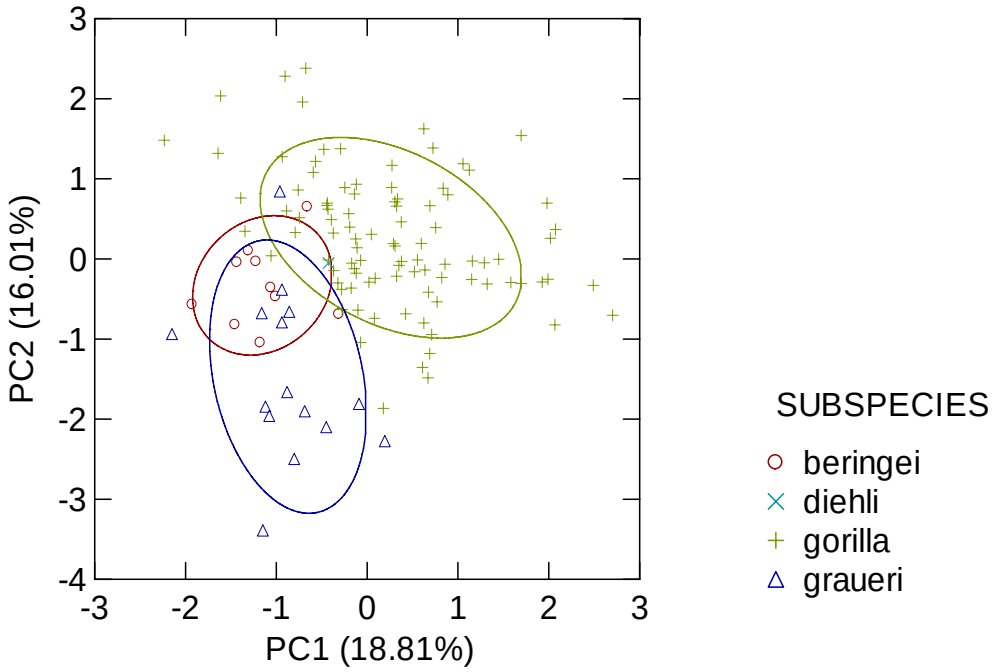
Figure 4.12. Female *G. beringei* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component Loadings

| | 1 | 2 |
|---|---|---|
| MTB | 0.8709 | 0.1167 |
| FPFS | 0.8198 | 0.4884 |
| CCFS | -0.7199 | -0.0576 |
| CCFD | 0.6884 | -0.3220 |
| MTAH | -0.5347 | 0.7073 |
| CCTW | 0.4736 | 0.6842 |
| XPMT | 0.0256 | 0.4439 |
| FPAH | -0.4433 | 0.1973 |
| XCMT | 0.3988 | -0.4805 |

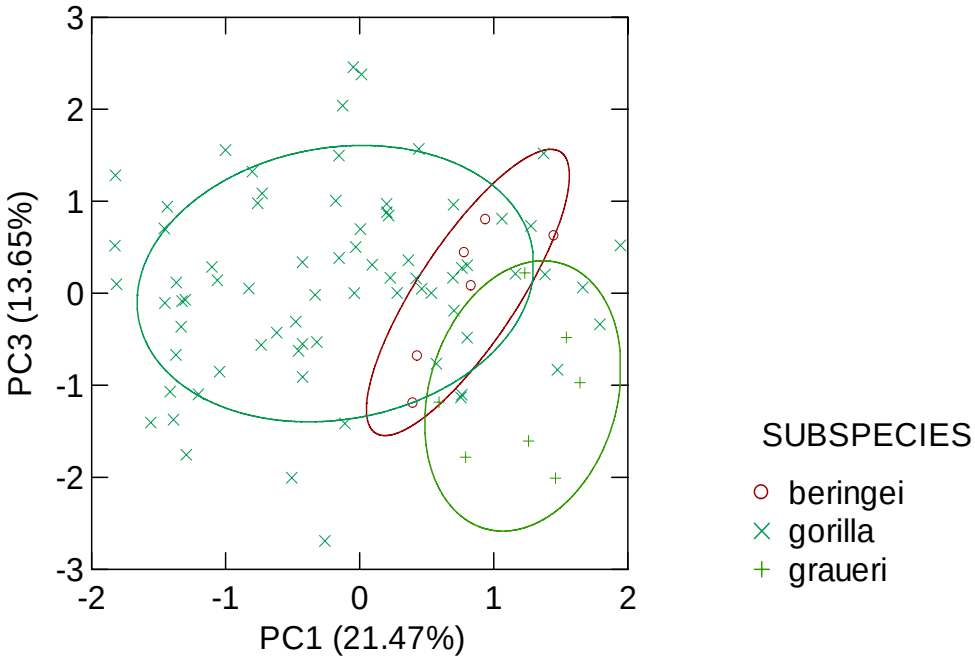
Figure 4.13. Male *Gorilla* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component Loadings

| | 1 | 2 |
|---|---|---|
| HPAH | 0.8013 | -0.0053 |
| HPMD | -0.6273 | 0.5196 |
| HPTW | -0.6105 | 0.2340 |
| MCB | 0.5281 | -0.1174 |
| XPMC | -0.2497 | -0.6599 |
| HPBD | -0.2693 | 0.5518 |
| MCDR | 0.4087 | 0.0912 |
| XHPL | -0.2410 | -0.0935 |
| MCAH | 0.1328 | -0.4718 |
| HPFS | -0.3600 | -0.4854 |
| MCHS | 0.3108 | 0.4741 |
| HPGT | 0.3713 | 0.4139 |
| MCM | 0.1266 | 0.3630 |

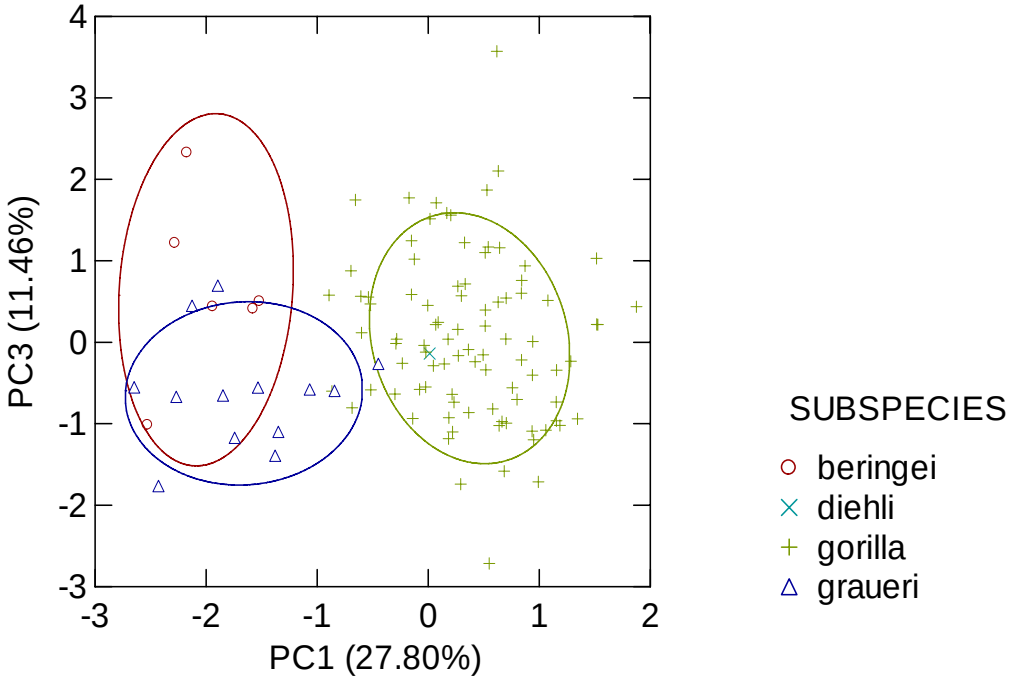
Figure 4.14. Female *Gorilla* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 3 |
|---|---|---|
| HPAH | -0.7383 | 0.0480 |
| HPTW | 0.7219 | 0.0795 |
| HPFS | 0.6567 | -0.0715 |
| MCB | -0.5823 | -0.2968 |
| MCDR | -0.5249 | 0.3406 |
| XPMC | 0.5058 | -0.1394 |
| HPBD | 0.4066 | 0.1098 |
| MCAH | -0.1868 | -0.3844 |
| XHPL | 0.0294 | -0.7704 |
| MCHS | -0.1150 | 0.7482 |
| HPMD | 0.3640 | -0.0908 |
| MCM | 0.2432 | 0.3613 |
| HPGT | 0.1336 | 0.2911 |

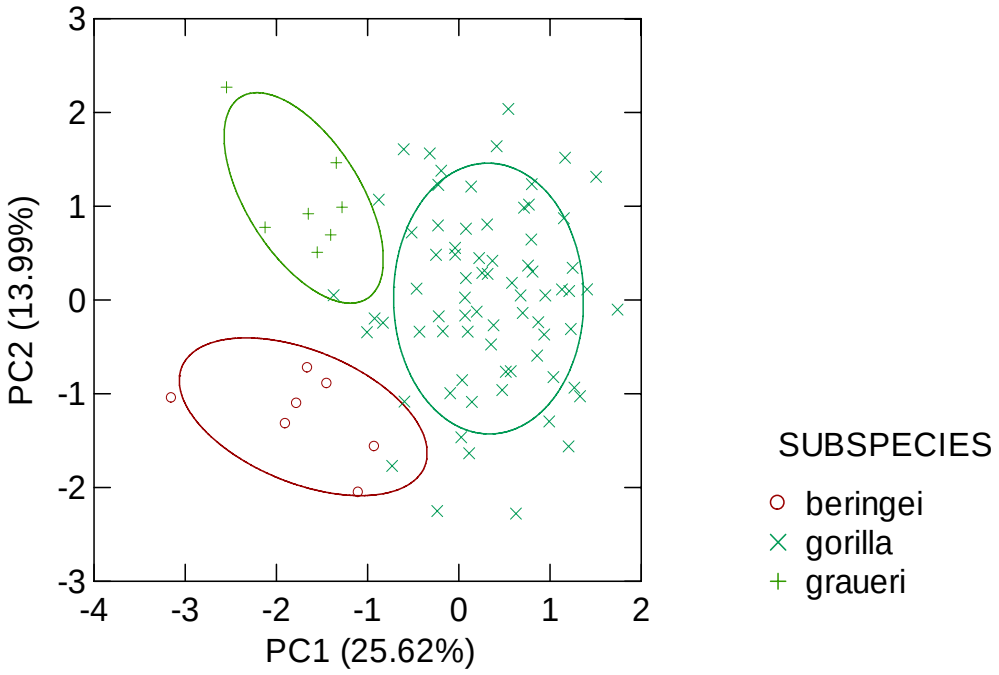
Figure 4.15. Male *Gorilla* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 3 |
|---|---|---|
| XCMT | -0.7283 | 0.0576 |
| FPFS | -0.7104 | -0.0982 |
| MTB | 0.6856 | -0.0871 |
| MTAH | -0.6567 | -0.0766 |
| XPMT | -0.5215 | 0.1440 |
| FPAH | 0.1281 | 0.2554 |
| CCFD | 0.3624 | 0.1719 |
| CCTW | 0.2904 | -0.6863 |
| CCFS | 0.2489 | 0.6469 |

Figure 4.16. Female *Gorilla* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 2 |
|---|---|---|
| XCMT | -0.7240 | -0.0215 |
| MTAH | -0.6766 | 0.2317 |
| FPFS | -0.5431 | 0.3563 |
| CCTW | 0.5131 | 0.5722 |
| XPMT | -0.5007 | 0.4471 |
| CCFD | 0.3561 | 0.5275 |
| CCFS | 0.0194 | -0.0608 |
| MTB | 0.4038 | 0.4646 |
| FPAH | 0.4742 | -0.2304 |

Figure 4.17. Male *P. troglodytes* hands by subspecies: Discriminant function analysis (backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

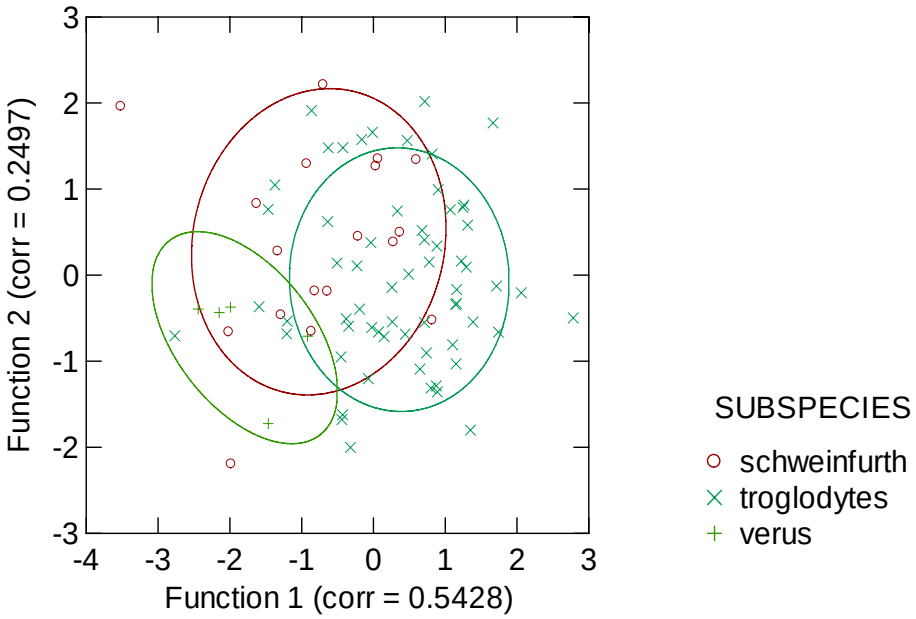


Figure 4.18. Female *P. troglodytes* hands by subspecies: Discriminant function analysis (forward stepwise model). The confidence ellipses for the samples are set at 68.27%.

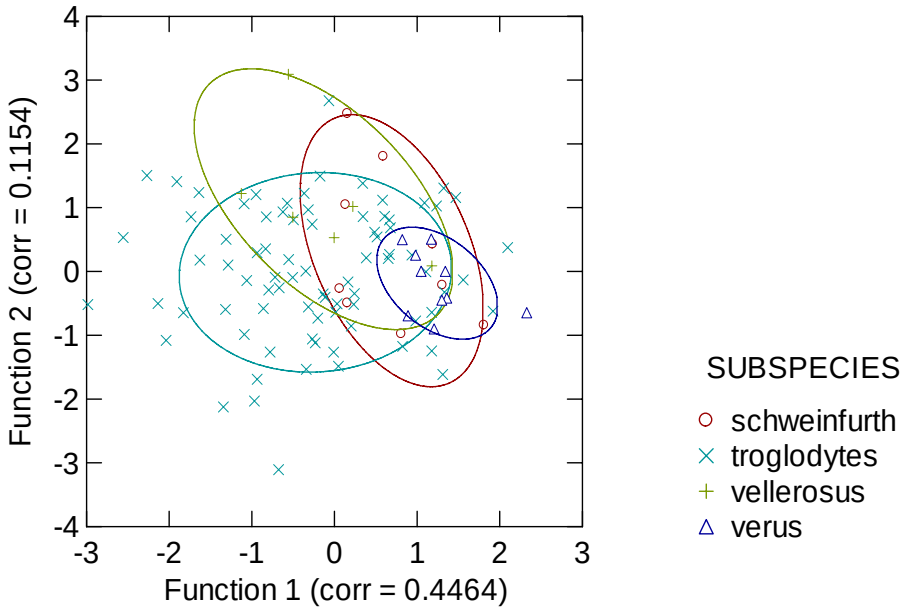


Figure 4.19. Male *P. troglodytes* feet by subspecies: Discriminant function analysis (forward/backward stepwise models). The confidence ellipses for the samples are set at 68.27%.

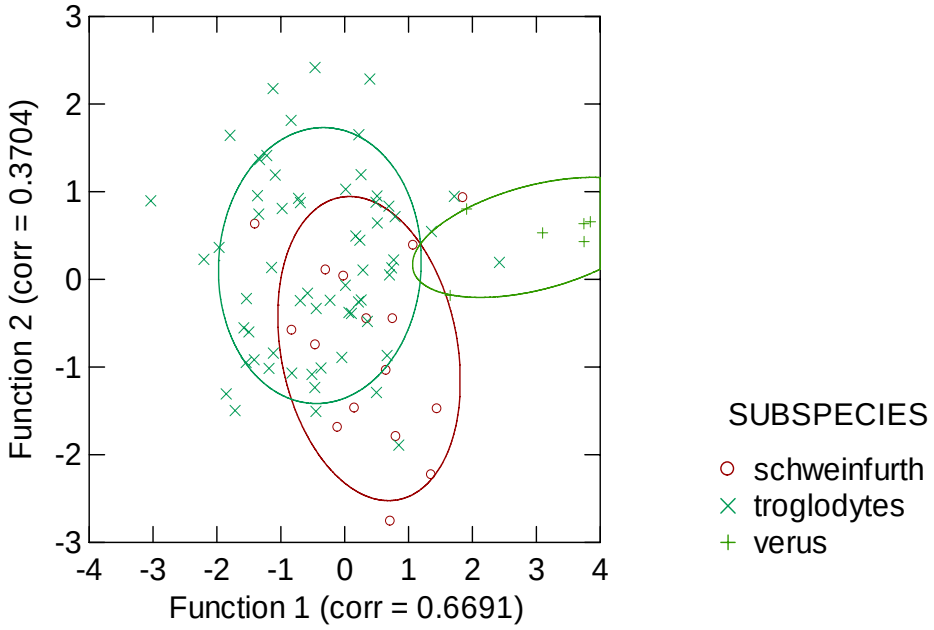


Figure 4.20. Female *P. troglodytes* feet by subspecies: Discriminant function analysis (forward/backward stepwise models). The confidence ellipses for the samples are set at 68.27%.

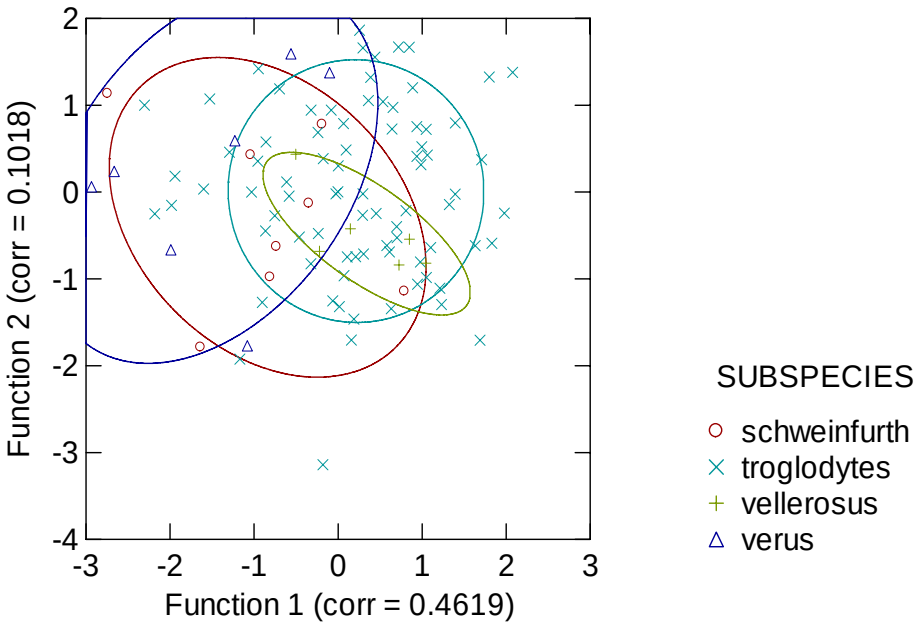


Figure 4.21. Male *P. troglodytes* hands by subspecies plus *P. paniscus*: Discriminant function analysis (backward stepwise model). The confidence ellipses for the samples are set at 68.27%.

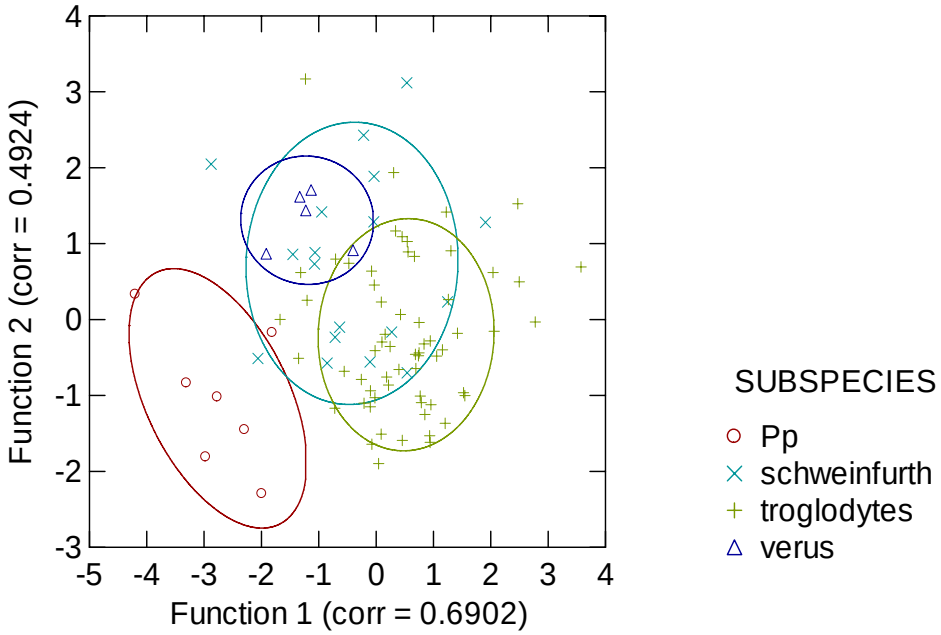


Figure 4.22. Female *P. troglodytes* hands by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models). The confidence ellipses for the samples are set at 68.27%.

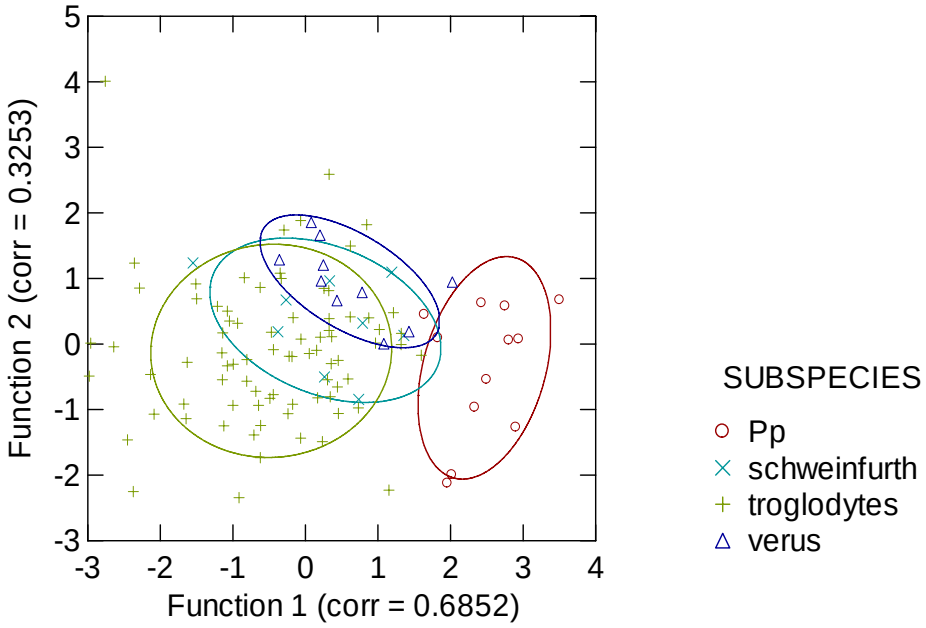


Figure 4.23. Male *P. troglodytes* feet by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models). The confidence ellipses for the samples are set at 68.27%.

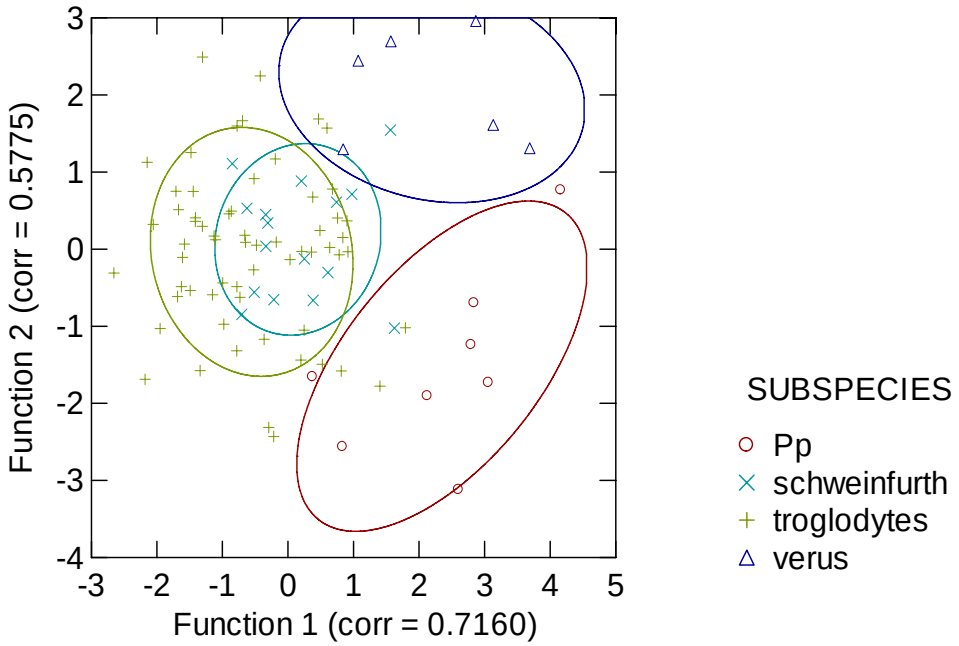


Figure 4.24. Female *P. troglodytes* feet by subspecies plus *P. paniscus*: Discriminant function analysis (forward/backward stepwise models). The confidence ellipses for the samples are set at 68.27%.

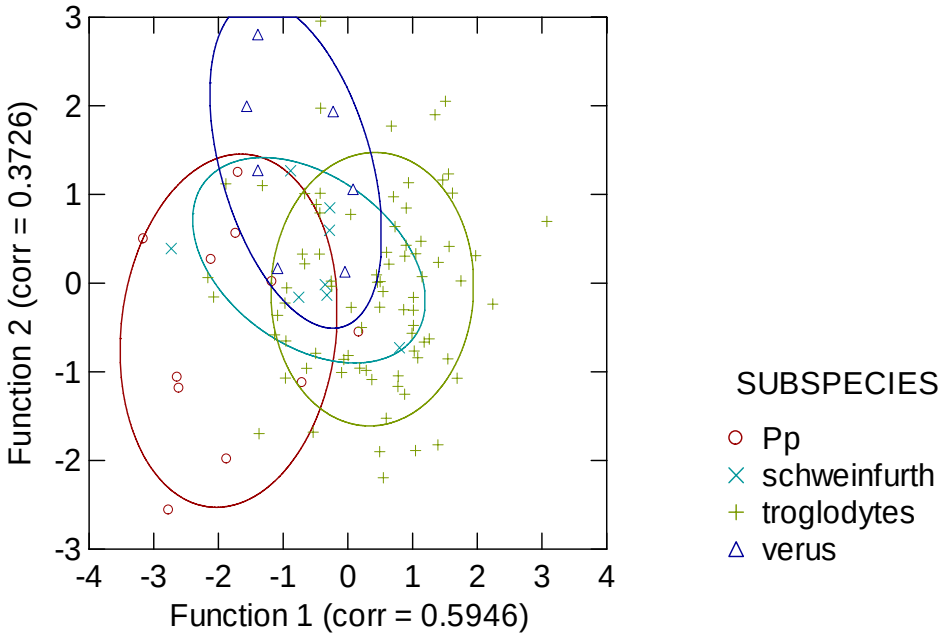
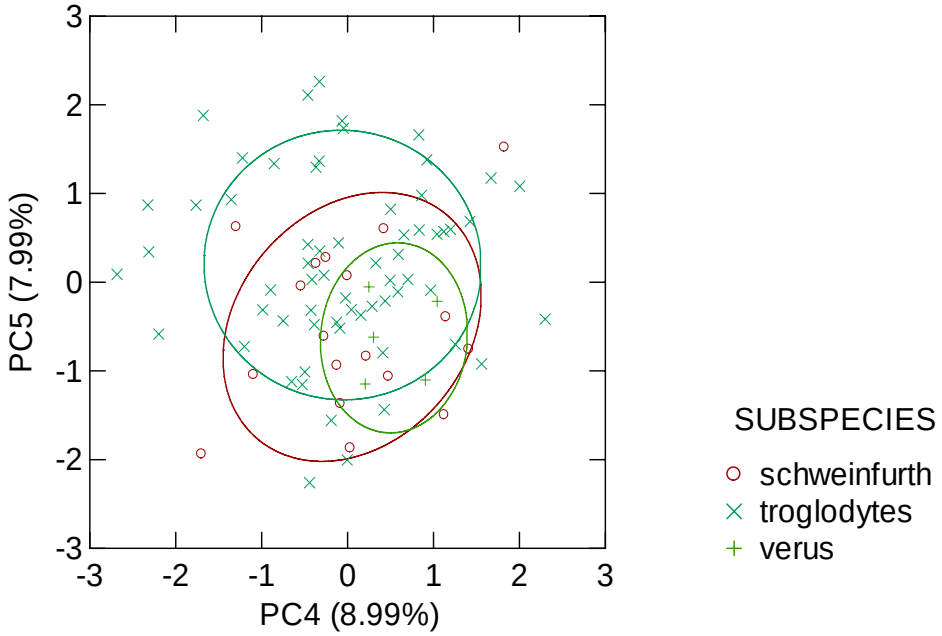


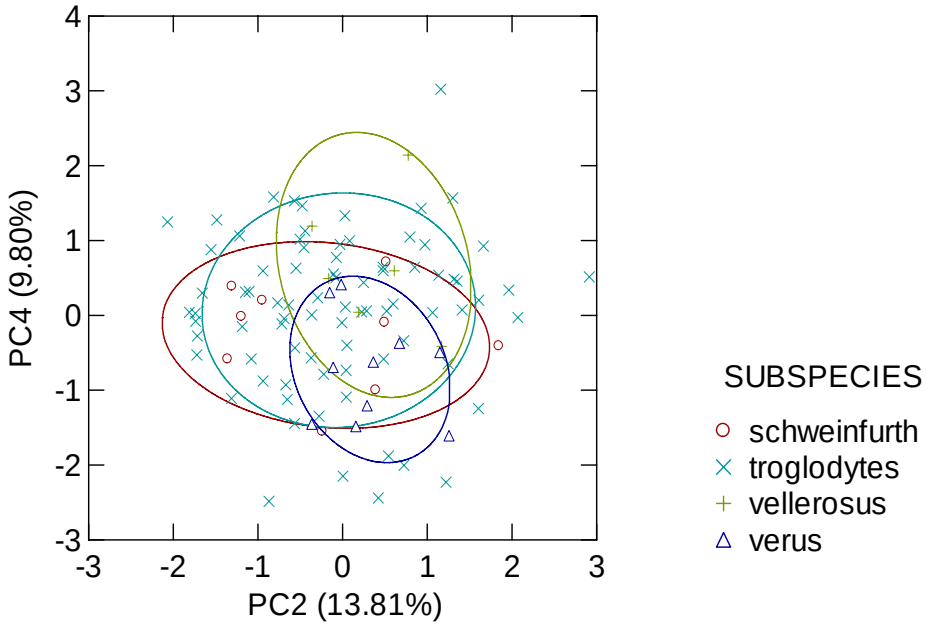
Figure 4.25. Male *P. troglodytes* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 4 | 5 |
|---|---|---|
| HPTW | 0.2493 | 0.0167 |
| HPBD | 0.1824 | 0.2154 |
| HPMD | -0.2024 | -0.2334 |
| HPAH | 0.0377 | 0.1185 |
| XHPL | -0.0737 | 0.1279 |
| MCHS | 0.1522 | 0.4026 |
| MCB | 0.1744 | -0.1813 |
| XPMC | -0.5065 | 0.0144 |
| MCM | -0.5689 | -0.0933 |
| HPGT | -0.2042 | 0.6532 |
| MCAH | 0.3126 | -0.1521 |
| MCDR | 0.3128 | -0.3680 |
| HPFS | 0.3930 | 0.3433 |

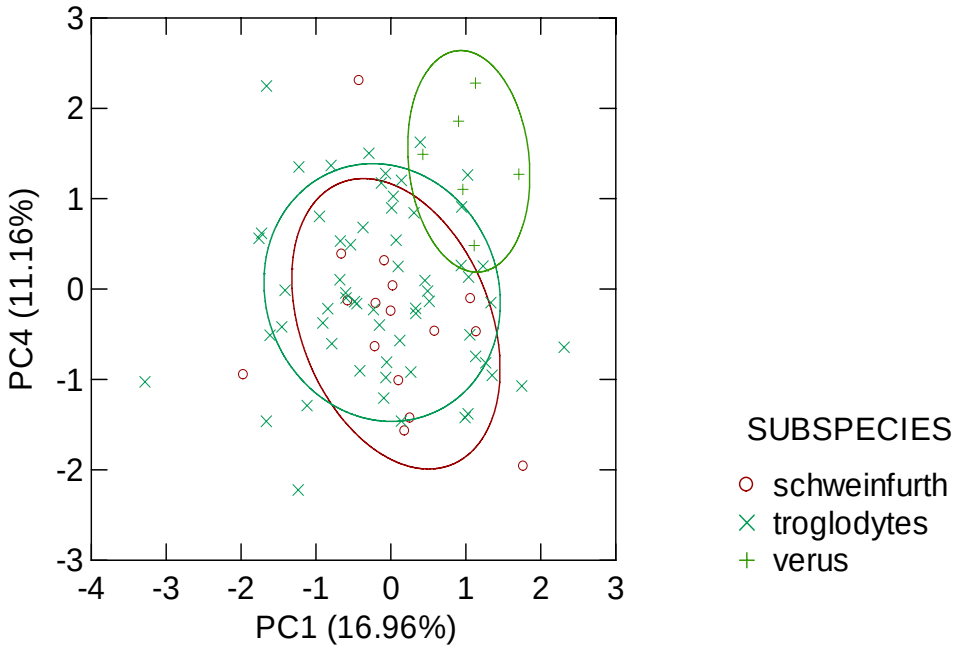
Figure 4.26. Female *P. troglodytes* hands by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 2 | 4 |
|---|---|---|
| HPBD | 0.5109 | -0.0226 |
| HPTW | 0.4556 | 0.1469 |
| HPFS | 0.1713 | 0.2177 |
| HPMD | 0.0612 | -0.2450 |
| HPAH | 0.3764 | 0.3432 |
| XHPL | 0.7311 | -0.1271 |
| MCAH | 0.5361 | -0.1210 |
| MCDR | -0.0415 | 0.1246 |
| MCHS | -0.3005 | 0.2514 |
| HPGT | 0.2406 | -0.3248 |
| MCB | -0.1875 | -0.7792 |
| MCM | 0.1125 | 0.3935 |
| XPMC | -0.3637 | 0.2215 |

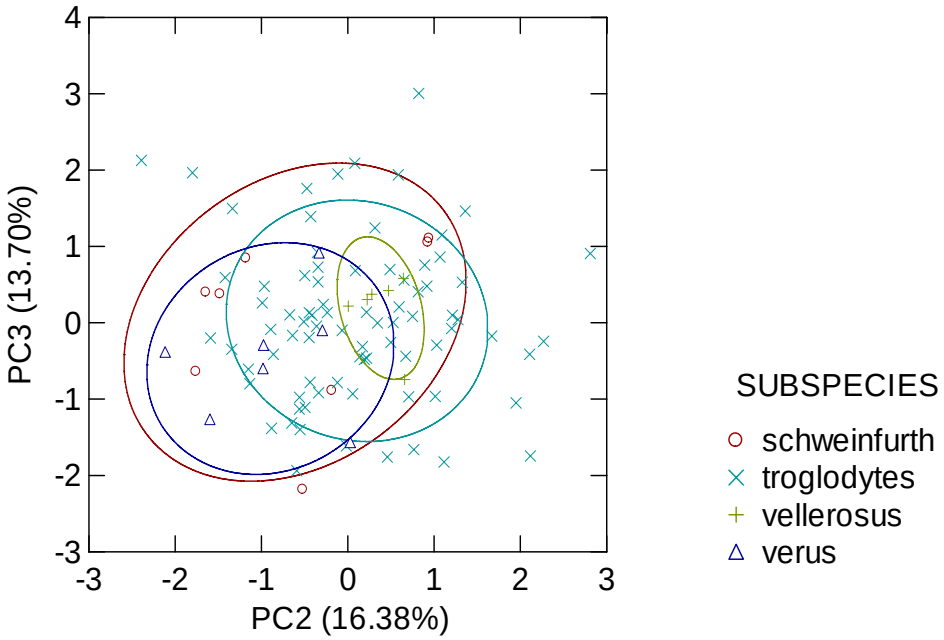
Figure 4.27. Male *P. troglodytes* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 4 |
|---|---|---|
| XPMT | -0.5687 | 0.0453 |
| FPAH | 0.5270 | -0.5269 |
| MTAH | 0.4861 | -0.0173 |
| MTB | 0.0579 | 0.2035 |
| CCTW | 0.2519 | 0.7331 |
| CCFS | -0.3140 | -0.3180 |
| FPFS | 0.4125 | 0.1768 |
| XCMT | -0.4435 | 0.1129 |
| CCFD | -0.3963 | 0.0185 |

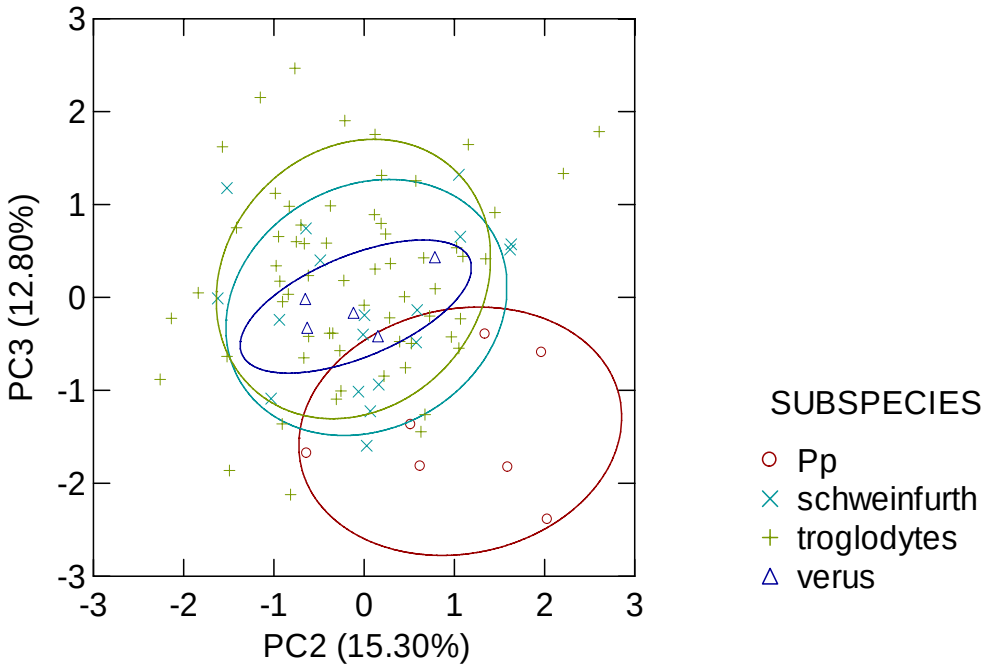
Figure 4.28. Female *P. troglodytes* feet by subspecies: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 2 | 3 |
|---|---|---|
| MTAH | 0.0271 | 0.3958 |
| FPFS | 0.3388 | -0.2447 |
| FPAH | 0.4478 | 0.1857 |
| CCFS | 0.5943 | 0.3233 |
| CCTW | 0.5217 | -0.3920 |
| XCMT | -0.0058 | 0.6213 |
| MTB | -0.3950 | 0.4485 |
| XPMT | 0.3903 | 0.3586 |
| CCFD | 0.4734 | 0.0891 |

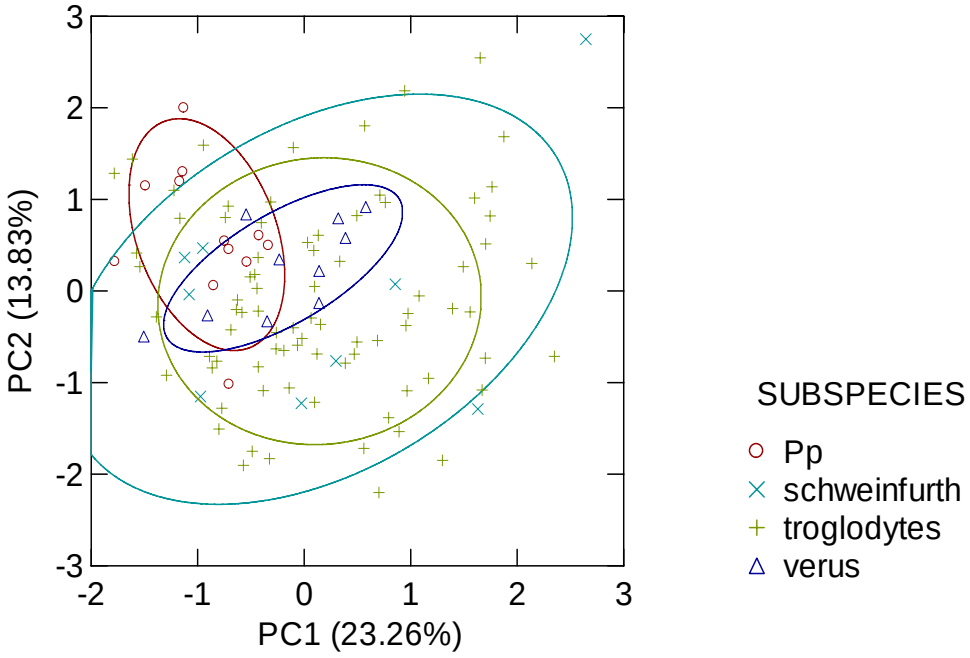
Figure 4.29. Male *P. troglodytes* hands by subspecies plus *P. paniscus*: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 2 | 3 |
|---|---|---|
| HPBD | 0.1084 | -0.0256 |
| HPTW | 0.2884 | -0.0725 |
| HPMD | 0.0463 | -0.3272 |
| HPAH | 0.2268 | 0.1689 |
| XHPL | 0.6692 | 0.1020 |
| MCHS | -0.6421 | -0.3576 |
| MCM | 0.5456 | 0.0596 |
| HPFS | 0.0964 | 0.6876 |
| MCB | -0.0086 | 0.6378 |
| MCAH | 0.4602 | 0.0607 |
| MCDR | -0.4659 | 0.1778 |
| HPGT | -0.3173 | 0.4799 |
| XPMC | -0.3784 | 0.4848 |

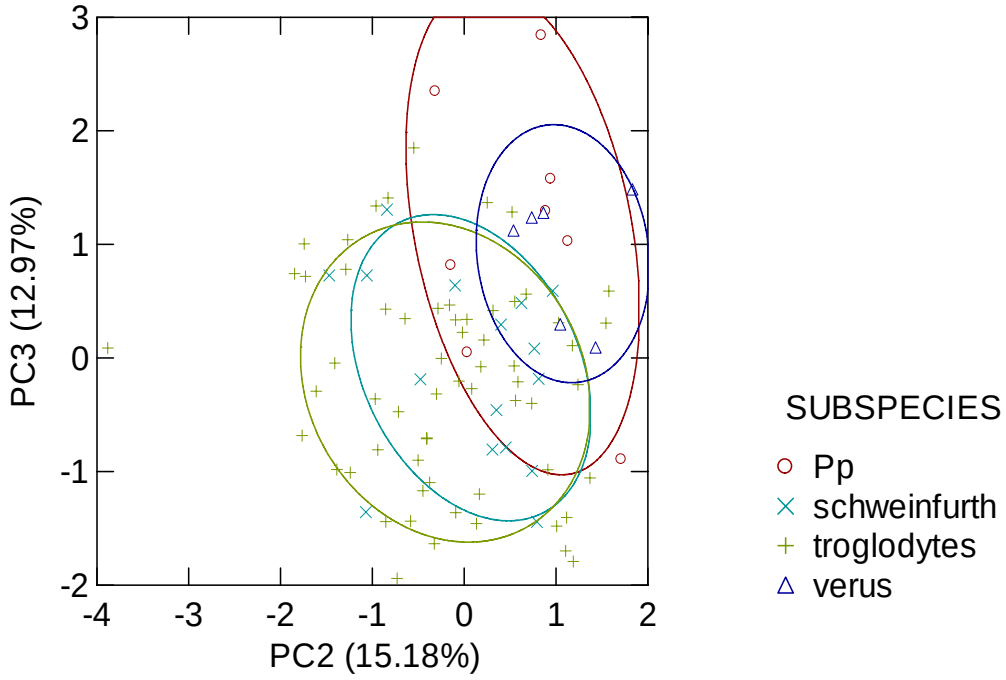
Figure 4.30. Female *P. troglodytes* hands by subspecies plus *P. paniscus*: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 2 |
|---|---|---|
| HPBD | 0.7263 | 0.5566 |
| HPFS | 0.6841 | 0.1693 |
| HPTW | 0.6837 | 0.5479 |
| HPAH | -0.5683 | 0.1985 |
| XHPL | -0.5213 | 0.6641 |
| XPMC | 0.5168 | -0.4263 |
| MCDR | 0.3421 | -0.1968 |
| MCB | 0.1642 | -0.0902 |
| MCM | 0.2140 | 0.0904 |
| HPGT | 0.3300 | -0.0075 |
| MCHS | 0.2431 | -0.4476 |
| MCAH | -0.3149 | 0.4476 |
| HPMD | 0.4924 | 0.2023 |

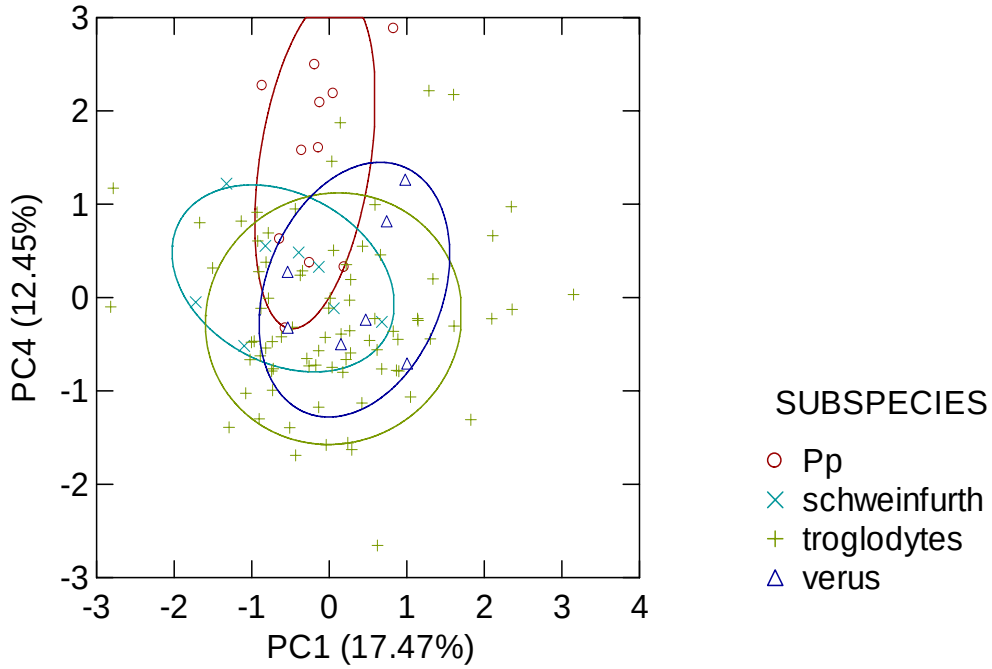
Figure 4.31. Male *P. troglodytes* feet by subspecies plus *P. paniscus*: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 2 | 3 |
|---|---|---|
| MTAH | 0.0651 | 0.0232 |
| FPAH | 0.2868 | -0.0094 |
| XPMT | -0.7157 | -0.2392 |
| CCFS | -0.5701 | 0.2000 |
| XCMT | -0.5138 | 0.2427 |
| MTB | 0.1370 | 0.7357 |
| CCFD | -0.2499 | 0.5618 |
| FPFS | 0.2859 | 0.3914 |
| CCTW | 0.1251 | -0.0287 |

Figure 4.32. Female *P. troglodytes* feet by subspecies plus *P. paniscus*: Principal components analysis. The confidence ellipses for the samples are set at 68.27%.




Component loadings

| | 1 | 4 |
|---|---|---|
| MTAH | 0.6198 | -0.3439 |
| FPFS | 0.5832 | 0.0501 |
| FPAH | 0.5634 | 0.1868 |
| CCFS | -0.1365 | 0.0544 |
| CCFD | -0.4386 | 0.3394 |
| XPMT | -0.2316 | -0.6174 |
| XCMT | -0.0177 | 0.5433 |
| MTB | 0.3260 | 0.4057 |
| CCTW | 0.3986 | -0.0769 |

# CHAPTER 5

# DISCUSSION AND CONCLUSIONS

## Introduction

Two approaches are used to address the questions posed in this study about geographic variation in African ape limb skeletons. The first approach is a set of analyses of raw variables (linear measurements) that generally describe the size and shape of ten bones of the forelimb and hindlimb, including bones of the hand and foot. The second approach is a set of analyses of ratios calculated from linear measurements of the hand and foot. These ratios were chosen because they were thought likely to reflect relative frequencies of certain positional behaviors.

The analyses of raw variables consist of comparisons of means and principal components analyses (PCAs). Patterns and extents of size variation between groups are evaluated based on results from both the univariate and multivariate statistics. Patterns and extents of shape variation between groups are explored primarily with the PCAs. Univariate analyses also suggest between-group shape differences as reflected in measurement proportions, based on observations of which variables are significantly different and which are not.

The analyses of ratios are made up of comparisons of means, discriminant function analyses (DFAs), and PCAs. The ratio data reflect shape differences, but not absolute size differences, between groups. The univariate analyses identify specific morphological differences between groups, while the multivariate analyses address patterns and extents of shape differences between groups, taking into account the entire set of variables and their inter-relationships.

Results from both sets of analyses, the set using raw variables and the set using ratios, contribute information about patterns of geographic variation in African ape limb bone morphology. In addition, because the ratio variables describe morphology that has been suggested to relate to functional adaptation, either due to selection or due to skeletal responses to functional stress, results from the analyses of ratios address questions about the functional significance of these variables and the role of adaptation in differentiating taxa and populations of African apes.

This chapter brings together the results of both sets of analyses to address the questions and predictions outlined at the end of Chapter 1. Subsequently, several implications for hominoid paleontology are discussed. The chapter concludes with a concise summary of findings.

## Questions and predictions

Results from the two sets of analyses are quite consistent in the patterns of geographic variation they reveal. Unless it is stated otherwise, summary statements made below should be understood to be on the basis of both sets of analyses, that of raw measurements from all ten limb bones and that of hand and foot bone ratios.

### *Primary questions*

The primary questions addressed in this study are:

1. Do African apes exhibit geographic variation, particularly at the levels of subspecies and populations, in forelimb and hindlimb skeletal morphology?
2. If so, how do *Gorilla* and *Pan* differ in the patterns and extents of such variation?

The results of this study demonstrate that both *Gorilla* and *Pan* exhibit geographic variation at the levels of species, subspecies, and population in forelimb and hindlimb skeletal morphology. This study made two major predictions, based on previous studies of craniodental morphology and genetics, that relate to these primary questions about patterns and extents of geographic variation:

1. *Gorilla* will show distinct separations between species, subspecies and populations, and populations will cluster according to subspecies.
2. *Pan* will show distinct separations between species, but subspecies and populations will be distinguished less clearly than in *Gorilla*, and populations of *P. troglodytes* will not cluster according to subspecies.

As predicted, both genera show distinct separations between species. This is best observed in the results of the DFAs, which directly address the question of how well groups can be discriminated, and in comparisons of means of both raw measurements and hand and foot ratios. In the DFAs, overall rates of correct classification are high for the species of both genera. The PCAs also reflect differences in multivariate distributions between the species of each genus, but the species of *Gorilla* are much better separated than the species of *Pan*, and the *P. paniscus* distribution is entirely or almost entirely contained within the distribution of *P. troglodytes* in every analysis on the components that best separates species. The PCA results might appear to suggest that the two species of *Pan* cannot be distinguished from one another and, therefore, are not taxonomically diagnosable on the basis of limb bone morphology; however, PCA takes into account all variation in the sample, not just variation between and within groups, and therefore does not directly address the question of how well groups can be discriminated (or

taxonomically diagnosed). Discriminant function analysis is more appropriate than PCA for this purpose.

As further predicted, *Gorilla* subspecies and populations are more clearly distinguished than subspecies and populations of *Pan*. It is interesting to observe that, although the eastern and western subspecies of *P. troglodytes* (*P. t. schweinfurthii* and *P. t. verus*, respectively) are much more geographically distant from one another than are the two subspecies of eastern gorilla (*G. b. beringei* and *G. b. graueri*), they are less morphologically distinct than these neighboring gorilla subspecies. At the population level, variation in hand and foot bone ratios between adjacent groups in west-central Africa is greater in *Gorilla* than in *Pan*, as predicted, but these populations are not well distinguished in either genus.

Direct comparisons between *Gorilla* and *Pan* of population-level differences are geographically limited because of small sample sizes from many localities. Comparisons of population clustering patterns, however, are possible across the ranges of both genera using PCAs of raw measurements. Populations of both *Gorilla* and *Pan* have a strong tendency to cluster by species, observed across all six separately-analyzed sets of variables. Populations of *Gorilla* (specifically *G. beringei*) also usually cluster by their currently-assigned subspecies, although each population varies in its own way. On the other hand, populations of *Pan* do not tend to cluster according to subspecies. Although a more geographically diverse and balanced sample would better address the nature of clustering patterns, these results are consistent with the predictions based on craniodental and genetic studies.

Potential explanations for these differences between *Gorilla* and *Pan* in patterns of geographic variation have been discussed by previous researchers. From the perspective of ecology, chimpanzees may be adapted to broader niches, resulting in less correspondence between subspecies and habitat (Shea and Coolidge, 1988), while gorillas may be less flexible in their adaptations, resulting in greater isolation in forest refugia during dry periods (Gagneux et al., 1999; Yu et al., 2004). From the perspective of demography, smaller group sizes in gorillas and greater dispersal distances in female chimpanzees may contribute to the observed differences (Gagneux et al., 1999). Additionally, genetic studies tell us that gorillas split from the chimp/human clade about three million years before chimps split from the human clade (Gagneux et al., 1999), which may have given gorillas more time to diversify (Taylor and Groves, 2003).

This study also put forward a set of minor predictions, based on previous studies, that relate to patterns of geographic variation but are more taxonomic in focus. Predictions related to *Gorilla* taxonomy are:

1. *G. beringei* will be discriminated from *G. gorilla* at least as well as *P. paniscus* will be discriminated from *P. troglodytes*.
2. *G. b. graueri* will group with *G. b. beringei* rather than with *G. g. gorilla*.
3. *G. g. diehli* will be discriminated from other *Gorilla* subspecies and will group with *G. g. gorilla* rather than with the subspecies of *G. beringei*.
4. Gorillas from Kahuzi and Tshiaberimu will group with gorillas from Mwenga-Fizi and Utu (*G. b. graueri*) and not with gorillas from the Virungas (*G. b. beringei*).

These predictions related to *Gorilla* taxonomy, made on the basis of previous craniodental and genetic work, largely hold true for forelimb and hindlimb skeletal morphology, as well.

Both sets of analyses find differences between eastern and western gorillas that are at least as strong as those between *P. paniscus* and *P. troglodytes*, supporting the species-level separation of these groups into *G. beringei* and *G. gorilla*, as proposed by Groves (2001). In fact, the most surprising result of this study may be that *G. beringei* and *G. gorilla*, which are not yet universally accepted as separate species, are consistently *better*-differentiated by the shape components of PCAs based on various sets of limb bone measurements than are *P. troglodytes* and *P. paniscus*, which have been widely accepted as separate species for several decades (e.g., Zihlman and Cramer, 1978). The result is not explained by shorter hands and feet in eastern gorillas, which is a long-recognized difference between the two species, or at least between *G. b. beringei* and *G. g. gorilla* (e.g., Schultz, 1934). Even the PCA of the set of *Gorilla* long bone variables, which does not include variables of the hand and foot, shows greater shape-based separation between eastern and western gorillas than the shape-based separation seen between chimpanzees and bonobos in the PCA of *Pan* long bone variables or any other set of variables. At the same time, DFA results show discrimination between *Pan* species to be almost as strong as discrimination between *Gorilla* species, in general, which suggests that the relatively weak separation between *Pan* species seen in the PCA results may be explained by the presence of more variation that is not due to group differences in the *Pan* sample than in the *Gorilla* sample. Variation from all sources is taken into account by PCAs, while DFAs evaluate only variation between and within groups.

Based on univariate tests, differences between the two species of gorilla in linear measurements of the limb skeletons are concentrated in the hands and feet. The hand and foot bones of *G. beringei* are significantly smaller, overall, than those of *G. gorilla*. In particular, the lengths of all five hand and foot ray bones included in the study are among the measurements that are significantly different between species in both males and females, with smaller measurements in *G. beringei*. This result is consistent with previous studies that have shown mountain gorilla hands and feet to be shorter than western lowland gorilla hands and feet (Schultz, 1934; Inouye, 1992; Sarmiento, 1994). In addition, univariate tests of hand and foot ratios find a number of variables, including inter-element length ratios, to be significantly different between species of *Gorilla* in one or both sexes.

Schultz (1934) reported that *G. beringei* has a shorter humerus and upper limb than *G. gorilla* and was so confident of his result that he wrote, "Indeed, the author does not hesitate to call *G. beringei* the *short-armed* gorilla" (p. 61, italics in original). His conclusion has been debated ever since, finding disagreement in the studies of Groves and Stott (1979) and Jungers and Susman (1984) and support in the study of Taylor (1997a). The present study finds mean humerus length to be smaller in *G. beringei* than in *G. gorilla* in both males and females (Table 3.1), but these differences are not significant (although the uncorrected p-value is low in males); however, it may be more relevant to look at subspecies-level comparisons, as Schultz's (1934) *G. beringei* sample consisted mostly of *G. b. beringei* specimens. Turning our attention to subspecies-level comparisons, humerus length is significantly smaller in male *G. b. beringei* than in male *G. g. gorilla* (Table 3.2), but humerus length in females of these two subspecies is not

significantly different, according to the present study. Differences in humerus length between *G. b. graueri* and *G. g. gorilla* are not significant in either sex (Table 3.3). It appears that Schultz's (1934) observation, made on a very small sample of eastern gorillas, does not stand up to tests using larger and more geographically representative samples of *G. beringei*, but it still holds true for comparisons between male mountain gorillas and male western lowland gorillas.

The prediction that *G. b. graueri* would group with *G. b. beringei* rather than with *G. g. gorilla* is strongly realized by the multivariate analyses of both raw variables and hand and foot ratios. Further, in both sets of univariate analyses, the greater similarity of the two eastern gorilla subspecies is seen in the much smaller number of significant differences between them in comparison with the number of significant differences between either of them and *G. g. gorilla*. Additionally, comparisons of means show that *G. g. gorilla* differs from each of the two eastern gorilla subspecies in many of the same ways, especially in measurements of the hand and foot. Although Groves' early (1970) study of cranial measurements concluded that eastern lowland gorillas appeared to be morphologically intermediate to mountain gorillas and western lowland gorillas, and results of some subsequent studies have been equivocal with regard to the separation between eastern and western gorillas (Uchida, 1998; Taylor and Groves, 2003), recent work has supported the similarity of *G. b. graueri* and *G. b. beringei* to the exclusion of *G. g. gorilla* in many craniodental measures (Groves, 2001).

The predictions regarding *G. g. diehli* could not be completely addressed, due to the very small size of the *G. g. diehli* sample. Three specimens were included in the study, and two were quite incomplete. Only the single complete specimen could be

included in the multivariate analyses. Based on multivariate analyses of raw measurements (PCA) and of hand and foot ratios (DFA and PCA), this single *G. g. diehli* specimen consistently groups with *G. g. gorilla* rather than with the subspecies of *G. beringei*, as predicted; however, DFA cannot attempt to discriminate a group from the others on the basis of a single specimen. Distributions of individual raw measurements also follow the prediction that *G. g. diehli* would group with *G. g. gorilla*. Measurements from the three *G. g. diehli* specimens always fall within the range of the *G. g. gorilla* sample, while they sometimes fall below or above the ranges of the eastern gorilla subspecies.

At the same time, inspection of univariate plots for the raw measurements that differ significantly between the two species of *Gorilla* hints that there might be differences between the two western gorilla subspecies in dimensions of the hand and foot ray bones. The one *G. g. diehli* specimen that includes hand and foot elements falls at the low end of the *G. g. gorilla* range, in the direction of the *G. beringei* mean, for such measurements of the hand and foot ray bones (including lengths), but it and the two *G. g. diehli* specimens without hand and foot bones fall near the middle of the *G. g. gorilla* range for such measurements of other limb elements. Sarmiento and Oates (2000) obtained similar results based on bone lengths alone; the present study extends their results to measurements of shafts and articular regions. Based on these limited observations, it appears that limb bone differences between *G. g. diehli* and *G. g. gorilla* may be concentrated in the hands and feet, as are differences between *G. beringei* and *G. g. gorilla*. Unfortunately, the very small sample of *G. g. diehli* postcranial skeletons makes it impossible to address the prediction, based mostly on studies of craniodental

morphology (Sarmiento and Oates, 2000; Stumpf et al., 2003; Pilbrow, 2003), that *G. g. diehli* would be differentiated from the other subspecies of *Gorilla*. The three available specimens, two of which are very incomplete, support a distinction between this subspecies and the subspecies of *G. beringei*, but differences between *G. g. diehli* and *G. g. gorilla* are only suggested by the single specimen that includes all elements in the study. In order to better characterize the postcranial skeleton of *G. g. diehli*, more gorilla skeletons from the Cross River region would be needed, but the sample is likely to remain very small.

Two predictions pertain to eastern gorilla populations whose subspecies memberships have been previously questioned. Populations from the high-altitude localities of Kahuzi and Tshiaberimu were predicted to group with gorillas from Mwenga-Fizi and Utu (*G. b. graueri*) and not with gorillas from the Virungas (*G. b. beringei*). Principal components analyses of raw measurements were used to inspect population clustering patterns across the *Gorilla* range using all six separately-analyzed sets of limb bone variables. Because the Mwenga-Fizi sample is larger than the Utu sample and better reflects the tendencies of the *G. b. graueri* sample as a whole, the Kahuzi and Tshiaberimu samples are compared to it and not to the Utu sample. Based on PCA components that best separate the two subspecies of *G. beringei*, the very small Kahuzi sample consistently clusters with the Mwenga-Fizi sample. The Tshiaberimu sample, also very small, is less consistent, clustering with the Virungas sample in some analyses and showing values at the opposite end of the *G. b. graueri* spectrum in others, but it clusters with the Mwenga-Fizi sample on most of these components. In summary, recognizing the limitations of these very small samples, the Kahuzi population groups

with the Mwenga-Fizi population and not with the Virungas population, while the Tshiaberimu population is more similar to the Mwenga-Fizi population than to the Virungas population but does not group reliably with Mwenga-Fizi. These results are consistent with other studies that find the Kahuzi and Tshiaberimu populations to be more similar to populations of *G. b. graueri* than to the Virungas population based on morphology (Groves and Stott, 1979; Pilbrow, 2003) and genetics (Saltonstall et al., 1998; Jensen-Seaman and Kidd, 2001), despite morphological ambiguities found by Groves (1970) and Groves and Stott (1979).

Several minor predictions relating to *Pan* taxonomy were also made at the beginning of this study. These predictions are (retaining their numbering from Chapter 1):

5. *P. t. verus* will be the most distinct subspecies of *P. troglodytes*.

6. *P. t. vellerosus* will be discriminated from other *P. troglodytes* subspecies. Evidence from mtDNA suggests it will be most similar to *P. t. verus*. Evidence from dental morphology suggests it will be most similar to *P. t. troglodytes*.

7. Chimpanzees from the northwestern and the southeastern parts of the eastern chimpanzee range will be distinguishable from one another.

Predictions relating to the distinctiveness of particular groups of *Pan* met with moderate success overall.

*Pan troglodytes verus* is the most distinct subspecies of *P. troglodytes*, as predicted. Although raw measurement means demonstrate that *P. t. troglodytes* has slightly larger limb bones than the other subspecies, most analyses find that its limb bones are poorly distinguished from *P. t. schweinfurthii* in terms of shape, whether based

on shape components of the raw measurement PCAs or on hand and foot ratio univariate and multivariate analyses. Differences between *P. t. verus* and the subspecies *P. t. schweinfurthii* and *P. t. troglodytes* are apparent on a low-numbered component in every raw measurement PCA, with loadings generally dominated by articular surface measurements and shaft widths, while differences between *P. t. schweinfurthii* and *P. t. troglodytes* are consistently weak. Several hand and foot ratios have significant differences between *P. t. verus* and *P. t. troglodytes*, while only one ratio has a significant difference between *P. t. troglodytes* and *P. t. schweinfurthii*. In addition, DFAs of male hand and foot ratios show *P. t. verus* to be the best-discriminated subspecies of *P. troglodytes*.

Taken together, all of these results suggest greater distinctiveness in *P. t. verus* limb bone morphology than was captured by the long bone length indices analyzed by Zihlman et al. (2007) in their comparison of chimpanzee skeletons from Taï (*P. t. verus*) and Gombe (*P. t. schweinfurthii*). Although they did not find the length indices to be significantly different between the two populations, it appears likely that further study of their samples, perhaps including articular surface measurements and shaft widths, would reveal stronger shape differences between the limb skeletons of the two populations.

While multivariate plots show that *P. t. verus* has a different distribution from the other subspecies, it is important to point out that its distribution usually greatly overlaps or is contained within the distributions of the other subspecies, rather than separating it from the others entirely. In addition, *P. t. verus* does not have the highest rate of correct classification in DFAs of female hand and foot ratios. While a number of previous studies have found *P. t. verus* to be the most distinctive subspecies of *P. troglodytes*, the

suggestion by Morin et al. (1994), based on mtDNA evidence, that *P. t. verus* might be different enough from the other chimpanzee subspecies to be considered a separate species has found little support in subsequent studies of craniodental morphology, and this taxonomic proposition is not supported by forelimb and hindlimb morphology, either.

Predictions regarding *P. t. vellerosus* must be addressed with caveats, as the sample included only females and only between three and six specimens per analysis (depending on the set of variables analyzed). Due to the limitations of the sample, *P. t. vellerosus* was not included in the samples used to derive the DFA functions that discriminate subspecies of *Pan*, and univariate statistics were not conducted; therefore, this study does not directly address whether this subspecies can be discriminated from the others. All the same, there are suggestions that it has its own distinctive tendencies. While *P. t. vellerosus* is not well-distinguished from the other subspecies in most PCAs, its distribution is particularly distinctive in the PCA of raw measurements from the foot. One of the components in this analysis that separates this subspecies from the others is driven by the cuboid facet depth of the calcaneus, a measurement for which *P. t. vellerosus* appears to have an exceptionally large mean.

Evidence from genetics and from dental morphology point to different predictions regarding the affinities of *P. t. vellerosus*. Findings based on mtDNA indicate that *P. t. vellerosus* is more closely related to *P. t. verus* than to the other subspecies (Gonder et al., 1997, 2006), while dental metrics support a closer relationship to *P. t. troglodytes* (Pilbrow, 2003, 2006b). In this study, results from both raw measurements and hand and foot ratios point in the same direction. Using DFAs of hand and foot ratios, and based on

the functions that best discriminate the other subspecies from one another, *P. t. vellerosus* is most frequently classified as *P. t. troglodytes* and least frequently classified as *P. t. verus*. This result is echoed by PCAs of hand and foot ratios, which show *P. t. vellerosus* especially separated from *P. t. verus*. The raw measurement in which *P. t. vellerosus* appears unusual, the cuboid facet depth of the calcaneus, is especially large in *P. t. vellerosus* relative to *P. t. verus*, and the PCA component of the foot analysis that is driven by this variable particularly separates these two subspecies. In summary, *P. t. vellerosus* hand and foot bone morphology appears to be more similar to that of *P. t. troglodytes* than that of *P. t. verus*.

These results regarding the affinities of *P. t. vellerosus* do not offer support for the suggestion by Gonder et al. (2006), based on mtDNA, that *P. t. verus* be sunk into *P. t. vellerosus*, to the exclusion of *P. t. troglodytes* and *P. t. schweinfurthii*. This suggestion is part of their proposal that *P. troglodytes* taxonomy be revised to include only two subspecies, *P. t. troglodytes* (into which *P. t. schweinfurthii* would be sunk) and *P. t. vellerosus* (in which *P. t. verus* would be sunk). The mtDNA data show two large monophyletic groups of *P. troglodytes*, converging near the Sanaga River (the approximate boundary between *P. t. vellerosus* and *P. t. troglodytes*, in Cameroon), but some haplotypes are found on both sides of the Sanaga, suggesting an explanation for the lack of agreement between patterns revealed by mtDNA data and morphological data. Perhaps *P. t. verus* and *P. t. vellerosus* are sister taxa, but *P. t. verus* became more isolated after their divergence from the rest of *P. troglodytes*, while *P. t. vellerosus* subsequently renewed occasional genetic contact with other subspecies.

The prediction that chimpanzees from the northwestern and the southeastern parts of the eastern chimpanzee range will be distinguishable from one another is generated by the proposition by Groves (2005), based on DFAs of cranial measurements, that these two populations should be considered separate subspecies. The northwestern population would retain the name *P. t. schweinfurthii*, while the southeastern population would assume the name *P. t. marungensis*. Principal components analyses of raw measurements permitted their differences on the basis of forelimb and hindlimb morphology to be explored, and the distributions of the two populations of eastern chimpanzee clearly differed in four of the six analyses. This could be interpreted as support for the presence of two subspecies in the eastern chimpanzee sample. At the same time, several analyses show similarities between the distribution of one of the eastern chimpanzee populations and one of the *P. t. troglodytes* populations, in various combinations, which warns against making taxonomic inferences based on the eastern chimpanzee variation observed in these PCAs.

*Secondary questions*

If the results of this study are to be useful in constructing models based on modern analogs to aid in the interpretation of variation between fossils, it is important to establish not only the existence of geographic variation in forelimb and hindlimb skeletal morphology but also the influence of various factors on the extent of variation detected between groups, the types of variables that contribute most to separating groups, and whether the variables responsible for differentiating geographic groups reflect differences between groups in positional behavior. In order to explore these issues, three secondary questions were posed at the beginning of this study:

1. Are there patterns of differences between taxonomic levels, anatomical regions, and sexes in relative strength of group discrimination?

2. Are there patterns in which variables, and which *types* of variables, best differentiate groups?

3. Do selected variables of the hand and foot vary according to known differences in frequencies of positional behaviors characteristic of arboreal and terrestrial substrate use?

The results of the analyses of hand and foot ratios are particularly well-suited to addressing these questions. First, the analyses of hand and foot ratios use DFAs, which specifically quantify discrimination of geographic groups, whereas the PCAs on which the analyses of raw measurements rely take into account variation from all sources. Second, the hand and foot ratios can be more easily sorted into types of variables that reflect shapes or proportions; differences in shapes or proportions are easier to grasp conceptually than differences in raw measurements, which must be considered in relation to all the other measurements in a given analysis. Third, the hand and foot ratios were selected for their potential functional significance, while the raw measurements were selected only to describe the general size and shape of each bone. The last section of Chapter 4 (Patterns and comparisons) brings the results of the analyses of hand and foot ratios to bear on the three secondary questions above. The present section briefly summarizes the conclusions in Chapter 4 and, where appropriate, complements them with results from the analyses of raw measurements.

The potential influence of taxonomic level of analysis, anatomical region (hand vs. foot), and sex were examined by comparing patterns of group discrimination (i.e., rates of correct classification) from the DFAs. The hierarchical relationships of the

taxonomic levels are generally reflected in the extents of variation between groups at each level, with the highest rates of discrimination at the genus level down to the lowest rates at the population level. The exception is that variation between gorilla subspecies is sometimes as high as variation between gorilla species and African ape genera. The PCAs of raw measurements also demonstrate a clear taxonomic hierarchy in the extents of group separation on low-numbered shape components.

Using the DFA results from hand and foot ratios, no general patterns of differences are found across genera on the basis of anatomical region (hand vs. foot). The raw measurement PCAs, however, favor the hindlimb, especially emphasizing the foot, over the forelimb for separating the species of both *Gorilla* and *Pan*. Similarities between the genera are not so strong when it comes to separation of subspecies with raw measurement PCAs, but one variable of the foot (cuboid facet depth of the calcaneus) plays a prominent role in separating subspecies of both *G. beringei* and *P. troglodytes*.

Why might the hindlimb, especially the foot, play a larger role than the forelimb in separating species of both *Gorilla* and *Pan*? Whether the morphological differences between taxa are due to genetic drift or to adaptations, the most obvious sources of explanation are the differences in the functional roles of the hand and foot. If the evolutionary mechanism responsible for the observed variation is primarily drift, perhaps the hand is buffered from the effects of drift by tight adaptive constraints resulting from the demands of knuckle-walking, which directs large forces through the lengths of several proximal phalanges and metacarpals and their joints, while the foot, which distributes forces more broadly through its skeleton, may be less constrained and more subject to the effects of drift. If the observed taxonomic variation is primarily due to

adaptations to different habitats and/or patterns of positional behavior, whether due to selection or due to plastic responses to functional stresses during an individual's lifetime, perhaps the foot reflects adaptive differences to a greater extent than the hand because the foot is more frequently bearing weight and in contact with the substrate during daily activities. If the foot does reflect adaptive differences to a greater extent than the hand, this may also contribute to the prominent role of the cuboid facet depth of the calcaneus in separating subspecies from both genera. This possibility is supported by the presence of the ratio for cuboid facet depth of the calcaneus (CCFD) on the list of four ratios that vary in a manner consistent with proposed functional interpretations in this study.

The hand and foot ratio DFAs do not find a general pattern of differences across the genera in which sex is better discriminated by the analyses, and the study did not distinguish between the sexes on the shape components of the raw measurement PCAs.

The variables and types of variables that best differentiate geographic groups were examined by bringing together results of comparisons of means and DFAs. The types of variables that are most informative at the species and subspecies levels, across both *Gorilla* and *Pan*, are inter-element length proportions and measure of tendon and ligament attachment sites. Four variables differentiate both species and subspecies in both genera: phalanx-metacarpal length ratio (XPMC), phalanx-metatarsal length ratio (XPMT), hand phalanx flexor sheath ridge size ratio (HPFS), and foot phalanx arch height (FPAH). Two are inter-element length proportions (XPMC and XPMT), one is a ligament attachment site measurement (HPFS), and one is an arch height (FPAH). Other variables, including another inter-element length proportion and five more

tendon/ligament attachment sites, differentiate only species or only subspecies in both genera.

Inter-element length proportions of the hand and foot appear to play the greatest role of any type of variable in differentiating groups. Two of the three inter-element length proportions included in the study are among the four variables that differentiate both species and subspecies in both *Gorilla* and *Pan*. The third inter-element length proportion in the study, calcaneal tuberosity-metatarsal length ratio (XCMT), differentiates only species in both genera. The phalanx-metacarpal length ratio (XPMC) and the phalanx-metatarsal length ratio (XPMT) both make large contributions to differentiating *Gorilla* populations, as well. Observations from the comparisons of means of raw measurements underscore the large part played by hand and foot bone lengths in differentiating groups. In both *Gorilla* and *Pan*, measurement means with significant differences between species include those of several hand and foot ray bone lengths. In particular, lengths of the third proximal phalanges of both the hand and foot are significantly different between species in both genera. Additionally, the hand and foot phalanges are significantly longer in *P. t. troglodytes* than in either *P. t. verus* or *P. t. schweinfurthii* (each in only one sex but not always the same sex), although *P. t. troglodytes* bones are not significantly longer in general.

Research in evolutionary developmental biology has the potential to shed light on the prominence of hand and foot bone lengths and length proportions in limb bone variation among geographic groups. A study by Hallgrímsson et al. (2002) of adult macaque limb segment lengths (humerus, radius, third metacarpal, femur, tibia, and third metatarsal) found the most distal segments, the third metacarpal and third metatarsal, to

have the greatest phenotypic variance. Elevated phenotypic variance of distal element lengths relative to more proximal element lengths in African ape limbs could potentially be a factor in greater geographic variation in the lengths of more distal elements. On the other hand, this study showed lower heritability in the distal element lengths. If the hand and foot element lengths have lower heritability, they are presumably less evolvable and, therefore, less likely to vary geographically, unless the geographic variation in these measurements is mediated by environmental, rather than genetic, differences. In fact, a study of fetal mouse limbs, reported in the same publication (Hallgrímsson et al., 2002), found no decrease in heritability along the proximal-distal limb axis, leading the authors to propose that the lesser heritability in distal elements of adult macaques reflected differential effects of the mechanical environment. The macaque sample is derived entirely from the Cayo Santiago free-ranging research colony, and no information is given on how the mechanical environment might differ among individuals, leaving open to broad speculation the question of how differences in metacarpal and metatarsal length among these macaques might be influenced by their mechanical environments. The Hallgrímsson et al. (2002) study suggests that work in evolutionary developmental biology may lead to a greater understanding of why hand and foot bone ray lengths and length proportions appear particularly variable among geographic groups of African apes, yet, if the effect is due to environmental differences and not divergences of the genotype, the nature of these environmental differences is an open question.

The potential relationship of variation in the hand and foot ratios to variation in frequencies of characteristically arboreal and characteristically terrestrial positional behaviors was investigated by examining their directions of variation in the comparisons

of means. First, widespread inconsistencies in the directions of variation within arboreal and terrestrial categories were seen at the levels of genus, species, and subspecies, making it clear that many, if not all, of the ratios did not reflect differences between group in frequencies of positional behaviors. Second, reasonably well-known behavioral contrasts between *Gorilla* and *Pan* and between *G. g. gorilla* and *G. b. beringei* were employed to look for ratios that follow the predicted direction of variation in both comparisons of taxa. Out of twenty-two hand and foot ratios, only four passed the test. These four variables are the metacarpal biepicondylar width ratio (MCB) and the hand phalanx base width ratio (HPBD) from the hand and the cuboid facet depth ratio of the calcaneus (CCFD) and calcaneal tendon facet width ratio (CCTW) from the foot.

The two hand ratios that vary in the directions predicted by functional interpretations of their significance are both related to the metacarpo-phalangeal joint. The metacarpal biepicondylar width ratio (MCB) measures the extent to which the epicondyles, which are attachment sites for the collateral ligaments of the joint, project beyond the width of the head. Because joint hyperextension during knuckle-walking is assumed to strain these ligaments, and ligament strain is assumed to influence development at the attachment sites, greater projection of the epicondyles is proposed to reflect greater frequencies of knuckle-walking. The hand phalanx base width ratio (HPBD) measures the width of the base relative to the narrowest part of the shaft. It is proposed to reflect the relative amount of load-bearing on the phalangeal base and, therefore, is also proposed to reflect relative frequencies of knuckle-walking.

The two foot ratios that may be functionally significant, on the basis of this study, are both based on measurements of the calcaneus. The cuboid facet depth ratio of the

calcaneus (CCFD) measures the depth of this articular region, where the cuboid articulates with the calcaneus, relative to its width. Because the cuboid pivots against the calcaneus within this facet, a deeper facet is proposed to reflect greater foot mobility and, therefore, greater frequencies of climbing. The calcaneal tendon facet width ratio (CCTW) measures the width of the attachment site for the calcaneal tendon (tendon for the gastrocnemius muscle, popularly known as the Achilles tendon) relative to the height of the calcaneal tuberosity. The gastrocnemius muscle functions in plantarflexion of the foot, as occurs in walking. Greater development of its attachment site is proposed to reflect greater frequencies of walking.

Not one of these four variables that vary in a manner consistent with functional interpretations is among the variables that differentiate both species and subspecies within both *Gorilla* and *Pan*. If these four variables do, in fact, reflect differences in positional behavior, then differences in positional behavior do not follow major geographic divisions in African apes.

**Implications for interpretation of hominoid fossils**

General model

The interpretation of variation among hominoid fossils depends on making comparisons with modern analog taxa. The results of this study permit a general model of variation in African ape forelimb and hindlimb skeletal morphology to be outlined. According to this model, morphological variation is present between geographic and taxonomic groups at every level of hierarchical organization, from the population to the genus, with increasing degrees of variation between groups as one ascends the hierarchy; this model holds true for both forelimbs and hindlimbs and for both males and females.

The morphological variation between subspecies is uncorrelated or only weakly correlated with body size, as long as body size variation between subspecies is within the limits of modern African apes. Length proportions and tendon and ligament attachment sites are particularly useful for separating species, subspecies, and populations.

If *Gorilla* and *Pan* are considered separately, the resulting models differ from one another in that geographic groups, especially subspecies and populations, are more distinct according to the *Gorilla* model. In addition, groups tend to cluster in a pattern consistent with their taxonomy when following the *Gorilla* model, while they do not cluster so predictably in the *Pan* model. The difference in patterns between the genera is likely to be related to differences in ecology and demography. *Gorilla* is considered to be less ecologically flexible than *Pan* with greater geographic restriction of populations and smaller groups, while *Pan* adaptations permit greater flexibility in resource exploitation accompanied by long-distance dispersal in females.

It is hoped that the information on geographic variation in African ape forelimb and hindlimb morphology provided by this study will have utility for the interpretation of variation among hominoid fossils. At the same time, the choice of whether to use a model based on *Gorilla* or *Pan* may influence such interpretations. Further, this choice carries with it implications for whether the fossil taxon is thought to have ecological and demographic characteristics more like *Gorilla* or more like *Pan*. Perhaps the most cautious approach would be for researchers to apply both *Gorilla* and *Pan* models and discuss any resulting interpretive differences in the context of the ecological and demographic implications of the two models.

Patterns of postcranial variation

Most of the geographic patterns of variation observed in previous studies of African ape craniodental morphology and genetics are reflected in this study of forelimb and hindlimb skeletal morphology. However, although these results are as *predicted*, based on patterns of variation in skulls, teeth, and DNA, they are not necessarily what would be *expected*. Bone is known to exhibit considerable plasticity in response to functional stresses during an individual's lifetime, and, among modern humans, activity-related variation in skeletal morphology has been documented especially well in limb bones (e.g., Ruff et al., 2006). In particular, one would expect hand and foot bones to reflect differences in positional behavior profiles between individuals, populations, and subspecies, as hands and feet interact directly with the behavioral substrate or superstrate. As widespread variation in habitat, and apparently related variation in positional behavior profiles, have been documented between African ape populations, it follows that the phylogeographic signal would run a great risk of being overpowered by the functional signal in the limb bones. Limb bone variables, including those of the hand and foot, appear to retain a stronger phylogeographic signal than their presumed plasticity would lead one to expect.

Further, one might expect a large amount of parallelism in limb bone morphology, for similar reasons. The forelimb and hindlimb skeletons would be expected to be under heavy directional selection due to variation in habitats, which would be likely to lead to parallelisms between populations in similar habitats, confusing the phylogeographic signal. In fact, the hominoid postcranium has been proposed to show high levels of parallelism and responsiveness to selective pressures (Larson, 1998), and researchers have noted a common assumption in the field that postcranial characters are less useful

than craniodental characters for detecting phylogenetic relationships among hominoids (Ward, 1997; Collard et al., 2001; Young, 2005; Jabbour pers. obs.).

Given that functional differences between populations and taxa do not appear to have overpowered the phylogeographic signal in African ape limb bone morphology, how do we interpret the morphological variation we see between geographic groups?

One possible explanation is that it represents genetic drift. Over the course of *Gorilla* and *Pan* evolutionary history, as populations separated from one another and reproductive contact between them became infrequent, the within-population frequencies of some alleles might have diverged due to chance events. Some of these alleles may have been related to aspects of limb bone morphology. The accumulation of random changes in allele frequencies and, consequently, limb bone morphology may have tracked the sequence of divergence between groups and the amount of time since the splits occurred, resulting in a geographic pattern which reflects the pattern detected in genetic data. The same geographic pattern is observed in craniodental morphology, suggesting that genetic drift may have been the evolutionary force shaping patterns of variation in skulls and teeth at the same time it was shaping patterns of variation in the limb skeletons. In other words, populations may have been simultaneously accumulating random changes in the frequencies of alleles related to morphology of the skull, teeth, and limb bones, resulting in patterns of geographic variation in all of these skeletal regions that track the same underlying phylogeography.

Another possible explanation is that functional and genetic divergences may not be as distinct as one might think. First, if two populations are reproductively separated from one another by a geographic barrier, such as a river, ecological conditions are

frequently different on the two sides of the barrier. Second, two adjacent populations in habitats with different selective pressures might conceivably have less reproductive contact as they diverge adaptively. In both cases, it might not be easy to disentangle divergences due to adaptive differences and divergences due to reproductive isolation or semi-isolation.

Regardless of the explanation for the observed geographic variation in African ape forelimb and hindlimb morphology, patterns of geographic variation revealed in this study are quite concordant with patterns of geographic variation found in previous studies of craniodental morphology, as well as studies of genetics. This has implications for the study of the hominoid fossil record. Although most taxonomic descriptions and interpretations are based on craniodental remains, and some hominoid paleontologists may consider postcranial remains to reflect functional contexts more than phylogenetic relationships, this study suggests that studies of variation in postcrania, particularly the limb skeletons, are likely to lead to the same conclusions.

Functional interpretations

The hand and foot ratios included in this study are informative simply as skeletal morphology that varies among geographic groups; however, they were chosen in the hope that they would provide the basis for future interpretation of the functional and environmental correlates of geographic variation. If a clear relationship could be found between variation in modern African ape morphology and variation in modern African ape habitats and positional behavior, it would provide a powerful tool for the ecological interpretation of morphological variation in fossil hominoids. Unfortunately, the results of this study demonstrate that very few, if any, of the selected ratios are likely to reflect

differences in frequencies of positional behaviors. Further, if the small number of ratios that vary in a manner consistent with functional interpretation do, in fact, vary with function, then geographic and taxonomic divisions within *Gorilla* and *Pan* do not correspond to differences in frequencies of characteristically arboreal and characteristically terrestrial positional behaviors.

Alternatively, it may be unreasonable to look for a clear-cut morphological "code" from which can be deciphered the relative frequencies of terrestrial or arboreal positional behaviors, or relative degrees of arboreality or terrestriality, in every comparison of groups at every taxonomic or geographic level. First of all, variables that best reflect behavioral differences between African ape genera may not be the same as variables that best reflect behavioral differences between species or subspecies within the genera, simply because there is a great size difference between *Gorilla* and *Pan*, and size varies much less between taxa within each genus. Variables that do not vary in the expected direction when comparing genera may still be functionally meaningful at lower levels of the hierarchy, where body size is more comparable between groups. Second, and quite importantly, natural selection is an opportunistic process subject to a large element of chance. Skeletal features which are largely under genetic control and shaped by selection are limited in their ability to adapt to new functional circumstances by their reliance on the chance appearance of advantageous variations. Not every advantageous variation will arise in every population, and not every individual with an advantageous variation will experience reproductive success. No matter how great an animal's locomotor advantages over other members of its population, it may still get caught in a snare trap and die before it leaves any offspring. Third, skeletal features that form predominantly in response to

mechanical loading during an individual's lifetime, such as muscle markings and cross-sectional geometry, are influenced by a number of factors (Lieberman, 1997; Weiss, 2003; Ruff et al., 2006). While numerous studies make it clear that such features are related to the response of bone to functional stresses, control over the expression of these features appears to be quite complicated, and we are not yet able to predict the exact nature of their expression under non-experimental conditions. For example, Carlson et al. (2006) concluded that, although they had quantitative data on the locomotor behavior of the chimpanzees in their study, they could not predict their differences in femoral and humeral cross-sectional geometry, most likely because the locomotor forces that had been experienced by these animals were too varied in their orientation. Further, the functional significance of variation in some muscle attachment sites may be unclear because the functional role of the muscle itself is poorly understood (e.g., Boyer et al., 2007).

While it is possible that universal signals may be found in hominoid bones that will indicate the relative frequencies of arboreal or terrestrial positional behaviors, most, if not all, of the hand and foot ratios analyzed in this study, based mostly on the literature of ape comparative morphology, do not provide such universal signals. These results urge caution in the attempt to make functional interpretations of fossil hominoid limb bone morphology.

From implications to applications

If paleontologists were routinely faced with large samples of relatively complete fossil hominoid skeletons from multiple localities, application of this study's results to the taxonomic interpretation of variation among the fossil samples would be straightforward, for the most part. The same set of data collected for this study could be

collected from the fossil specimens, and it could be analyzed in the same manner. For taxonomic interpretations, the most appropriate set of variables to use would be hand and foot ratios, as the DFAs in this study were based on hand and foot ratios, and DFAs directly address the question of how well groups can be discriminated from one another. Comparisons of means and DFAs could be conducted on hand and foot ratios from the fossil samples, and the extents of differences between the fossil samples in the analyses could be compared to the extents of differences between geographic groups of *Gorilla* and *Pan*. The researcher could then determine whether the fossil samples were different enough to be considered separate species, based on the modern analog taxa. This would be simple if differences between the fossil samples were greater than differences between the species of either *Gorilla* or *Pan*. This would be less simple if differences between the fossil samples were within the range of differences between species or subspecies of the living genera, because the taxonomic interpretation would differ depending on which genus was used as a model. In this case, the researcher could make taxonomic interpretations on the basis of each model and then perhaps assess, on the basis of accessory information, whether the fossil taxon is more likely to resemble *Gorilla* or *Pan* in relevant aspects of ecology and demography.

Unfortunately, most paleontologists work with small samples and incomplete skeletal material. Direct comparisons with the results of this study are unlikely to be possible in most cases. Under these circumstances, how can a paleontologist apply the results of this study to the interpretation of variation, and particularly the identification of species, in fossil hominoid limb bones?

First, the general model developed by this study, based on modern African apes, simply sets the stage for an analysis of fossil hominoid limb bones. It confirms that information about evolutionary relationships and divergences among congeneric groups is present in the limb bones. Further, it demonstrates that differences between groups are present at every level of the geographic and taxonomic hierarchy, from populations to species, and generally increase as the hierarchy is ascended. The researcher is cautioned that the presence of readily-detectable variation, even between large samples, is not sufficient to indicate a species-level difference, as comparisons of means find significant differences between subspecies and even populations.

Second, the results of this study suggest that certain types of variables are more useful than others for distinguishing African ape groups from one another. Bone lengths, bone length proportions, and measurements of tendon and ligament attachment sites play particularly large roles in differentiating groups. Even if the fossils under analysis are not the same elements analyzed here or are too incomplete to permit many of the measurements used in this study, researchers might focus on these types of variables to best discover differences between geographic groups.

Third, most hand and foot ratios proposed in this study to reflect functional differences between African ape groups do not appear to consistently indicate relative frequencies of characteristically arboreal and terrestrial positional behaviors. Until further studies identify limb bone variables that reliably track functional differences between individuals or groups, caution should be exercised in making functional interpretations of differences between fossil specimens in limb bone morphology.

Fourth, bolstered by the knowledge that limb bone morphology does, in fact, vary at the levels of species, subspecies and populations in modern African apes, a hominoid paleontologist could collect new data, different from that analyzed here and more directly applicable to the fossils under study, and compare differences between the fossils to the patterns of geographic variation found in modern African apes based on the new data.

Finally, in many cases the researcher will still be faced with the issue of different patterns of geographic variation in *Gorilla* and *Pan*. Skeletal correlates of the general ecological and demographic patterns seen in *Gorilla* and *Pan*, and thought to be responsible for their differences in patterns of geographic variation, could be brought to bear in assessing which modern patterns are more likely to apply to a fossil taxon. Perhaps large body size in a fossil taxon is a good indicator of a vegetation-dependent diet like that of *Gorilla*, and perhaps a *Gorilla*-like pattern of demography and geographic variation can be reasonably extrapolated. If a fossil taxon has smaller body size and an absence of dental adaptations associated with heavy folivory, this might imply a diet, pattern of dispersal behavior, and pattern of geographic variation more like that of *Pan*. The ability of hominoid paleontologists to choose appropriate modern analogs would be enhanced by further study of the relationship between aspects of the hominoid skeleton and patterns of ecology, demography, and geographic variation.

**Summary of findings**

Analysis of variation in raw linear measurements of the forelimb and hindlimb skeletons and ratios of linear measurements of hand and foot bones finds that *Gorilla* and *Pan* exhibit geographic variation in these variables at the levels of species, subspecies,

and population. At all three levels, those of species, subspecies, and populations, separation between groups is greater and more consistent in *Gorilla* than in *Pan*.

In both *Gorilla* and *Pan*, the taxonomic hierarchy is generally reflected in the extents of group separation, with stronger separation of species than of subspecies and with stronger separation of subspecies than of populations with a subspecies, although some analyses find the separation between the subspecies of *G. beringei* to be as great as the separation between the species of *Gorilla*. Patterns of group clustering also reflect taxonomic divisions in *Gorilla*, but group clustering patterns are weaker in *Pan*. In *Gorilla*, subspecies consistently cluster by species and populations usually cluster by subspecies, while *Pan* subspecies usually, but not always, cluster by species, and *Pan* populations usually cluster by species but not by subspecies.

The two species of *Gorilla*, *G. gorilla* and *G. beringei*, are generally better-differentiated than the two species of *Pan*, *P. troglodytes* and *P. paniscus*. This is surprising, as the proposal that *Gorilla* includes two species is not yet the consensus opinion, while the existence of two species of *Pan* has been accepted for several decades. In further support for a deep split within *Gorilla*, the two subspecies of *G. beringei* (*G. b. beringei* and *G. b. graueri*) consistently group with one another, to the exclusion of *G. g. gorilla*.

The subspecific affinities of two high-altitude populations of *G. beringei*, Kahuzi and Tshiaberimu, have remained ambiguous in some previous studies. In this study, Kahuzi specimens cluster comfortably with *G. b. graueri*, while Tshiaberimu specimens are more like *G. b. graueri* than like *G. b. beringei* but do not cluster consistently with either.

The recently-revived subspecies *G. g. diehli* groups with *G. g. gorilla* rather than with the subspecies of *G. beringei*. The analysis is constrained by a very small sample but it hints that this group may have its own unique morphological tendencies.

The most distinct subspecies of *P. troglodytes* is *P. t. verus*, but its separation from the other subspecies is not great. The recently-revived subspecies *P. t. vellerosus* is more similar to *P. t. troglodytes* than to *P. t. verus*, agreeing with results based on craniodental morphology rather than results based on genetics. The small sample of *P. t. vellerosus* in this study is not well-distinguished but shows signs of individual trends. Chimpanzee populations from the northwestern and southeastern parts of the *P. t. schweinfurthii* range differ from one another, but the observed separation of the populations offers only weak support for the proposal that they be considered separate subspecies, both because the separation between these two groups is weak and because populations of *P. t. schweinfurthii* and *P. t. troglodytes* are poorly sorted from one another in general.

Findings related to the distinctiveness of specific geographic groups and their relationships to one another, as well as general differences between *Gorilla* and *Pan* in the extents and patterns of observed geographic variation, are quite concordant overall with results from studies of craniodental morphology and genetics.

Based on analyses of hand and foot bone ratios, inter-element length proportions and measurements of tendon and ligament attachment sites appear to play particularly large roles is distinguishing species and subspecies, when results are compared from both *Gorilla* and *Pan* analyses. The prominent role of hand and foot bone lengths in separating geographic groups is also seen in the analyses of raw measurements from all

ten forelimb and hindlimb bones in the study. No strong patterns are found across the analyses in whether groups are better separated by hands or feet, or by forelimbs or hindlimbs, although the analyses of raw measurements point to especially strong differences between groups in the foot skeleton.

The potential relationship of the hand and foot bone ratios to variation in frequencies of characteristically arboreal and characteristically terrestrial positional behaviors was examined, and, based on directions of variation in two pairs of taxa with well-established contrasts in positional behavior, only four ratios could possibly reflect differences in positional behavior across African ape taxa. These four ratios do not correspond to those that play the greatest roles in differentiating African ape taxa, across both species and subspecies and both *Gorilla* and *Pan*; therefore, if they do reflect functional differences, African ape taxonomic divisions do not correspond to these functional differences.

The results of this study have implications for the interpretation of variation in hominoid fossils. Although taxonomic and systematic interpretations of the hominoid fossil record are usually based on craniodental morphology, postcranial morphology, specifically morphology of the forelimb and hindlimb, is likely to reflect the same patterns of variation between geographic groups. In the hands and feet, bone lengths and measurements of attachment sites for tendons and ligaments are particularly useful types of variables for differentiating geographic groups. Many features of the hand and foot that have been proposed to reflect differences among hominoids in positional behavior and substrate/superstrate use do not appear to be reliable indicators of functional differences between taxa of African apes.

Differences between *Gorilla* and *Pan* in their patterns and extents of geographic variation may reflect ecological and demographic differences between the two genera. *Gorilla* groups are less ecologically flexible, and groups tend to be smaller and more isolated, which may have resulted in the greater differentiation observed between geographic groups of *Gorilla*. *Pan* is more flexible in its adaptations, and individuals (especially females) are known to disperse great distances, which may have resulted in the much greater admixture and much weaker population structuring seen in *Pan*. In this light, the choice of an extant model taxon on which to base taxonomic interpretations of fossil hominoids should be understood to entail a hypothesis about the ecology and demography of the extinct taxon, and taxonomic interpretations will differ depending on whether a *Gorilla* model or a *Pan* model is chosen.

## APPENDIX 1: Sources and proposed functional relevance of hand and foot ratios

Hand and foot variables identified as "arboreal" are proposed to reflect the relative frequency of climbing and suspension. Hand and foot variables identified as "terrestrial" are proposed to reflect the relative frequency of knuckle-walking. Each variable defined below is a ratio of two linear measurements, which are defined in Appendix 3.

Note that these variables are not interpreted along a continuum from arboreal to terrestrial. Each variable is proposed to reflect the frequency of positional behaviors that are either distinctively arboreal or distinctively terrestrial. Therefore, each variable is expressed along a continuum of lesser or greater arboreality or lesser or greater terrestriality.

Skeletal elements are abbreviated as follows: third metacarpal (MC3), third proximal hand phalanx (HP3), third metatarsal (MT3), third proximal foot phalanx (FP3), and calcaneus (CALC).

### *Hand*

Arboreal

- MC3 arch height ratio (MCAH) = MC3 height of arch/length

MCAH is intended to measure metacarpal curvature. The metacarpals have been thought to experience strong bending forces during climbing and suspension, which are resisted by curvature of the shaft (Preuschoft, 1973; Susman, 1979). Susman (1979) observed greater metacarpal shaft curvature in orangutans than in African apes, suggesting that

increased curvature may be related to increased arboreality. The ratio definition is based on Langdon's (1986) index for arch of shaft in the metatarsal.

- HP3 flexor sheath ridge size ratio (HPFS) = HP3 maximum shaft width/minimum shaft width

HPFS is intended to reflect the development of the flexor sheath ridges, which probably develop in response to contraction of the long digital flexors during climbing and suspension (Susman and Stern, 1979). The flexor sheath ridges are attachments for the flexor sheaths, ligamentous sheets that hold the flexor tendons against the phalanges and resist their tendency to pull away from the bones when the muscle contracts and interphalangeal joints flex. Susman (1979) found flexor sheath ridge height to be among variables that particularly distinguished hylobatids from other apes in a discriminant function analysis, suggesting a relationship to arboreal locomotor behaviors. HPFS measures flexor sheath ridge development in a radioulnar direction, rather than measuring ridge height, due to difficulties in measuring the height of a single ridge (not an average of the two ridges) with the caliper's depth gauge.

- HP3 arch height ratio (HPAH) = HP3 height of arch/length

HPAH is intended to measure proximal hand phalanx curvature, which has been associated with strong bending forces during climbing and suspension (Preuschoft, 1973; Susman, 1979; Richmond, 2007). Using a measure of curvature in radians, Susman (1979) found that the proximal hand phalanges of gorillas were less curved than those of orangutans, and those of chimpanzees and bonobos were intermediate, suggesting a

relationship to arboreality. The ratio definition is based on Langdon's (1986) index for arch of shaft in the metatarsal.

- phalanx-metacarpal length ratio (XPMC) = HP3 length/MC3 length

XPMC is intended to reflect the proportional length of the proximal hand phalanx. The ratio definition is the same as that used by Susman (1979), who found that the proximal phalanges of African apes were shorter relative to the metacarpals than those of orangutans or hylobatids, and gorilla proximal phalanges were relatively shorter than those of chimpanzees. These comparisons suggest that relatively longer proximal phalanges are associated with greater arboreality. Inouye (1992) also found African apes to have relatively shorter proximal phalanges than orangutans, and gorillas to have relatively shorter proximal phalanges than chimpanzees, using various size surrogates. In contrast, Napier and Davis (1959) conclude that brachiators, defined as primates that raise the arms above the head during locomotion, are specialized by having both long hand phalanges and long metacarpals. Similarly, Schultz (1930) found the index of third ray phalangeal length to total third ray length to be unexpectedly constant across hominoids, indicating that the metacarpal and the phalanges maintain the same proportional relationship to one another regardless of hand length.

It could be argued that shorter phalanges are an adaptation for terrestriality (e.g., Tuttle, 1970), rather than longer phalanges being an adaptation for arboreality. One does not necessarily exclude the other. Variation in phalangeal length is here interpreted in terms of arboreal behavior to be consistent with Susman (1979), who defined the ratio used here.

Terrestrial

- MC3 midshaft diameter ratio (MCM) = MC3 dorso-palmar midshaft diameter/radio-ulnar midshaft diameter

MCM is intended to reflect the amount of dorsopalmarly-directed bending stress relative to the amount of radioulnarly-directed bending stress in the metacarpal. Bending stresses related to knuckle-walking would be expected to be directed primarily in a dorso-palmar direction, and dorso-palmar midshaft diameter would be expected to increase in order to resist these bending stresses. Susman (1979) found dorsopalmar midshaft diameter to be among measurements that array the apes from more terrestrial, associated with higher values, to more arboreal, associated with lower values, using discriminant function analysis. Similarly, the means of an index of dorsopalmar midshaft diameter to metacarpal length array the apes from more terrestrial to more arboreal.

- MC3 dorsal ridge height ratio (MCDR) = MC3 head height plus ridge/head height

MCDR is intended to measure the development of the dorsal ridge of the metacarpal, which has been related to buttressing of the metacarpophalangeal joint during knuckle-walking (Tuttle, 1970; Susman, 1979). The dorsal ridge has also been considered a plastic response to compressive forces on the hyperextended joint during knuckle-walking (Inouye, 1990). Dorsal ridge expression in the African apes is greatest in gorillas and least in bonobos, and dorsal ridges are absent in orangutans and hylobatids (Susman, 1979; Inouye, 2003).

- MC3 head shape ratio (MCHS) = MC3 head width/head height

MCHS is intended to reflect the amount of load-bearing on the metacarpal head (Susman, 1979) during knuckle-walking. Susman (1979) did not find radioulnar head diameter to contribute much to arraying or separating the ape taxa in a discriminant function analysis; however, he did find the heads of MC3 and MC4 to exhibit radioulnar expansion of their dorsal aspects, relative to their palmar aspects, in African apes but not in orangutans or hylobatids, suggesting that a relationship to knuckle-walking might exist.

- MC3 biepicondylar width ratio (MCB) = MC3 biepicondylar width/head width

MCB is intended to measure the development of the collateral ligament attachments at the metacarpal head, which seems likely to be associated with strain at the attachment sites during the joint hyperextension characteristic of knuckle-walking. Susman (1979) considers the epicondyles to participate in buttressing the metacarpophalangeal joint during knuckle-walking. Susman (1979) found that a ratio of biepicondylar diameter to metacarpal length arrays apes along a behavioral continuum from arboreality to terrestriality, with the highest values in gorillas. The denominator was changed in the current study so the ratio could more directly reflect the projection of the epicondyles beyond the sides of the metacarpal head.

- HP3 midshaft diameter ratio (HPMD) = HP3 dorso-palmar midshaft diameter/radio-ulnar midshaft diameter

HPMD is intended to reflect the amount of dorsopalmarly-directed bending stress relative to the amount of radioulnarly-directed bending stress in the proximal hand phalanx. Bending stresses related to knuckle-walking would be expected to be directed primarily in a dorso-palmar direction, and dorso-palmar midshaft diameter would be expected to

increase in order to resist these bending stresses. Susman (1979) included dorsopalmar midshaft diameter of the proximal hand phalanx in his study, but it did not contribute greatly to separation of groups in the discriminant function analysis; however, support for the relationship of terrestriality and increased dorsopalmar midshaft diameter of the metacarpal (see MCM) justifies the further investigation of dorsopalmar midshaft diameter of the proximal hand phalanx.

- HP3 base width ratio (HPBD) = HP3 base width/minimum shaft width

HPBD is intended to reflect relative amounts of load-bearing on the phalangeal base during knuckle-walking. Susman (1979) found large radioulnar base diameters, among other measurements, to distinguish African apes from orangutans and hylobatids in a discriminant function analysis, supporting a relationship to knuckle-walking. In addition, radioulnar base diameter is the measurement that contributes the most to separation of hylobatids from other apes in the same analysis.

- HP3 trochlear width ratio (HPTW) = HP3 trochlear width/minimum shaft width

HPTW is intended to measure expansion of the trochlea of the proximal phalanx, which could reflect weight-bearing during knuckle-walking. Susman (1979) found radioulnar width of the trochlea to be among measurements that distinguish African apes from orangutans and hylobatids, with larger values in the African apes, using discriminant function analysis.

- HP3 glenoid plate tubercle size ratio (HPGT) = HP3 maximum base height/articular base height

HPGT is intended to reflect the development of the glenoid plate tubercles, which are likely to form in response to strain at the attachment sites for the glenoid plate during hyperextension of the metacarpophalangeal joint during knuckle-walking. Susman (1979) observed the presence of the fibrocartilaginous glenoid plate and ligament on the palmar surface of the metacarpophalangeal joint capsule in chimpanzees and gorillas but not in orangutans. He did not measure the associated tubercles, and an original measurement ratio is used in this study.

- hand power arm:load arm ratio (XHPL) = MC3 head height(1/2)/HP3 length

XHPL is intended to measure the biomechanical relationship between the power arm and the load arm of the hand during knuckle-walking (Susman, 1979). The ratio definition is the same as that used by Susman (1979), who found it to array apes along a continuum, with higher values associated with greater terrestriality and lower values associated with greater arboreality.

***Foot***

Arboreal

- MT3 arch height ratio (MTAH) = MT3 height of arch/length

MTAH is intended to measure metatarsal curvature. As curvature of the metacarpals and the hand and foot phalanges is thought to be a response to bending forces experienced during arboreal behaviors (Preuschoft, 1973; Susman, 1979; Stern and Susman, 1983), and as the metatarsals are intimately involved with climbing, as well, a measure of metatarsal curvature seemed appropriate. The ratio is the same as that used by Langdon (1986), but he considered metatarsal shaft arching to reflect use of the metatarsals as a

lever, which sounds as if he were referring to terrestrial locomotion although he did not specify. Langdon (1986) found hominoid third metatarsals to be more arched than those of monkeys and African ape third metatarsals to be more arched than those of orangutans.

- FP3 flexor sheath ridge size ratio (FPFS) = FP3 maximum shaft width/minimum shaft width

FPFS is intended to reflect the development of the flexor sheath ridges of the foot phalanx. The explanation given for HPFS of likely functional significance and measurement method applies to FPFS, as well.

- FP3 arch height ratio (FPAH) = FP3 height of arch/length

FPAH is intended to reflect foot phalanx curvature, which has been related to grasping and arboreality (Preuschoft, 1973; Stern and Susman, 1983). Using a different measure of curvature from that used in this study, Stern and Susman (1983) found the third proximal foot phalanx of gorillas to be less curved than that of chimpanzees and bonobos. The ratio definition is based on Langdon's (1986) arch height index for the metatarsal.

- CALC cuboid facet shape ratio (CCFS) = CALC cuboid facet height/cuboid facet width

CCFS is intended to reflect foot mobility related to arboreal behaviors (Gebo, 1992). The ratio definition is the same as that used by Gebo (1992), but the orientation of the calcaneus in this study follows Langdon (1986), which results in a different orientation of the cuboid facet from the orientation depicted by Gebo (1992). Gebo (1992) found this ratio to array the great apes from most to least arboreal, with the highest values for orangutans.

- CALC cuboid facet depth ratio (CCFD) = CALC cuboid facet depth/cuboid facet width

CCFD is intended to reflect foot mobility related to arboreal behaviors (Langdon, 1986; Gebo, 1992). The ratio definition is the same as that used by Langdon (1986), who found it to array great apes from most to least arboreal, with the highest values for orangutans. Gebo (1992) also observed that that this indented facet, in which the cuboid pivots on the calcaneus, is flatter in gorillas than in chimpanzees, indicating less mobility in the gorilla foot.

- phalanx-metatarsal length ratio (XPMT) = FP3 length/MT3 length

XPMT is intended to reflect the proportional length of the proximal foot phalanx. Longer toe bones have been associated with arboreality (Langdon, 1986; Gebo, 1992). Schultz (1963) measured the total length of third ray phalanges relative to the length of the third metatarsal and found that orangutans have longer toes than African apes and chimpanzees have longer toes than gorillas. The ratio definition is an adaptation of that used by Schultz (1963).

<u>Terrestrial</u>

- MT3 biepicondylar width ratio (MTB) = MT3 biepicondylar width/head width

MTB is intended to measure the development of the collateral ligament attachments at the metatarsal head. Although reports vary on how African apes use their toes during walking (Tuttle, 1970; Tuttle and Watts, 1985; Sarmiento, 1994), it appears that at least sometimes they extend or hyperextend the metatarsophalangeal joint and bear weight on the toes. At these times, the collateral ligaments are likely to experience strain, which is

likely to be reflected in the development of their attachment sites at the epicondyles. As the epicondyles contribute to the dorsal ridges of both the metatarsals and metacarpals, when dorsal ridges are present, it is relevant to note that Inouye (2003) found a higher frequency of third metatarsal dorsal ridges in *Gorilla* than in *Pan*.

- CALC calcaneal tendon facet width ratio (CCTW) = CALC tendon facet width/tuberosity height

CCTW is intended to reflect the relative amount of plantarflexion of the foot by the gastrocnemius muscle, as occurs in walking. The relative width of the facet for attachment of the calcaneal tendon, which is the tendon for the gastrocnemius, seems likely to increase with increased muscle function. The ratio definition is original to this study. Greater calcaneal *tuberosity* width has been widely discussed as reflecting terrestriality (Langdon, 1986; Gebo, 1992; Sarmiento, 1994), and measurements of calcaneal tuberosity width were collected, but the measurement endpoints were frequently not homologous between specimens. Tendon facet width appeared to be a more anatomically interpretable measurement.

- calcaneal tuberosity-metatarsal length ratio (XCMT) = CALC tuberosity length/MT3 length

XCMT is intended to approximate the ratio of biomechanical power arm to load arm in plantarflexion (Schultz, 1963; Langdon, 1986). A longer calcaneal tuberosity is thought to permit stronger, but slower, muscle action, which appears to be associated with terrestrial plantigrady in apes (Langdon, 1986; Gebo, 1992; Sarmiento, 1994). Various measures of the ratio of power arm to load arm or of the power arm alone have shown

gorillas to have a greater power arm than chimpanzees and both African apes to have greater power arms than orangutans (Schultz, 1963; Langdon, 1986; Gebo, 1992). The ratio definition follows Langdon (1986) in using calcaneal tuberosity length to represent the power arm, and metatarsal length was chosen to represent load arm as a modification of Schultz's (1963) load arm, which included the entire third ray and most of the tarsus.

# APPENDIX 2: Sample sizes

## *Raw measurements*

Table 1. *Gorilla* species and subspecies sample sizes for raw measurements (pooled sexes)

| | All variables | Forelimb | Hindlimb | Long bones | Hand | Foot |
|---|---|---|---|---|---|---|
| *G. beringei* | 25 | 29 | 28 | 37 | 38 | 33 |
| *beringei* | 9 | 12 | 11 | 17 | 16 | 13 |
| *graueri* | 16 | 17 | 17 | 20 | 22 | 20 |
| *G. gorilla* | 105 | 123 | 111 | 132 | 173 | 164 |
| *gorilla* | 104 | 122 | 110 | 131 | 172 | 163 |
| *diehli* | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gorilla* total | 130 | 152 | 139 | 169 | 211 | 197 |

Table 2. *Pan* species and subspecies sample sizes for raw measurements (pooled sexes)

| | All variables | Forelimb | Hindlimb | Long bones | Hand | Foot |
|---|---|---|---|---|---|---|
| *P. troglodytes* | 121 | 151 | 130 | 164 | 196 | 185 |
| *troglodytes* | 93 | 110 | 99 | 111 | 146 | 143 |
| *schweinfurthii* | 17 | 22 | 17 | 32 | 28 | 23 |
| *verus* | 8 | 13 | 11 | 18 | 16 | 13 |
| *vellerosus* | 3 | 6 | 3 | 3 | 6 | 6 |
| *P. paniscus* | 17 | 17 | 19 | 20 | 19 | 19 |
| *Pan* total | 138 | 168 | 149 | 184 | 215 | 204 |

Table 3. Sample sizes of *Gorilla* populations for PCAs of raw measurements (pooled sexes)

| | All variables | Forelimb | Hindlimb | Long bones | Hand | Foot |
|---|---|---|---|---|---|---|
| *G. b. beringei* | | | | | | |
| 1-Virungas | 9 | 12 | 11 | 17 | 16 | 13 |
| *G. b. graueri* | | | | | | |
| 2-Mwenga-Fizi | 9 | 10 | 9 | 9 | 12 | 12 |
| 3-Kahuzi | 2 | 2 | 2 | 3 | 2 | 2 |
| 4-Tshiaberimu | 2 | 2 | 2 | 4 | 4 | 2 |
| 5-Utu | 3 | 3 | 4 | 4 | 4 | 4 |
| *G. g. gorilla* | | | | | | |
| 6-Coast | 14 | 18 | 15 | 21 | 29 | 26 |
| 7-Ebolowa | 38 | 42 | 39 | 45 | 49 | 46 |
| 8-Abong Mbang/Metet | 26 | 32 | 29 | 35 | 39 | 36 |
| 9-Batouri/Lomie | 22 | 25 | 23 | 26 | 47 | 47 |
| 10-Sangha | 4 | 5 | 4 | 4 | 8 | 8 |
| *G. g. diehli* | | | | | | |
| 11-Cross River | 1 | 1 | 1 | 1 | 1 | 1 |
| *Gorilla* total | 130 | 152 | 139 | 169 | 211 | 197 |

Table 4. Sample sizes of *Pan* populations for PCAs of raw measurements (pooled sexes)

| | All variables | Forelimb | Hindlimb | Long bones | Hand | Foot |
|---|---|---|---|---|---|---|
| *P. t. schweinfurthii* | | | | | | |
| 1-NW eastern | 9 | 12 | 9 | 20 | 15 | 12 |
| 2-SE eastern | 8 | 10 | 8 | 12 | 13 | 11 |
| *P. t. troglodytes* | | | | | | |
| 3-Coast | 23 | 29 | 25 | 27 | 32 | 32 |
| 4-Ebolowa | 32 | 32 | 33 | 37 | 36 | 37 |
| 5-Abong Mbang/Metet | 12 | 14 | 14 | 14 | 16 | 16 |
| 6-Batouri/Lomie | 17 | 20 | 17 | 18 | 41 | 42 |
| 7-Sangha | 2 | 3 | 2 | 4 | 7 | 6 |
| *P. t. vellerosus* | | | | | | |
| 8-North of Sanaga River | 3 | 6 | 3 | 3 | 6 | 6 |
| *P. t. verus* | | | | | | |
| 9-Ivory Coast and Liberia | 8 | 13 | 11 | 18 | 16 | 13 |
| *P. paniscus* | | | | | | |
| 10-South of Congo River | 17 | 17 | 19 | 20 | 19 | 19 |
| *Pan* total | | | | | | |

***Hand and foot ratios***

In the analyses of hand and foot bone measurement ratios, the total number of *Gorilla* individuals was 221, and the total number of *Pan* individuals was 227; however, these numbers are greater than either the total number of hands or the total number of feet, because some individuals preserved only one or the other.

Table 5. *Gorilla* species and subspecies sample sizes for hand and foot ratios

| | male hand | female hand | male foot | female foot |
|---|---|---|---|---|
| *Gorilla beringei* | 25 | 13 | 19 | 14 |
| *beringei* | 10 | 6 | 6 | 7 |
| *graueri* | 15 | 7 | 13 | 7 |
| *Gorilla gorilla* | 97 | 74 | 91 | 73 |
| *gorilla* | 96 | 74 | 90 | 73 |
| *diehli* | 1 | 0 | 1 | 0 |
| *Gorilla* total | 122 | 87 | 110 | 87 |

Table 6. *Pan* species and subspecies sample sizes for hand and foot ratios

| | male hand | female hand | male foot | female foot |
|---|---|---|---|---|
| *Pan troglodytes* | 86 | 106 | 84 | 102 |
| *troglodytes* | 63 | 81 | 62 | 81 |
| *schweinfurthii* | 18 | 9 | 16 | 8 |
| *verus* | 5 | 10 | 6 | 7 |
| *vellerosus* | 0 | 6 | 0 | 6 |
| *Pan paniscus* | 7 | 12 | 8 | 11 |
| *Pan* total | 93 | 118 | 92 | 113 |

Table 7. Sample sizes of *Gorilla* populations from west-central Africa, for direct comparison with *Pan* (hand and foot ratios)

| | male hand | female hand | male foot | female foot |
|---|---|---|---|---|
| Coast | 18 | 9 | 16 | 10 |
| Cameroon Interior | 43 | 43 | 42 | 42 |
| Ebolowa | 29 | 20 | 26 | 19 |

Table 8. Sample sizes of *Pan* populations from west-central Africa, for direct comparison with *Gorilla* (hand and foot ratios)

| | male hand | female hand | male foot | female foot |
|---|---|---|---|---|
| Coast | 16 | 14 | 17 | 14 |
| Cameroon Interior | 15 | 42 | 15 | 43 |
| Ebolowa | 20 | 16 | 21 | 16 |

## APPENDIX 3: Abbreviations and descriptive names of variables

Tables in Chapters 3 and 4 use abbreviations to refer to variables in the analyses. These abbreviations can be found in the tables that define the variables (Table 2.4 for raw measurements, Tables 2.5 and 2.6 for hand and foot ratios), but these tables list the descriptive names first. For ease of reference, Tables 1 and 2 below list each variable by its abbreviation, with descriptive names in parentheses.

Note that Tables 1 and 2 are organized by skeletal element. Each abbreviation begins with a prefix of one or more letters indicating the skeletal element under which it is listed. The correspondence between prefixes and skeletal elements should be intuitive, except in the case of inter-element ratios, which begin with the letter "X".

Table 1. Abbreviations and descriptive names for measurements used in analyses of raw measurements

***Forelimb***

Humerus

HUM_LENGTH (length)
HUM_ML_MID (medio-lateral midshaft diameter)
HUM_AP_MID (antero-posterior midshaft diameter)
HUM_SI_HEAD (head height)
HUM_DISTARTWD (distal articular width)
HUM_BIEPI (biepicondylar width)

Radius

RAD_LENGTH (length)
RAD_ML_MID (medio-lateral midshaft diameter)
RAD_AP_MID (antero-posterior midshaft diameter)
RAD_ML_HEAD (medio-lateral head diameter)
RAD_DISTALWD (distal width)

Metacarpal 3

MC_LENGTH (length)
MC_RU_MID (radio-ulnar midshaft diameter)
MC_DP_MID (dorso-palmar midshaft diameter)
MC_RU_HEAD (head width)
MC_BIEPI (biepicondylar width)

Proximal hand phalanx 3

HP_LENGTH (length)
HP_RU_MAX (maximum shaft width)
HP_RU_MIN (minimum shaft width)
HP_RU_BASE (base width)
HP_RU_TROCH (trochlear width)

***Hindlimb***

Femur

FEM_LENGTH (length)
FEM_ML_MID (medio-lateral midshaft diameter)
FEM_AP_MID (antero-posterior midshaft diameter)
FEM_HEAD_HT (head height)
FEM_BICON_WD (bicondylar width)

Tibia

TIB_LENGTH (length)
TIB_ML_MID (medio-lateral midshaft diameter)
TIB_AP_MID (antero-posterior midshaft diameter)
TIB_PLATEAU (plateau width)

Calcaneus

C_LENGTH (length)
C_TUB_LENGTH (tuberosity length)
C_TUB_HTADJ (tuberosity height)
C_TENDON_WD (tendon facet width)
C_CUB_WD (cuboid facet width)
C_CUB_DPADJ (cuboid facet depth)

Metatarsal 1

MT1_LENGTH (length)

Metatarsal 3

MT3_LENGTH (length)
MT3_ML_HEAD (head width)
MT3_BIEPI (biepicondylar width)

Proximal foot phalanx 3

FP_LENGTH (length)
FP_MAXSHAFT (maximum shaft width)
FP_MINSHAFT (minimum shaft width)

Table 2. Abbreviations and descriptive names for hand and foot ratios

***Hand***
Metacarpal 3
MCAH (arch height ratio)
MCM (midshaft diameter ratio)
MCDR (dorsal ridge height ratio)
MCHS (head shape ratio)
MCB (biepicondylar width ratio)
Proximal hand phalanx 3
HPFS (flexor sheath ridge size ratio)
HPAH (arch height ratio)
HPMD (midshaft diameter ratio)
HPBD (base width ratio)
HPTW (trochlear width ratio)
HPGT (glenoid plate tubercle size ratio)
Inter-element
XPMC (phalanx-metacarpal length ratio)
XHPL (hand power arm:load arm ratio)

***Foot***
Metatarsal 3
MTAH (arch height ratio)
MTB (biepicondylar width ratio)
Proximal foot phalanx 3
FPFS (flexor sheath ridge size ratio)
FPAH (arch height ratio)
Calcaneus
CCFS (cuboid facet shape ratio)
CCFD (cuboid facet depth ratio)
CCTW (calcaneal tendon facet width ratio)
Inter-element
XPMT (phalanx-metatarsal length ratio)
XCMT (calcaneal tuberosity-metatarsal length ratio)

## APPENDIX 4: Descriptive statistics

Table 1. Descriptive statistics for raw measurements in *Gorilla* by sex and species

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | | | | |
| N of cases | 31 | 87 | 20 | 61 |
| Minimum | 366.84 | 392.38 | 340.25 | 331.86 |
| Maximum | 468.59 | 492.44 | 399.82 | 417.28 |
| Mean | 434.41 | 444.36 | 365.78 | 371.56 |
| SD | 19.87 | 21.95 | 14.04 | 16.89 |
| HUM_ML_MID | | | | |
| N of cases | 31 | 88 | 20 | 61 |
| Minimum | 28.56 | 29.09 | 24.78 | 20.57 |
| Maximum | 38.13 | 41.19 | 32.98 | 33.50 |
| Mean | 34.13 | 35.37 | 26.85 | 27.89 |
| SD | 2.34 | 2.64 | 1.83 | 2.68 |
| HUM_AP_MID | | | | |
| N of cases | 31 | 88 | 20 | 61 |
| Minimum | 25.05 | 24.47 | 23.10 | 17.08 |
| Maximum | 33.79 | 34.68 | 28.81 | 29.28 |
| Mean | 30.32 | 30.55 | 25.02 | 25.23 |
| SD | 1.72 | 1.91 | 1.36 | 2.21 |
| HUM_SI_HEAD | | | | |
| N of cases | 31 | 88 | 20 | 62 |
| Minimum | 45.15 | 47.49 | 43.66 | 38.21 |
| Maximum | 64.35 | 67.03 | 58.65 | 52.31 |
| Mean | 58.71 | 57.93 | 48.32 | 46.13 |
| SD | 3.72 | 3.81 | 3.15 | 3.03 |
| | | | | |
| | | | | |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| HUM_DISTARTWD | | | | |
| N of cases | 31 | 88 | 18 | 61 |
| Minimum | 53.19 | 52.82 | 46.07 | 44.07 |
| Maximum | 76.97 | 75.45 | 57.35 | 59.81 |
| Mean | 64.72 | 66.12 | 50.39 | 51.67 |
| SD | 5.17 | 3.99 | 3.07 | 3.36 |
| HUM_BIEPI | | | | |
| N of cases | 31 | 87 | 18 | 62 |
| Minimum | 81.65 | 84.73 | 73.50 | 69.16 |
| Maximum | 117.80 | 120.35 | 84.42 | 87.17 |
| Mean | 100.92 | 101.39 | 79.47 | 78.26 |
| SD | 7.58 | 6.59 | 2.91 | 4.22 |
| *Radius* | | | | |
| RAD_LENGTH | | | | |
| N of cases | 28 | 90 | 16 | 63 |
| Minimum | 278.82 | 306.86 | 278.11 | 267.31 |
| Maximum | 380.13 | 400.28 | 312.06 | 321.88 |
| Mean | 350.38 | 356.21 | 291.33 | 298.03 |
| SD | 19.27 | 18.01 | 10.05 | 11.30 |
| RAD_ML_MID | | | | |
| N of cases | 28 | 90 | 17 | 63 |
| Minimum | 18.15 | 17.14 | 16.05 | 13.36 |
| Maximum | 27.35 | 28.11 | 21.68 | 21.42 |
| Mean | 22.33 | 22.13 | 17.80 | 17.00 |
| SD | 2.21 | 2.01 | 1.40 | 1.75 |
| RAD_AP_MID | | | | |
| N of cases | 28 | 90 | 17 | 63 |
| Minimum | 14.40 | 14.19 | 11.94 | 12.60 |
| Maximum | 20.29 | 22.42 | 14.94 | 17.70 |
| Mean | 17.43 | 18.34 | 13.45 | 14.67 |
| SD | 1.38 | 1.59 | 0.86 | 1.20 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| RAD_ML_HEAD | | | | |
| N of cases | 29 | 89 | 18 | 63 |
| Minimum | 27.69 | 24.03 | 23.39 | 23.04 |
| Maximum | 37.59 | 38.52 | 30.60 | 29.26 |
| Mean | 33.57 | 32.75 | 26.46 | 25.56 |
| SD | 2.29 | 2.39 | 1.74 | 1.57 |
| RAD_DISTALWD | | | | |
| N of cases | 28 | 90 | 16 | 63 |
| Minimum | 33.82 | 32.51 | 29.36 | 28.96 |
| Maximum | 48.43 | 51.22 | 36.88 | 40.93 |
| Mean | 40.89 | 42.39 | 33.45 | 35.06 |
| SD | 3.03 | 3.28 | 2.14 | 2.53 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | | | | |
| N of cases | 27 | 100 | 15 | 80 |
| Minimum | 74.83 | 86.61 | 69.61 | 75.97 |
| Maximum | 100.51 | 112.75 | 80.43 | 92.94 |
| Mean | 88.21 | 99.35 | 74.97 | 84.31 |
| SD | 5.16 | 4.97 | 3.35 | 3.60 |
| MC_RU_MID | | | | |
| N of cases | 27 | 100 | 15 | 80 |
| Minimum | 9.54 | 9.67 | 8.39 | 7.98 |
| Maximum | 13.57 | 13.94 | 11.04 | 11.57 |
| Mean | 11.49 | 11.63 | 9.61 | 9.57 |
| SD | 1.14 | 0.94 | 0.87 | 0.83 |
| MC_DP_MID | | | | |
| N of cases | 27 | 100 | 15 | 80 |
| Minimum | 10.16 | 10.76 | 9.01 | 7.86 |
| Maximum | 14.96 | 16.60 | 13.04 | 13.32 |
| Mean | 13.03 | 13.56 | 10.80 | 10.81 |
| SD | 1.21 | 1.17 | 1.07 | 1.07 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| MC_RU_HEAD | | | | |
| N of cases | 27 | 100 | 14 | 80 |
| Minimum | 13.63 | 17.00 | 13.20 | 13.51 |
| Maximum | 23.25 | 23.98 | 17.58 | 18.52 |
| Mean | 18.93 | 20.08 | 15.01 | 15.80 |
| SD | 1.74 | 1.39 | 1.14 | 0.98 |
| MC_BIEPI | | | | |
| N of cases | 27 | 101 | 14 | 80 |
| Minimum | 15.82 | 20.28 | 14.85 | 15.09 |
| Maximum | 23.65 | 28.11 | 17.69 | 21.74 |
| Mean | 20.94 | 23.92 | 16.34 | 18.53 |
| SD | 1.71 | 1.76 | 0.80 | 1.45 |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | | | | |
| N of cases | 25 | 101 | 14 | 77 |
| Minimum | 50.73 | 54.37 | 48.20 | 49.37 |
| Maximum | 64.35 | 71.15 | 54.24 | 59.33 |
| Mean | 59.83 | 63.83 | 51.00 | 54.41 |
| SD | 2.72 | 3.39 | 1.84 | 2.45 |
| HP_RU_MAX | | | | |
| N of cases | 25 | 101 | 14 | 77 |
| Minimum | 14.46 | 16.11 | 14.12 | 13.91 |
| Maximum | 25.03 | 24.64 | 16.63 | 18.24 |
| Mean | 20.34 | 20.47 | 15.46 | 16.00 |
| SD | 1.98 | 1.48 | 0.86 | 1.02 |
| HP_RU_MIN | | | | |
| N of cases | 25 | 101 | 14 | 77 |
| Minimum | 12.16 | 14.72 | 11.56 | 12.09 |
| Maximum | 20.52 | 21.12 | 14.50 | 16.45 |
| Mean | 17.05 | 18.36 | 13.13 | 14.13 |
| SD | 1.46 | 1.27 | 0.67 | 0.91 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| HP_RU_BASE | | | | |
| N of cases | 25 | 99 | 13 | 77 |
| Minimum | 16.02 | 20.67 | 16.09 | 16.58 |
| Maximum | 24.58 | 27.49 | 18.00 | 21.49 |
| Mean | 21.65 | 24.17 | 17.16 | 19.15 |
| SD | 1.74 | 1.40 | 0.57 | 1.08 |
| HP_RU_TROCH | | | | |
| N of cases | 25 | 101 | 14 | 77 |
| Minimum | 11.86 | 14.48 | 11.96 | 12.15 |
| Maximum | 17.61 | 19.83 | 13.74 | 15.30 |
| Mean | 15.86 | 16.84 | 12.86 | 13.72 |
| SD | 1.18 | 1.01 | 0.56 | 0.76 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | | | | |
| N of cases | 27 | 80 | 18 | 62 |
| Minimum | 356.67 | 325.83 | 289.05 | 290.18 |
| Maximum | 396.60 | 418.31 | 329.17 | 334.44 |
| Mean | 374.24 | 374.21 | 313.15 | 312.85 |
| SD | 11.92 | 17.85 | 11.56 | 10.56 |
| FEM_ML_MID | | | | |
| N of cases | 28 | 80 | 19 | 62 |
| Minimum | 37.35 | 34.66 | 29.83 | 27.45 |
| Maximum | 46.80 | 46.20 | 38.73 | 39.43 |
| Mean | 40.90 | 41.49 | 32.76 | 33.74 |
| SD | 2.52 | 2.25 | 2.16 | 3.02 |
| FEM_AP_MID | | | | |
| N of cases | 28 | 80 | 19 | 62 |
| Minimum | 30.12 | 24.38 | 24.88 | 22.10 |
| Maximum | 37.00 | 36.43 | 34.06 | 30.63 |
| Mean | 33.71 | 30.85 | 27.68 | 25.87 |
| SD | 1.65 | 2.21 | 2.22 | 2.06 |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| FEM_HEAD_HT | | | | |
| N of cases | 31 | 81 | 19 | 62 |
| Minimum | 39.85 | 40.72 | 37.16 | 35.65 |
| Maximum | 57.73 | 56.59 | 45.84 | 44.75 |
| Mean | 51.27 | 49.84 | 40.44 | 40.16 |
| SD | 3.65 | 2.67 | 2.05 | 1.94 |
| FEM_BICON_WD | | | | |
| N of cases | 28 | 80 | 17 | 61 |
| Minimum | 76.72 | 72.38 | 62.95 | 60.63 |
| Maximum | 100.11 | 96.67 | 77.13 | 78.78 |
| Mean | 88.56 | 86.84 | 69.75 | 69.72 |
| SD | 5.30 | 4.99 | 4.38 | 4.22 |
| *Tibia* | | | | |
| TIB_LENGTH | | | | |
| N of cases | 29 | 80 | 18 | 61 |
| Minimum | 284.32 | 270.32 | 231.29 | 235.26 |
| Maximum | 322.07 | 353.33 | 263.93 | 290.68 |
| Mean | 301.77 | 313.78 | 249.50 | 259.76 |
| SD | 10.25 | 16.24 | 8.21 | 10.61 |
| TIB_ML_MID | | | | |
| N of cases | 29 | 80 | 18 | 61 |
| Minimum | 19.25 | 18.01 | 14.19 | 14.76 |
| Maximum | 23.92 | 25.63 | 21.19 | 21.24 |
| Mean | 21.53 | 21.91 | 16.67 | 17.59 |
| SD | 1.18 | 1.49 | 1.60 | 1.61 |
| TIB_AP_MID | | | | |
| N of cases | 29 | 80 | 18 | 61 |
| Minimum | 26.32 | 25.23 | 23.11 | 20.75 |
| Maximum | 36.92 | 40.03 | 27.38 | 30.69 |
| Mean | 31.07 | 31.72 | 25.40 | 24.94 |
| SD | 2.73 | 2.42 | 1.26 | 2.12 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| TIB_PLATEAU | | | | |
| N of cases | 29 | 80 | 17 | 61 |
| Minimum | 77.27 | 71.58 | 60.43 | 58.78 |
| Maximum | 97.34 | 97.50 | 76.18 | 83.13 |
| Mean | 87.79 | 87.03 | 69.63 | 70.18 |
| SD | 4.80 | 5.10 | 4.20 | 4.32 |
| *Calcaneus* | | | | |
| C_LENGTH | | | | |
| N of cases | 23 | 95 | 14 | 80 |
| Minimum | 66.78 | 80.32 | 61.07 | 62.66 |
| Maximum | 94.05 | 102.58 | 72.35 | 78.63 |
| Mean | 85.49 | 89.17 | 68.14 | 71.12 |
| SD | 5.74 | 4.69 | 3.43 | 3.68 |
| C_TUB_LENGTH | | | | |
| N of cases | 23 | 95 | 15 | 81 |
| Minimum | 31.42 | 31.88 | 25.55 | 24.36 |
| Maximum | 48.78 | 49.56 | 37.92 | 40.32 |
| Mean | 42.79 | 41.89 | 32.78 | 32.76 |
| SD | 4.37 | 3.36 | 3.17 | 2.72 |
| C_TUB_HTADJ | | | | |
| N of cases | 23 | 97 | 15 | 81 |
| Minimum | 30.49 | 39.30 | 29.40 | 28.49 |
| Maximum | 51.29 | 59.72 | 38.54 | 41.19 |
| Mean | 44.61 | 46.42 | 33.10 | 34.68 |
| SD | 4.32 | 3.55 | 2.64 | 2.53 |
| C_TENDON_WD | | | | |
| N of cases | 23 | 96 | 15 | 81 |
| Minimum | 17.57 | 16.88 | 14.76 | 13.50 |
| Maximum | 27.89 | 29.37 | 19.35 | 22.62 |
| Mean | 23.41 | 25.56 | 16.59 | 19.06 |
| SD | 2.22 | 2.03 | 1.43 | 1.76 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| C_CUB_WD | | | | |
| N of cases | 24 | 93 | 15 | 80 |
| Minimum | 22.36 | 24.83 | 20.82 | 20.65 |
| Maximum | 30.68 | 39.66 | 25.15 | 31.30 |
| Mean | 27.58 | 30.49 | 23.51 | 24.85 |
| SD | 1.83 | 2.43 | 1.37 | 2.03 |
| C_CUB_DPADJ | | | | |
| N of cases | 24 | 93 | 15 | 79 |
| Minimum | 2.11 | 2.35 | 1.73 | 1.57 |
| Maximum | 5.42 | 7.61 | 3.92 | 6.39 |
| Mean | 3.54 | 4.93 | 3.09 | 4.07 |
| SD | 0.83 | 1.18 | 0.64 | 1.01 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | | | | |
| N of cases | 23 | 99 | 14 | 81 |
| Minimum | 50.40 | 58.56 | 46.46 | 48.27 |
| Maximum | 66.13 | 78.40 | 54.15 | 61.01 |
| Mean | 60.78 | 66.63 | 50.72 | 54.85 |
| SD | 3.31 | 3.81 | 2.26 | 2.71 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | | | | |
| N of cases | 24 | 99 | 14 | 81 |
| Minimum | 61.53 | 73.42 | 55.86 | 64.92 |
| Maximum | 80.63 | 97.00 | 67.63 | 78.05 |
| Mean | 73.37 | 83.71 | 62.37 | 70.30 |
| SD | 4.62 | 4.46 | 3.39 | 3.24 |
| MT3_ML_HEAD | | | | |
| N of cases | 24 | 101 | 14 | 81 |
| Minimum | 9.22 | 11.08 | 7.75 | 8.65 |
| Maximum | 14.22 | 15.85 | 11.09 | 15.58 |
| Mean | 12.03 | 13.28 | 9.52 | 10.55 |
| SD | 1.21 | 0.94 | 0.92 | 0.99 |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *G. beringei* | *G. gorilla* | *G. beringei* | *G. gorilla* |
| MT3_BIEPI | | | | |
| N of cases | 24 | 100 | 14 | 81 |
| Minimum | 9.31 | 11.15 | 8.50 | 9.35 |
| Maximum | 12.94 | 16.98 | 10.35 | 14.51 |
| Mean | 11.27 | 14.06 | 9.24 | 11.27 |
| SD | 0.91 | 1.14 | 0.53 | 1.21 |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | | | | |
| N of cases | 19 | 99 | 14 | 76 |
| Minimum | 37.29 | 41.67 | 35.16 | 37.53 |
| Maximum | 47.93 | 54.53 | 39.45 | 45.59 |
| Mean | 43.84 | 48.45 | 37.21 | 41.36 |
| SD | 2.29 | 2.67 | 1.59 | 2.08 |
| FP_MAXSHAFT | | | | |
| N of cases | 19 | 99 | 14 | 76 |
| Minimum | 9.04 | 11.70 | 7.81 | 8.78 |
| Maximum | 13.25 | 16.08 | 10.48 | 14.28 |
| Mean | 11.73 | 13.33 | 9.02 | 10.67 |
| SD | 0.99 | 0.96 | 0.77 | 0.98 |
| FP_MINSHAFT | | | | |
| N of cases | 19 | 99 | 14 | 76 |
| Minimum | 7.67 | 10.02 | 5.95 | 7.23 |
| Maximum | 10.91 | 14.98 | 8.71 | 11.88 |
| Mean | 9.40 | 11.84 | 7.03 | 9.19 |
| SD | 0.95 | 0.92 | 0.78 | 0.93 |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

Table 2. Descriptive statistics for raw measurements in *Gorilla* by sex and subspecies

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| ***Forelimb*** | | | | | | |
| *Humerus* | | | | | | |
| HUM_LENGTH | | | | | | |
| N of cases | 16 | 15 | 85 | 13 | 7 | 61 |
| Minimum | 403.02 | 366.84 | 392.38 | 340.25 | 348.83 | 331.86 |
| Maximum | 443.44 | 468.59 | 492.44 | 399.82 | 388.92 | 417.28 |
| Mean | 426.96 | 442.36 | 444.40 | 363.67 | 369.69 | 371.56 |
| SD | 9.72 | 24.78 | 22.20 | 13.69 | 14.90 | 16.89 |
| HUM_ML_MID | | | | | | |
| N of cases | 16 | 15 | 86 | 13 | 7 | 61 |
| Minimum | 29.89 | 28.56 | 29.09 | 25.19 | 24.78 | 20.57 |
| Maximum | 38.13 | 36.98 | 41.19 | 32.98 | 28.39 | 33.50 |
| Mean | 33.46 | 34.86 | 35.39 | 27.28 | 26.05 | 27.89 |
| SD | 2.26 | 2.28 | 2.66 | 2.01 | 1.15 | 2.68 |
| HUM_AP_MID | | | | | | |
| N of cases | 16 | 15 | 86 | 13 | 7 | 61 |
| Minimum | 27.49 | 25.05 | 24.47 | 23.10 | 23.47 | 17.08 |
| Maximum | 33.79 | 33.22 | 34.68 | 28.81 | 25.29 | 29.28 |
| Mean | 30.14 | 30.52 | 30.60 | 25.25 | 24.59 | 25.23 |
| SD | 1.66 | 1.83 | 1.90 | 1.59 | 0.71 | 2.21 |
| HUM_SI_HEAD | | | | | | |
| N of cases | 16 | 15 | 86 | 13 | 7 | 62 |
| Minimum | 52.34 | 45.15 | 47.49 | 43.66 | 44.94 | 38.21 |
| Maximum | 64.35 | 62.02 | 67.03 | 58.65 | 50.01 | 52.31 |
| Mean | 58.96 | 58.45 | 57.91 | 48.38 | 48.19 | 46.13 |
| SD | 3.44 | 4.10 | 3.85 | 3.75 | 1.82 | 3.03 |
| HUM_DISTARTWD | | | | | | |
| N of cases | 16 | 15 | 86 | 11 | 7 | 61 |
| Minimum | 53.19 | 55.78 | 52.82 | 46.07 | 48.60 | 44.07 |
| Maximum | 70.89 | 76.97 | 75.45 | 56.15 | 57.35 | 59.81 |
| Mean | 62.10 | 67.52 | 66.19 | 49.65 | 51.56 | 51.67 |
| SD | 4.03 | 4.86 | 4.01 | 3.04 | 2.93 | 3.36 |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| HUM_BIEPI | | | | | | |
| N of cases | 16 | 15 | 85 | 11 | 7 | 62 |
| Minimum | 84.31 | 81.65 | 84.73 | 73.50 | 77.38 | 69.16 |
| Maximum | 108.67 | 117.80 | 120.35 | 83.85 | 84.42 | 87.17 |
| Mean | 98.73 | 103.26 | 101.41 | 79.18 | 79.93 | 78.26 |
| SD | 5.34 | 9.01 | 6.63 | 3.12 | 2.70 | 4.22 |
| *Radius* | | | | | | |
| RAD_LENGTH | | | | | | |
| N of cases | 14 | 14 | 88 | 9 | 7 | 62 |
| Minimum | 337.32 | 278.82 | 306.86 | 281.24 | 278.11 | 267.31 |
| Maximum | 363.71 | 380.13 | 400.28 | 312.06 | 299.48 | 321.88 |
| Mean | 352.25 | 348.52 | 356.16 | 295.03 | 286.58 | 298.01 |
| SD | 8.09 | 26.43 | 18.14 | 9.64 | 9.03 | 11.40 |
| RAD_ML_MID | | | | | | |
| N of cases | 14 | 14 | 88 | 10 | 7 | 62 |
| Minimum | 18.60 | 18.15 | 17.14 | 16.39 | 16.05 | 13.36 |
| Maximum | 25.78 | 27.35 | 28.11 | 21.68 | 18.61 | 21.42 |
| Mean | 22.25 | 22.40 | 22.15 | 18.25 | 17.17 | 17.03 |
| SD | 2.21 | 2.29 | 2.03 | 1.48 | 1.07 | 1.74 |
| RAD_AP_MID | | | | | | |
| N of cases | 14 | 14 | 88 | 10 | 7 | 62 |
| Minimum | 14.71 | 14.40 | 14.19 | 11.94 | 12.09 | 12.60 |
| Maximum | 20.29 | 19.77 | 22.42 | 14.94 | 14.02 | 17.70 |
| Mean | 17.37 | 17.50 | 18.35 | 13.77 | 12.99 | 14.67 |
| SD | 1.41 | 1.41 | 1.60 | 0.91 | 0.57 | 1.21 |
| RAD_ML_HEAD | | | | | | |
| N of cases | 15 | 14 | 87 | 11 | 7 | 62 |
| Minimum | 29.95 | 27.69 | 24.03 | 23.39 | 25.47 | 23.04 |
| Maximum | 37.17 | 37.59 | 38.52 | 30.60 | 28.56 | 29.26 |
| Mean | 33.67 | 33.47 | 32.75 | 26.26 | 26.79 | 25.60 |
| SD | 1.78 | 2.80 | 2.42 | 2.05 | 1.18 | 1.55 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| RAD_DISTALWD | | | | | | |
| N of cases | 14 | 14 | 88 | 9 | 7 | 62 |
| Minimum | 35.43 | 33.82 | 32.51 | 29.36 | 32.42 | 28.96 |
| Maximum | 48.43 | 44.56 | 51.22 | 36.01 | 36.88 | 40.93 |
| Mean | 40.73 | 41.06 | 42.48 | 32.41 | 34.80 | 35.13 |
| SD | 3.24 | 2.91 | 3.25 | 1.98 | 1.57 | 2.48 |
| *Metacarpal 3* | | | | | | |
| MC_LENGTH | | | | | | |
| N of cases | 11 | 16 | 99 | 8 | 7 | 80 |
| Minimum | 85.79 | 74.83 | 86.61 | 73.38 | 69.61 | 75.97 |
| Maximum | 94.26 | 100.51 | 112.75 | 80.43 | 76.14 | 92.94 |
| Mean | 89.35 | 87.42 | 99.42 | 76.88 | 72.79 | 84.31 |
| SD | 3.14 | 6.16 | 4.94 | 2.39 | 3.02 | 3.60 |
| MC_RU_MID | | | | | | |
| N of cases | 11 | 16 | 99 | 8 | 7 | 80 |
| Minimum | 9.73 | 9.54 | 9.67 | 9.13 | 8.39 | 7.98 |
| Maximum | 13.38 | 13.57 | 13.94 | 11.04 | 10.02 | 11.57 |
| Mean | 11.74 | 11.32 | 11.64 | 10.13 | 9.02 | 9.57 |
| SD | 1.20 | 1.10 | 0.94 | 0.75 | 0.58 | 0.83 |
| MC_DP_MID | | | | | | |
| N of cases | 11 | 16 | 99 | 8 | 7 | 80 |
| Minimum | 11.86 | 10.16 | 10.76 | 9.71 | 9.01 | 7.86 |
| Maximum | 14.96 | 14.33 | 16.60 | 13.04 | 12.06 | 13.32 |
| Mean | 13.36 | 12.81 | 13.58 | 11.13 | 10.42 | 10.81 |
| SD | 1.16 | 1.23 | 1.16 | 1.10 | 0.99 | 1.07 |
| MC_RU_HEAD | | | | | | |
| N of cases | 11 | 16 | 99 | 7 | 7 | 80 |
| Minimum | 16.93 | 13.63 | 17.00 | 13.20 | 13.79 | 13.51 |
| Maximum | 23.25 | 20.70 | 23.98 | 17.58 | 15.99 | 18.52 |
| Mean | 19.70 | 18.40 | 20.10 | 15.45 | 14.57 | 15.80 |
| SD | 1.62 | 1.66 | 1.38 | 1.32 | 0.80 | 0.98 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| MC_BIEPI | | | | | | |
| N of cases | 11 | 16 | 100 | 7 | 7 | 80 |
| Minimum | 18.35 | 15.82 | 20.28 | 14.85 | 15.47 | 15.09 |
| Maximum | 22.76 | 23.65 | 28.11 | 17.69 | 16.96 | 21.74 |
| Mean | 20.88 | 20.98 | 23.95 | 16.55 | 16.12 | 18.53 |
| SD | 1.39 | 1.94 | 1.74 | 0.97 | 0.58 | 1.45 |
| *Proximal hand phalanx 3* | | | | | | |
| HP_LENGTH | | | | | | |
| N of cases | 10 | 15 | 100 | 7 | 7 | 77 |
| Minimum | 55.66 | 50.73 | 54.37 | 48.50 | 48.20 | 49.37 |
| Maximum | 61.77 | 64.35 | 71.15 | 54.24 | 53.28 | 59.33 |
| Mean | 59.38 | 60.14 | 63.86 | 51.14 | 50.87 | 54.41 |
| SD | 1.94 | 3.17 | 3.40 | 1.85 | 1.97 | 2.45 |
| HP_RU_MAX | | | | | | |
| N of cases | 10 | 15 | 100 | 7 | 7 | 77 |
| Minimum | 18.89 | 14.46 | 16.11 | 14.53 | 14.12 | 13.91 |
| Maximum | 22.63 | 25.03 | 24.64 | 16.46 | 16.63 | 18.24 |
| Mean | 19.94 | 20.60 | 20.49 | 15.45 | 15.46 | 16.00 |
| SD | 1.12 | 2.39 | 1.47 | 0.86 | 0.93 | 1.02 |
| HP_RU_MIN | | | | | | |
| N of cases | 10 | 15 | 100 | 7 | 7 | 77 |
| Minimum | 15.17 | 12.16 | 14.72 | 12.76 | 11.56 | 12.09 |
| Maximum | 18.21 | 20.52 | 21.12 | 14.50 | 13.53 | 16.45 |
| Mean | 16.75 | 17.26 | 18.37 | 13.35 | 12.90 | 14.13 |
| SD | 0.96 | 1.72 | 1.26 | 0.60 | 0.70 | 0.91 |
| HP_RU_BASE | | | | | | |
| N of cases | 10 | 15 | 98 | 6 | 7 | 77 |
| Minimum | 19.31 | 16.02 | 20.67 | 16.86 | 16.09 | 16.58 |
| Maximum | 23.96 | 24.58 | 27.49 | 18.00 | 17.67 | 21.49 |
| Mean | 21.53 | 21.73 | 24.20 | 17.42 | 16.94 | 19.15 |
| SD | 1.29 | 2.02 | 1.38 | 0.47 | 0.59 | 1.08 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| HP_RU_TROCH | | | | | | |
| N of cases | 10 | 15 | 100 | 7 | 7 | 77 |
| Minimum | 14.38 | 11.86 | 14.48 | 12.19 | 11.96 | 12.15 |
| Maximum | 17.31 | 17.61 | 19.83 | 13.74 | 13.32 | 15.30 |
| Mean | 16.00 | 15.76 | 16.85 | 12.95 | 12.77 | 13.72 |
| SD | 0.92 | 1.35 | 1.01 | 0.63 | 0.50 | 0.76 |
| ***Hindlimb*** | | | | | | |
| *Femur* | | | | | | |
| FEM_LENGTH | | | | | | |
| N of cases | 13 | 14 | 78 | 11 | 7 | 62 |
| Minimum | 360.62 | 356.67 | 325.83 | 289.05 | 299.71 | 290.18 |
| Maximum | 386.27 | 396.60 | 418.31 | 329.17 | 328.54 | 334.44 |
| Mean | 371.22 | 377.05 | 374.14 | 312.91 | 313.53 | 312.85 |
| SD | 8.86 | 13.94 | 18.06 | 12.27 | 11.29 | 10.56 |
| FEM_ML_MID | | | | | | |
| N of cases | 14 | 14 | 78 | 12 | 7 | 62 |
| Minimum | 37.35 | 37.88 | 34.66 | 30.49 | 29.83 | 27.45 |
| Maximum | 44.64 | 46.80 | 46.20 | 38.73 | 33.54 | 39.43 |
| Mean | 40.34 | 41.45 | 41.50 | 33.43 | 31.61 | 33.74 |
| SD | 2.67 | 2.32 | 2.27 | 2.29 | 1.38 | 3.02 |
| FEM_AP_MID | | | | | | |
| N of cases | 14 | 14 | 78 | 12 | 7 | 62 |
| Minimum | 30.12 | 31.77 | 24.38 | 25.41 | 24.88 | 22.10 |
| Maximum | 37.00 | 35.97 | 36.43 | 34.06 | 28.80 | 30.63 |
| Mean | 34.30 | 33.12 | 30.84 | 28.52 | 26.22 | 25.87 |
| SD | 1.78 | 1.30 | 2.23 | 2.21 | 1.36 | 2.06 |
| FEM_HEAD_HT | | | | | | |
| N of cases | 17 | 14 | 79 | 12 | 7 | 62 |
| Minimum | 39.85 | 46.07 | 40.72 | 37.16 | 39.48 | 35.65 |
| Maximum | 53.95 | 57.73 | 56.59 | 45.84 | 42.53 | 44.75 |
| Mean | 49.85 | 52.99 | 49.85 | 40.26 | 40.74 | 40.16 |
| SD | 3.52 | 3.12 | 2.70 | 2.42 | 1.30 | 1.94 |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| FEM_BICON_WD | | | | | | |
| N of cases | 14 | 14 | 78 | 10 | 7 | 61 |
| Minimum | 76.72 | 85.40 | 72.38 | 62.95 | 66.48 | 60.63 |
| Maximum | 94.57 | 100.11 | 96.67 | 77.13 | 75.14 | 78.78 |
| Mean | 86.41 | 90.70 | 87.03 | 68.50 | 71.54 | 69.72 |
| SD | 4.89 | 4.94 | 4.92 | 4.82 | 3.17 | 4.22 |
| *Tibia* | | | | | | |
| TIB_LENGTH | | | | | | |
| N of cases | 15 | 14 | 79 | 11 | 7 | 61 |
| Minimum | 284.32 | 288.96 | 270.32 | 231.29 | 240.35 | 235.26 |
| Maximum | 307.04 | 322.07 | 353.33 | 263.93 | 258.42 | 290.68 |
| Mean | 297.54 | 306.31 | 313.86 | 250.80 | 247.46 | 259.76 |
| SD | 7.05 | 11.41 | 16.33 | 9.01 | 6.91 | 10.61 |
| TIB_ML_MID | | | | | | |
| N of cases | 15 | 14 | 79 | 11 | 7 | 61 |
| Minimum | 19.25 | 19.68 | 18.01 | 15.44 | 14.19 | 14.76 |
| Maximum | 23.92 | 23.74 | 25.63 | 21.19 | 16.91 | 21.24 |
| Mean | 21.49 | 21.58 | 21.94 | 17.42 | 15.50 | 17.59 |
| SD | 1.25 | 1.13 | 1.48 | 1.52 | 0.88 | 1.61 |
| TIB_AP_MID | | | | | | |
| N of cases | 15 | 14 | 79 | 11 | 7 | 61 |
| Minimum | 27.82 | 26.32 | 25.23 | 23.11 | 23.30 | 20.75 |
| Maximum | 36.61 | 36.92 | 40.03 | 27.38 | 26.58 | 30.69 |
| Mean | 31.22 | 30.90 | 31.74 | 25.75 | 24.86 | 24.94 |
| SD | 2.53 | 3.01 | 2.42 | 1.27 | 1.11 | 2.12 |
| TIB_PLATEAU | | | | | | |
| N of cases | 15 | 14 | 79 | 10 | 7 | 61 |
| Minimum | 77.27 | 82.89 | 71.58 | 60.43 | 67.02 | 58.78 |
| Maximum | 93.88 | 97.34 | 97.50 | 76.18 | 74.66 | 83.13 |
| Mean | 86.07 | 89.64 | 87.09 | 68.12 | 71.81 | 70.18 |
| SD | 4.34 | 4.70 | 5.11 | 4.53 | 2.61 | 4.32 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| *Calcaneus* | | | | | | |
| C_LENGTH | | | | | | |
| N of cases | 7 | 16 | 94 | 7 | 7 | 80 |
| Minimum | 80.22 | 66.78 | 80.32 | 61.07 | 63.23 | 62.66 |
| Maximum | 91.06 | 94.05 | 102.58 | 72.35 | 71.66 | 78.63 |
| Mean | 85.93 | 85.29 | 89.19 | 68.11 | 68.17 | 71.12 |
| SD | 3.99 | 6.47 | 4.71 | 4.33 | 2.60 | 3.68 |
| C_TUB_LENGTH | | | | | | |
| N of cases | 7 | 16 | 94 | 8 | 7 | 81 |
| Minimum | 37.89 | 31.42 | 31.88 | 25.55 | 29.21 | 24.36 |
| Maximum | 47.85 | 48.78 | 49.56 | 37.92 | 35.63 | 40.32 |
| Mean | 42.07 | 43.11 | 41.91 | 32.45 | 33.16 | 32.76 |
| SD | 3.07 | 4.88 | 3.37 | 4.03 | 2.05 | 2.72 |
| C_TUB_HTADJ | | | | | | |
| N of cases | 7 | 16 | 96 | 8 | 7 | 81 |
| Minimum | 44.54 | 30.49 | 39.30 | 29.76 | 29.40 | 28.49 |
| Maximum | 50.16 | 51.29 | 59.72 | 38.54 | 32.71 | 41.19 |
| Mean | 47.78 | 43.22 | 46.40 | 34.63 | 31.35 | 34.68 |
| SD | 1.76 | 4.40 | 3.56 | 2.67 | 1.11 | 2.53 |
| C_TENDON_WD | | | | | | |
| N of cases | 7 | 16 | 95 | 8 | 7 | 81 |
| Minimum | 20.23 | 17.57 | 16.88 | 15.02 | 14.76 | 13.50 |
| Maximum | 25.01 | 27.89 | 29.37 | 17.80 | 19.35 | 22.62 |
| Mean | 22.93 | 23.61 | 25.57 | 16.10 | 17.15 | 19.06 |
| SD | 1.63 | 2.45 | 2.04 | 0.94 | 1.74 | 1.76 |
| C_CUB_WD | | | | | | |
| N of cases | 8 | 16 | 92 | 8 | 7 | 80 |
| Minimum | 25.07 | 22.36 | 24.83 | 20.82 | 22.81 | 20.65 |
| Maximum | 29.94 | 30.68 | 39.66 | 25.15 | 25.08 | 31.30 |
| Mean | 27.78 | 27.48 | 30.49 | 23.18 | 23.89 | 24.85 |
| SD | 1.57 | 1.99 | 2.44 | 1.58 | 1.07 | 2.03 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| C_CUB_DPADJ | | | | | | |
| N of cases | 8 | 16 | 92 | 8 | 7 | 79 |
| Minimum | 2.11 | 2.56 | 2.35 | 1.73 | 3.06 | 1.57 |
| Maximum | 4.25 | 5.42 | 7.61 | 3.40 | 3.92 | 6.39 |
| Mean | 3.01 | 3.80 | 4.92 | 2.69 | 3.55 | 4.07 |
| SD | 0.70 | 0.77 | 1.18 | 0.59 | 0.30 | 1.01 |
| *Metatarsal 1* | | | | | | |
| MT1_LENGTH | | | | | | |
| N of cases | 7 | 16 | 98 | 7 | 7 | 81 |
| Minimum | 58.71 | 50.40 | 58.56 | 48.46 | 46.46 | 48.27 |
| Maximum | 65.21 | 66.13 | 78.40 | 54.15 | 52.38 | 61.01 |
| Mean | 61.64 | 60.41 | 66.69 | 51.52 | 49.92 | 54.85 |
| SD | 2.19 | 3.70 | 3.79 | 2.08 | 2.29 | 2.71 |
| *Metatarsal 3* | | | | | | |
| MT3_LENGTH | | | | | | |
| N of cases | 8 | 16 | 98 | 7 | 7 | 81 |
| Minimum | 68.86 | 61.53 | 73.42 | 58.44 | 55.86 | 64.92 |
| Maximum | 76.56 | 80.63 | 97.00 | 65.10 | 67.63 | 78.05 |
| Mean | 72.38 | 73.86 | 83.80 | 62.33 | 62.40 | 70.30 |
| SD | 2.67 | 5.34 | 4.39 | 2.54 | 4.30 | 3.24 |
| MT3_ML_HEAD | | | | | | |
| N of cases | 8 | 16 | 100 | 7 | 7 | 81 |
| Minimum | 10.88 | 9.22 | 11.08 | 9.26 | 7.75 | 8.65 |
| Maximum | 14.22 | 13.67 | 15.85 | 11.09 | 9.80 | 15.58 |
| Mean | 12.72 | 11.69 | 13.31 | 10.10 | 8.93 | 10.55 |
| SD | 0.98 | 1.19 | 0.92 | 0.67 | 0.77 | 0.99 |
| MT3_BIEPI | | | | | | |
| N of cases | 8 | 16 | 99 | 7 | 7 | 81 |
| Minimum | 10.11 | 9.31 | 11.15 | 8.50 | 8.94 | 9.35 |
| Maximum | 12.27 | 12.94 | 16.98 | 10.35 | 10.02 | 14.51 |
| Mean | 11.42 | 11.19 | 14.08 | 9.23 | 9.26 | 11.27 |
| SD | 0.71 | 1.01 | 1.14 | 0.69 | 0.35 | 1.21 |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *beringei* | *graueri* | *gorilla* | *beringei* | *graueri* | *gorilla* |
| *Proximal foot phalanx 3* | | | | | | |
| FP_LENGTH | | | | | | |
| N of cases | 6 | 13 | 98 | 7 | 7 | 76 |
| Minimum | 42.81 | 37.29 | 41.67 | 35.16 | 35.24 | 37.53 |
| Maximum | 46.64 | 47.93 | 54.53 | 38.87 | 39.45 | 45.59 |
| Mean | 44.44 | 43.56 | 48.48 | 37.15 | 37.27 | 41.36 |
| SD | 1.43 | 2.60 | 2.67 | 1.47 | 1.81 | 2.08 |
| FP_MAXSHAFT | | | | | | |
| N of cases | 6 | 13 | 98 | 7 | 7 | 76 |
| Minimum | 10.44 | 9.04 | 11.70 | 7.81 | 8.06 | 8.78 |
| Maximum | 12.31 | 13.25 | 16.08 | 9.82 | 10.48 | 14.28 |
| Mean | 11.63 | 11.77 | 13.34 | 8.82 | 9.22 | 10.67 |
| SD | 0.73 | 1.12 | 0.96 | 0.65 | 0.88 | 0.98 |
| FP_MINSHAFT | | | | | | |
| N of cases | 6 | 13 | 98 | 7 | 7 | 76 |
| Minimum | 8.68 | 7.67 | 10.02 | 6.10 | 5.95 | 7.23 |
| Maximum | 10.91 | 10.70 | 14.98 | 8.71 | 7.73 | 11.88 |
| Mean | 9.72 | 9.26 | 11.85 | 7.35 | 6.71 | 9.19 |
| SD | 0.91 | 0.97 | 0.92 | 0.78 | 0.68 | 0.93 |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

Table 3. Data for raw measurements in *G. g. diehli* specimens

| **Variables**[1] | NHM-L[2] ZD 1948.436 | ZMB[2] 12791 | ZMB 12791[3] |
|---|---|---|---|
| | Male | Male | Female? |
| ***Forelimb*** | | | |
| *Humerus* | L side | R side | not present |
| HUM_LENGTH | 439.59 | 445.96 | |
| HUM_ML_MID | 36.22 | 33.62 | |
| HUM_AP_MID | 27.64 | 29.15 | |
| HUM_SI_HEAD | 60.33 | 57.48 | |
| HUM_DISTARTWD | 62.14 | 64.02 | |
| HUM_BIEPI | 105.38 | 96.26 | |
| *Radius* | L side | R side | L side |
| RAD_LENGTH | 348.02 | 368.69 | 298.97 |
| RAD_ML_MID | 22.05 | 20.46 | 14.70 |
| RAD_AP_MID | 18.09 | 17.49 | 14.67 |
| RAD_ML_HEAD | 33.06 | 31.81 | 23.14 |
| RAD_DISTALWD | 40.78 | 36.33 | 30.44 |
| *Metacarpal 3* | R side | not present | not present |
| MC_LENGTH | 91.63 | | |
| MC_RU_MID | 10.78 | | |
| MC_DP_MID | 11.73 | | |
| MC_RU_HEAD | 17.85 | | |
| MC_BIEPI | 20.71 | | |
| *Proximal hand phalanx 3* | R side | not present | not present |
| HP_LENGTH | 60.92 | | |
| HP_RU_MAX | 18.35 | | |
| HP_RU_MIN | 16.58 | | |
| HP_RU_BASE | 21.34 | | |
| HP_RU_TROCH | 15.78 | | |
| ***Hindlimb*** | | | |
| *Femur* | R side | R side | not present |
| FEM_LENGTH | 382.19 | 371.82 | |
| FEM_ML_MID | 41.25 | 40.58 | |
| FEM_AP_MID | 29.80 | 32.25 | |
| FEM_HEAD_HT | 50.01 | 48.90 | |
| FEM_BICON_WD | 80.55 | 78.68 | |

| **Variables**[1] | NHM-L[2] ZD 1948.436 | ZMB[2] 12791 | ZMB 12791[3] |
|---|---|---|---|
| | Male | Male | Female? |
| *Tibia* | R side | not present | not present |
| TIB_LENGTH | 307.62 | | |
| TIB_ML_MID | 19.87 | | |
| TIB_AP_MID | 29.79 | | |
| TIB_PLATEAU | 82.32 | | |
| *Calcaneus* | R side | not present | not present |
| C_LENGTH | 86.84 | | |
| C_TUB_LENGTH | 39.69 | | |
| C_TUB_HTADJ | 48.33 | | |
| C_TENDON_WD | 25.30 | | |
| C_CUB_WD | 30.91 | | |
| C_CUB_DPADJ | 5.42 | | |
| *Metatarsal 1* | R side | not present | not present |
| MT1_LENGTH | 60.80 | | |
| *Metatarsal 3* | R side | not present | not present |
| MT3_LENGTH | 74.77 | | |
| MT3_ML_HEAD | 11.26 | | |
| MT3_BIEPI | 12.79 | | |
| *Proximal foot phalanx 3* | R side | not present | not present |
| FP_LENGTH | 45.80 | | |
| FP_MAXSHAFT | 12.07 | | |
| FP_MINSHAFT | 10.72 | | |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

[2] NHM-L = Natural History Museum (London); ZMB = Zoological Museum of Berlin, Humboldt University

[3] This is one of three radii included with the specimen ZMB 12791. The other two are much larger. All three radii are marked "Gorilla 5 Oboni", presumably a field or accession number. Oboni is the locality from which the specimen was collected.

Table 4. Descriptive statistics for raw measurements in *Pan* by sex and species

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| ***Forelimb*** | | | | |
| *Humerus* | | | | |
| HUM_LENGTH | | | | |
| N of cases | 9 | 97 | 11 | 101 |
| Minimum | 272.79 | 272.43 | 252.87 | 249.26 |
| Maximum | 297.71 | 336.64 | 297.91 | 334.47 |
| Mean | 283.76 | 304.00 | 284.54 | 294.42 |
| SD | 9.74 | 13.55 | 12.88 | 14.93 |
| HUM_ML_MID | | | | |
| N of cases | 9 | 96 | 11 | 102 |
| Minimum | 16.84 | 18.56 | 15.83 | 17.12 |
| Maximum | 21.77 | 28.68 | 19.52 | 26.16 |
| Mean | 18.96 | 23.21 | 17.84 | 21.30 |
| SD | 1.66 | 2.13 | 1.21 | 1.95 |
| HUM_AP_MID | | | | |
| N of cases | 9 | 96 | 11 | 102 |
| Minimum | 17.60 | 18.63 | 15.68 | 17.88 |
| Maximum | 19.61 | 29.62 | 20.67 | 26.08 |
| Mean | 18.87 | 21.83 | 19.19 | 21.05 |
| SD | 0.68 | 1.66 | 1.37 | 1.59 |
| HUM_SI_HEAD | | | | |
| N of cases | 9 | 97 | 11 | 101 |
| Minimum | 31.66 | 31.62 | 30.68 | 32.16 |
| Maximum | 39.42 | 44.89 | 37.03 | 45.47 |
| Mean | 35.03 | 39.58 | 33.71 | 37.34 |
| SD | 1.98 | 2.53 | 2.17 | 2.55 |
| HUM_DISTARTWD | | | | |
| N of cases | 9 | 97 | 11 | 102 |
| Minimum | 37.51 | 35.93 | 32.60 | 35.71 |
| Maximum | 44.12 | 52.81 | 42.03 | 49.29 |
| Mean | 39.77 | 45.40 | 37.91 | 41.90 |
| SD | 1.90 | 3.07 | 2.62 | 2.71 |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| HUM_BIEPI | | | | |
| N of cases | 9 | 97 | 11 | 101 |
| Minimum | 53.45 | 52.41 | 45.58 | 49.58 |
| Maximum | 64.65 | 71.49 | 58.38 | 70.94 |
| Mean | 58.44 | 63.67 | 54.03 | 58.65 |
| SD | 3.14 | 3.94 | 3.96 | 3.69 |
| *Radius* | | | | |
| RAD_LENGTH | | | | |
| N of cases | 9 | 93 | 11 | 98 |
| Minimum | 250.60 | 244.96 | 230.16 | 234.26 |
| Maximum | 277.56 | 318.71 | 276.04 | 303.76 |
| Mean | 264.48 | 280.20 | 260.33 | 268.47 |
| SD | 8.32 | 14.81 | 12.17 | 14.38 |
| RAD_ML_MID | | | | |
| N of cases | 9 | 92 | 11 | 98 |
| Minimum | 12.46 | 13.14 | 10.31 | 11.56 |
| Maximum | 14.90 | 19.72 | 14.08 | 19.03 |
| Mean | 13.56 | 15.93 | 12.77 | 14.76 |
| SD | 0.85 | 1.42 | 1.01 | 1.60 |
| RAD_AP_MID | | | | |
| N of cases | 9 | 92 | 11 | 98 |
| Minimum | 10.61 | 10.72 | 9.77 | 10.38 |
| Maximum | 12.81 | 18.66 | 13.08 | 16.97 |
| Mean | 11.80 | 14.56 | 11.70 | 13.44 |
| SD | 0.80 | 1.39 | 0.89 | 1.20 |
| RAD_ML_HEAD | | | | |
| N of cases | 9 | 93 | 11 | 99 |
| Minimum | 19.54 | 20.25 | 17.77 | 19.30 |
| Maximum | 22.64 | 28.36 | 22.01 | 25.88 |
| Mean | 21.23 | 24.32 | 20.41 | 22.51 |
| SD | 0.83 | 1.67 | 1.49 | 1.44 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| RAD_DISTALWD | | | | |
| N of cases | 9 | 93 | 11 | 98 |
| Minimum | 28.61 | 26.94 | 23.88 | 24.98 |
| Maximum | 31.10 | 36.71 | 31.19 | 34.73 |
| Mean | 29.86 | 31.29 | 28.50 | 28.98 |
| SD | 1.09 | 1.97 | 2.19 | 1.88 |
| *Metacarpal 3* | | | | |
| MC_LENGTH | | | | |
| N of cases | 8 | 97 | 12 | 121 |
| Minimum | 77.94 | 77.78 | 75.76 | 74.93 |
| Maximum | 94.45 | 103.29 | 89.34 | 98.85 |
| Mean | 87.55 | 89.57 | 85.32 | 87.55 |
| SD | 5.01 | 5.38 | 3.73 | 5.32 |
| MC_RU_MID | | | | |
| N of cases | 8 | 97 | 12 | 119 |
| Minimum | 6.86 | 7.43 | 6.15 | 6.66 |
| Maximum | 8.19 | 10.38 | 8.61 | 9.95 |
| Mean | 7.47 | 8.76 | 7.41 | 8.23 |
| SD | 0.45 | 0.65 | 0.76 | 0.69 |
| MC_DP_MID | | | | |
| N of cases | 8 | 97 | 12 | 119 |
| Minimum | 7.74 | 7.76 | 6.79 | 7.53 |
| Maximum | 8.62 | 10.71 | 9.09 | 10.64 |
| Mean | 8.20 | 9.26 | 7.92 | 8.76 |
| SD | 0.37 | 0.67 | 0.68 | 0.66 |
| MC_RU_HEAD | | | | |
| N of cases | 8 | 97 | 12 | 121 |
| Minimum | 10.24 | 11.91 | 9.99 | 11.39 |
| Maximum | 13.74 | 16.76 | 13.96 | 16.58 |
| Mean | 12.21 | 14.12 | 11.85 | 13.39 |
| SD | 1.16 | 0.99 | 1.16 | 1.03 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| MC_BIEPI | | | | |
| N of cases | 8 | 97 | 12 | 121 |
| Minimum | 13.02 | 13.98 | 12.73 | 13.31 |
| Maximum | 15.60 | 19.80 | 16.69 | 20.44 |
| Mean | 14.50 | 17.24 | 14.31 | 16.02 |
| SD | 0.95 | 1.22 | 1.26 | 1.30 |
| *Proximal hand phalanx 3* | | | | |
| HP_LENGTH | | | | |
| N of cases | 8 | 90 | 12 | 112 |
| Minimum | 49.91 | 51.97 | 46.34 | 51.67 |
| Maximum | 58.03 | 68.14 | 58.06 | 67.44 |
| Mean | 54.12 | 60.21 | 53.02 | 59.41 |
| SD | 2.90 | 3.62 | 3.07 | 3.62 |
| HP_RU_MAX | | | | |
| N of cases | 8 | 89 | 12 | 112 |
| Minimum | 9.33 | 10.56 | 9.17 | 8.51 |
| Maximum | 11.26 | 17.74 | 12.19 | 16.66 |
| Mean | 10.52 | 14.19 | 10.78 | 13.18 |
| SD | 0.62 | 1.29 | 0.90 | 1.31 |
| HP_RU_MIN | | | | |
| N of cases | 8 | 90 | 12 | 112 |
| Minimum | 9.02 | 9.38 | 7.90 | 6.74 |
| Maximum | 9.72 | 13.85 | 10.86 | 13.39 |
| Mean | 9.37 | 11.40 | 9.27 | 10.49 |
| SD | 0.23 | 0.97 | 0.77 | 0.99 |
| HP_RU_BASE | | | | |
| N of cases | 8 | 90 | 12 | 113 |
| Minimum | 13.31 | 14.18 | 12.74 | 13.76 |
| Maximum | 16.08 | 19.16 | 15.41 | 20.89 |
| Mean | 14.59 | 16.99 | 13.85 | 16.02 |
| SD | 1.02 | 1.02 | 0.89 | 1.06 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| HP_RU_TROCH | | | | |
| N of cases | 8 | 90 | 12 | 112 |
| Minimum | 10.03 | 10.97 | 9.29 | 10.45 |
| Maximum | 11.83 | 15.26 | 11.98 | 17.71 |
| Mean | 11.08 | 12.75 | 10.75 | 12.17 |
| SD | 0.54 | 0.78 | 0.91 | 0.86 |
| ***Hindlimb*** | | | | |
| *Femur* | | | | |
| FEM_LENGTH | | | | |
| N of cases | 10 | 91 | 12 | 92 |
| Minimum | 271.98 | 262.41 | 261.08 | 249.70 |
| Maximum | 315.03 | 334.31 | 300.60 | 335.25 |
| Mean | 290.85 | 297.39 | 287.53 | 289.17 |
| SD | 11.90 | 13.84 | 10.69 | 14.78 |
| FEM_ML_MID | | | | |
| N of cases | 10 | 90 | 12 | 93 |
| Minimum | 20.62 | 22.68 | 18.75 | 20.52 |
| Maximum | 26.24 | 30.96 | 23.39 | 29.19 |
| Mean | 22.77 | 25.98 | 21.77 | 24.61 |
| SD | 1.75 | 1.53 | 1.30 | 1.87 |
| FEM_AP_MID | | | | |
| N of cases | 10 | 90 | 12 | 93 |
| Minimum | 19.31 | 19.09 | 18.43 | 18.04 |
| Maximum | 23.80 | 26.56 | 22.33 | 27.90 |
| Mean | 21.84 | 22.62 | 20.92 | 22.02 |
| SD | 1.42 | 1.56 | 1.00 | 1.94 |
| FEM_HEAD_HT | | | | |
| N of cases | 10 | 92 | 12 | 92 |
| Minimum | 29.13 | 28.85 | 25.40 | 26.34 |
| Maximum | 35.10 | 38.91 | 32.66 | 37.11 |
| Mean | 30.91 | 33.78 | 29.78 | 31.64 |
| SD | 1.86 | 2.00 | 1.93 | 2.13 |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| FEM_BICON_WD | | | | |
| N of cases | 10 | 91 | 12 | 93 |
| Minimum | 50.63 | 51.54 | 47.46 | 47.63 |
| Maximum | 63.29 | 64.62 | 54.12 | 65.20 |
| Mean | 54.56 | 57.88 | 51.73 | 54.24 |
| SD | 4.16 | 3.00 | 2.43 | 3.05 |
| *Tibia* | | | | |
| TIB_LENGTH | | | | |
| N of cases | 10 | 90 | 12 | 88 |
| Minimum | 235.89 | 221.41 | 215.22 | 213.02 |
| Maximum | 270.09 | 288.16 | 249.90 | 273.06 |
| Mean | 247.58 | 252.74 | 237.79 | 243.77 |
| SD | 10.83 | 13.36 | 9.13 | 13.45 |
| TIB_ML_MID | | | | |
| N of cases | 10 | 89 | 12 | 88 |
| Minimum | 13.27 | 12.35 | 12.47 | 12.17 |
| Maximum | 18.13 | 19.03 | 16.39 | 19.47 |
| Mean | 14.60 | 15.40 | 14.21 | 14.88 |
| SD | 1.41 | 1.28 | 1.15 | 1.49 |
| TIB_AP_MID | | | | |
| N of cases | 10 | 89 | 12 | 88 |
| Minimum | 20.58 | 19.32 | 17.41 | 17.54 |
| Maximum | 26.96 | 27.88 | 24.23 | 28.11 |
| Mean | 23.37 | 23.30 | 20.80 | 21.86 |
| SD | 1.80 | 1.63 | 1.74 | 1.95 |
| TIB_PLATEAU | | | | |
| N of cases | 10 | 90 | 12 | 89 |
| Minimum | 53.09 | 53.31 | 48.32 | 45.42 |
| Maximum | 63.54 | 68.07 | 55.83 | 64.82 |
| Mean | 56.78 | 59.80 | 53.29 | 55.99 |
| SD | 3.65 | 3.09 | 2.54 | 3.18 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| *Calcaneus* | | | | |
| C_LENGTH | | | | |
| N of cases | 9 | 100 | 12 | 118 |
| Minimum | 51.06 | 46.38 | 46.82 | 45.87 |
| Maximum | 59.28 | 64.98 | 54.28 | 62.44 |
| Mean | 54.81 | 54.80 | 51.80 | 52.65 |
| SD | 3.14 | 3.27 | 1.98 | 3.42 |
| C_TUB_LENGTH | | | | |
| N of cases | 9 | 98 | 12 | 117 |
| Minimum | 18.33 | 14.43 | 17.62 | 13.74 |
| Maximum | 24.14 | 27.09 | 21.12 | 27.26 |
| Mean | 21.53 | 20.12 | 19.59 | 19.29 |
| SD | 1.96 | 2.30 | 1.19 | 2.41 |
| C_TUB_HTADJ | | | | |
| N of cases | 9 | 100 | 12 | 118 |
| Minimum | 25.47 | 28.71 | 25.43 | 25.58 |
| Maximum | 36.38 | 41.48 | 30.85 | 39.52 |
| Mean | 30.83 | 33.50 | 28.40 | 31.41 |
| SD | 3.16 | 2.54 | 1.57 | 2.51 |
| C_TENDON_WD | | | | |
| N of cases | 9 | 100 | 12 | 118 |
| Minimum | 15.20 | 14.73 | 13.12 | 12.57 |
| Maximum | 19.52 | 22.45 | 18.64 | 21.07 |
| Mean | 17.23 | 18.37 | 15.85 | 17.07 |
| SD | 1.45 | 1.62 | 1.67 | 1.41 |
| C_CUB_WD | | | | |
| N of cases | 9 | 99 | 12 | 118 |
| Minimum | 18.41 | 17.95 | 17.50 | 17.23 |
| Maximum | 23.58 | 25.16 | 22.50 | 24.71 |
| Mean | 20.32 | 21.53 | 19.12 | 20.26 |
| SD | 1.80 | 1.58 | 1.43 | 1.48 |
| | | | | |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| C_CUB_DPADJ | | | | |
| N of cases | 9 | 97 | 12 | 116 |
| Minimum | 3.10 | 1.64 | 2.80 | 2.06 |
| Maximum | 5.93 | 7.11 | 5.08 | 6.94 |
| Mean | 4.26 | 4.34 | 4.12 | 3.90 |
| SD | 0.99 | 0.91 | 0.77 | 0.86 |
| *Metatarsal 1* | | | | |
| MT1_LENGTH | | | | |
| N of cases | 10 | 95 | 12 | 120 |
| Minimum | 45.34 | 48.15 | 44.04 | 46.71 |
| Maximum | 55.07 | 63.62 | 51.89 | 64.80 |
| Mean | 50.58 | 56.06 | 48.77 | 54.72 |
| SD | 3.12 | 3.43 | 2.30 | 3.60 |
| *Metatarsal 3* | | | | |
| MT3_LENGTH | | | | |
| N of cases | 10 | 99 | 12 | 118 |
| Minimum | 60.18 | 57.40 | 58.80 | 56.54 |
| Maximum | 73.00 | 80.72 | 69.13 | 77.70 |
| Mean | 67.69 | 69.94 | 65.48 | 68.28 |
| SD | 4.13 | 4.53 | 2.62 | 4.48 |
| MT3_ML_HEAD | | | | |
| N of cases | 10 | 99 | 12 | 118 |
| Minimum | 7.54 | 8.08 | 7.56 | 8.15 |
| Maximum | 11.75 | 12.41 | 10.10 | 11.77 |
| Mean | 9.42 | 10.53 | 8.88 | 9.96 |
| SD | 1.41 | 0.86 | 0.99 | 0.79 |
| MT3_BIEPI | | | | |
| N of cases | 10 | 99 | 12 | 118 |
| Minimum | 7.53 | 7.90 | 7.32 | 7.74 |
| Maximum | 10.53 | 11.56 | 10.27 | 13.23 |
| Mean | 9.09 | 9.70 | 8.56 | 9.34 |
| SD | 0.99 | 0.78 | 0.82 | 0.84 |
| | | | | |
| | | | | |

| **Variables**[1] | Males | | Females | |
|---|---|---|---|---|
| | *P. paniscus* | *P. troglodytes* | *P. paniscus* | *P. troglodytes* |
| *Proximal foot phalanx 3* | | | | |
| FP_LENGTH | | | | |
| N of cases | 9 | 88 | 12 | 109 |
| Minimum | 34.59 | 35.85 | 33.79 | 35.33 |
| Maximum | 42.48 | 48.96 | 42.08 | 50.22 |
| Mean | 38.66 | 42.83 | 38.17 | 42.42 |
| SD | 2.59 | 2.74 | 2.17 | 2.88 |
| FP_MAXSHAFT | | | | |
| N of cases | 9 | 88 | 12 | 109 |
| Minimum | 6.11 | 7.06 | 6.05 | 6.03 |
| Maximum | 8.94 | 9.89 | 7.56 | 10.44 |
| Mean | 7.20 | 8.43 | 6.80 | 7.84 |
| SD | 0.81 | 0.66 | 0.49 | 0.68 |
| FP_MINSHAFT | | | | |
| N of cases | 9 | 88 | 12 | 109 |
| Minimum | 4.79 | 6.07 | 5.34 | 5.34 |
| Maximum | 7.18 | 9.09 | 7.01 | 9.37 |
| Mean | 6.19 | 7.46 | 5.97 | 6.76 |
| SD | 0.69 | 0.64 | 0.55 | 0.65 |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

Table 5. Descriptive statistics for raw measurements in *P. troglodytes* by sex and subspecies (not including *P. t. vellerosus*)

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| ***Forelimb*** | | | | | | |
| *Humerus* | | | | | | |
| HUM_LENGTH | | | | | | |
| N of cases | 23 | 66 | 8 | 13 | 67 | 15 |
| Minimum | 272.43 | 280.24 | 279.51 | 249.26 | 267.17 | 276.96 |
| Maximum | 332.26 | 336.64 | 323.22 | 323.79 | 334.47 | 309.30 |
| Mean | 303.64 | 304.70 | 299.28 | 293.33 | 295.50 | 291.56 |
| SD | 14.69 | 13.31 | 12.81 | 21.84 | 14.73 | 9.79 |
| HUM_ML_MID | | | | | | |
| N of cases | 22 | 66 | 8 | 13 | 68 | 15 |
| Minimum | 19.57 | 18.56 | 18.73 | 17.59 | 17.12 | 18.01 |
| Maximum | 28.68 | 28.62 | 23.03 | 25.32 | 26.16 | 24.22 |
| Mean | 23.36 | 23.48 | 20.54 | 21.56 | 21.52 | 20.04 |
| SD | 2.12 | 2.00 | 1.42 | 2.45 | 1.86 | 1.57 |
| HUM_AP_MID | | | | | | |
| N of cases | 22 | 66 | 8 | 13 | 68 | 15 |
| Minimum | 18.63 | 19.34 | 20.19 | 18.18 | 17.88 | 19.56 |
| Maximum | 24.50 | 29.62 | 23.50 | 26.08 | 25.46 | 23.63 |
| Mean | 20.92 | 22.18 | 21.49 | 21.09 | 21.08 | 21.13 |
| SD | 1.44 | 1.67 | 1.20 | 2.22 | 1.54 | 1.16 |
| HUM_SI_HEAD | | | | | | |
| N of cases | 23 | 66 | 8 | 13 | 67 | 15 |
| Minimum | 31.62 | 34.00 | 36.64 | 32.98 | 32.85 | 33.53 |
| Maximum | 44.08 | 44.89 | 41.98 | 40.99 | 45.47 | 40.09 |
| Mean | 38.55 | 40.06 | 38.60 | 37.31 | 37.68 | 36.30 |
| SD | 2.86 | 2.38 | 1.71 | 2.63 | 2.57 | 2.09 |
| HUM_DISTARTWD | | | | | | |
| N of cases | 23 | 66 | 8 | 13 | 68 | 15 |
| Minimum | 35.93 | 40.81 | 39.08 | 37.16 | 35.71 | 36.26 |
| Maximum | 52.51 | 52.81 | 51.41 | 44.48 | 49.29 | 45.58 |
| Mean | 44.22 | 46.00 | 43.91 | 41.43 | 42.17 | 41.16 |
| SD | 3.51 | 2.63 | 3.98 | 2.57 | 2.70 | 2.83 |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| HUM_BIEPI | | | | | | |
| N of cases | 23 | 66 | 8 | 13 | 68 | 14 |
| Minimum | 52.41 | 56.85 | 58.28 | 50.57 | 49.58 | 52.85 |
| Maximum | 69.26 | 71.49 | 70.33 | 63.64 | 70.94 | 64.07 |
| Mean | 61.24 | 64.51 | 63.81 | 57.09 | 58.89 | 59.34 |
| SD | 4.07 | 3.52 | 4.47 | 4.56 | 3.66 | 3.16 |
| *Radius* | | | | | | |
| RAD_LENGTH | | | | | | |
| N of cases | 22 | 63 | 8 | 12 | 66 | 14 |
| Minimum | 244.96 | 257.87 | 248.19 | 234.26 | 241.16 | 252.59 |
| Maximum | 300.83 | 318.71 | 300.71 | 294.39 | 303.76 | 278.42 |
| Mean | 275.91 | 282.87 | 270.91 | 261.39 | 270.62 | 264.81 |
| SD | 16.05 | 13.64 | 15.50 | 17.75 | 14.74 | 9.03 |
| RAD_ML_MID | | | | | | |
| N of cases | 21 | 63 | 8 | 12 | 66 | 14 |
| Minimum | 13.14 | 13.15 | 13.61 | 12.38 | 11.56 | 12.30 |
| Maximum | 19.72 | 19.07 | 16.12 | 17.37 | 19.03 | 17.65 |
| Mean | 16.01 | 16.06 | 14.75 | 14.64 | 14.88 | 14.29 |
| SD | 1.71 | 1.31 | 0.80 | 1.74 | 1.60 | 1.55 |
| RAD_AP_MID | | | | | | |
| N of cases | 21 | 63 | 8 | 12 | 66 | 14 |
| Minimum | 10.72 | 11.31 | 12.25 | 10.38 | 10.78 | 11.95 |
| Maximum | 17.73 | 18.66 | 16.58 | 15.03 | 16.97 | 16.17 |
| Mean | 14.50 | 14.61 | 14.28 | 12.94 | 13.52 | 13.59 |
| SD | 1.41 | 1.42 | 1.25 | 1.40 | 1.23 | 1.03 |
| RAD_ML_HEAD | | | | | | |
| N of cases | 22 | 63 | 8 | 12 | 66 | 15 |
| Minimum | 20.25 | 20.45 | 22.35 | 19.35 | 19.30 | 20.39 |
| Maximum | 26.35 | 28.36 | 25.78 | 25.53 | 25.88 | 24.48 |
| Mean | 23.12 | 24.76 | 24.14 | 21.59 | 22.67 | 22.50 |
| SD | 1.64 | 1.53 | 1.28 | 1.60 | 1.42 | 1.03 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| RAD_DISTALWD | | | | | | |
| N of cases | 22 | 63 | 8 | 12 | 66 | 14 |
| Minimum | 26.99 | 26.94 | 28.44 | 25.56 | 24.98 | 27.04 |
| Maximum | 34.08 | 36.71 | 34.02 | 31.69 | 34.73 | 30.99 |
| Mean | 30.56 | 31.62 | 30.69 | 28.03 | 29.04 | 29.38 |
| SD | 2.08 | 1.86 | 2.09 | 1.98 | 1.97 | 1.18 |
| *Metacarpal 3* | | | | | | |
| MC_LENGTH | | | | | | |
| N of cases | 24 | 65 | 8 | 14 | 88 | 13 |
| Minimum | 77.78 | 80.25 | 78.89 | 78.16 | 75.22 | 74.93 |
| Maximum | 103.29 | 100.02 | 94.66 | 97.54 | 98.85 | 90.68 |
| Mean | 87.90 | 90.39 | 87.95 | 86.91 | 88.27 | 84.64 |
| SD | 6.46 | 4.88 | 4.78 | 6.62 | 5.09 | 4.10 |
| MC_RU_MID | | | | | | |
| N of cases | 24 | 65 | 8 | 14 | 86 | 13 |
| Minimum | 7.43 | 7.84 | 7.53 | 6.80 | 6.66 | 7.19 |
| Maximum | 9.73 | 10.38 | 9.53 | 9.95 | 9.61 | 8.84 |
| Mean | 8.50 | 8.89 | 8.52 | 8.07 | 8.30 | 8.17 |
| SD | 0.63 | 0.62 | 0.68 | 0.89 | 0.67 | 0.56 |
| MC_DP_MID | | | | | | |
| N of cases | 24 | 65 | 8 | 14 | 86 | 13 |
| Minimum | 7.99 | 7.76 | 7.96 | 7.53 | 7.57 | 7.70 |
| Maximum | 10.71 | 10.69 | 9.45 | 10.26 | 10.64 | 9.36 |
| Mean | 9.12 | 9.37 | 8.79 | 8.60 | 8.80 | 8.55 |
| SD | 0.73 | 0.63 | 0.52 | 0.92 | 0.63 | 0.49 |
| MC_RU_HEAD | | | | | | |
| N of cases | 24 | 65 | 8 | 14 | 88 | 13 |
| Minimum | 11.96 | 11.91 | 12.71 | 11.39 | 11.65 | 12.65 |
| Maximum | 15.81 | 16.76 | 14.97 | 15.84 | 16.58 | 13.97 |
| Mean | 13.77 | 14.30 | 13.77 | 12.75 | 13.52 | 13.34 |
| SD | 1.07 | 0.94 | 0.77 | 1.24 | 1.01 | 0.44 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| MC_BIEPI | | | | | | |
| N of cases | 24 | 65 | 8 | 14 | 88 | 13 |
| Minimum | 13.98 | 14.75 | 15.60 | 13.53 | 13.31 | 14.60 |
| Maximum | 19.80 | 19.58 | 19.37 | 18.31 | 20.44 | 17.82 |
| Mean | 16.80 | 17.40 | 17.20 | 15.27 | 16.17 | 16.22 |
| SD | 1.49 | 1.07 | 1.35 | 1.43 | 1.28 | 0.93 |
| *Proximal hand phalanx 3* | | | | | | |
| HP_LENGTH | | | | | | |
| N of cases | 19 | 65 | 6 | 11 | 85 | 10 |
| Minimum | 53.04 | 51.97 | 53.62 | 51.98 | 51.67 | 53.66 |
| Maximum | 68.14 | 67.64 | 63.55 | 64.47 | 67.44 | 60.18 |
| Mean | 58.21 | 60.90 | 59.10 | 59.05 | 59.82 | 56.30 |
| SD | 4.04 | 3.28 | 3.71 | 4.15 | 3.66 | 1.97 |
| HP_RU_MAX | | | | | | |
| N of cases | 19 | 64 | 6 | 11 | 85 | 10 |
| Minimum | 10.56 | 12.24 | 11.94 | 8.51 | 10.56 | 11.73 |
| Maximum | 16.29 | 17.74 | 14.05 | 15.80 | 16.66 | 14.06 |
| Mean | 13.54 | 14.48 | 13.13 | 12.65 | 13.39 | 12.35 |
| SD | 1.54 | 1.14 | 0.78 | 1.93 | 1.23 | 0.77 |
| HP_RU_MIN | | | | | | |
| N of cases | 19 | 65 | 6 | 11 | 85 | 10 |
| Minimum | 9.38 | 9.83 | 9.68 | 6.74 | 7.80 | 9.41 |
| Maximum | 13.37 | 13.85 | 11.97 | 12.30 | 13.39 | 11.39 |
| Mean | 10.91 | 11.60 | 10.78 | 10.37 | 10.53 | 10.42 |
| SD | 1.18 | 0.83 | 0.97 | 1.39 | 0.97 | 0.58 |
| HP_RU_BASE | | | | | | |
| N of cases | 19 | 65 | 6 | 11 | 85 | 11 |
| Minimum | 14.59 | 14.18 | 15.47 | 14.00 | 13.76 | 14.88 |
| Maximum | 18.60 | 19.16 | 18.27 | 17.65 | 20.89 | 16.45 |
| Mean | 16.34 | 17.21 | 16.60 | 15.59 | 16.13 | 15.79 |
| SD | 1.09 | 0.91 | 1.10 | 1.01 | 1.11 | 0.50 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| HP_RU_TROCH | | | | | | |
| N of cases | 19 | 65 | 6 | 11 | 84 | 11 |
| Minimum | 11.14 | 10.97 | 12.29 | 11.23 | 10.45 | 11.76 |
| Maximum | 14.02 | 15.26 | 13.64 | 13.01 | 17.71 | 13.02 |
| Mean | 12.56 | 12.79 | 12.93 | 11.68 | 12.22 | 12.20 |
| SD | 0.90 | 0.77 | 0.53 | 0.56 | 0.93 | 0.32 |
| ***Hindlimb*** | | | | | | |
| *Femur* | | | | | | |
| FEM_LENGTH | | | | | | |
| N of cases | 23 | 58 | 10 | 13 | 63 | 12 |
| Minimum | 266.41 | 262.41 | 287.48 | 249.70 | 262.22 | 265.29 |
| Maximum | 334.31 | 322.21 | 319.09 | 335.25 | 322.36 | 299.84 |
| Mean | 297.63 | 297.56 | 295.81 | 291.26 | 290.05 | 283.93 |
| SD | 16.61 | 13.54 | 8.71 | 23.49 | 13.61 | 9.98 |
| FEM_ML_MID | | | | | | |
| N of cases | 22 | 58 | 10 | 13 | 63 | 13 |
| Minimum | 23.04 | 22.68 | 24.40 | 20.52 | 21.25 | 22.61 |
| Maximum | 28.66 | 30.96 | 27.68 | 27.16 | 29.11 | 29.19 |
| Mean | 25.23 | 26.21 | 26.32 | 23.67 | 24.81 | 24.67 |
| SD | 1.61 | 1.50 | 0.92 | 2.03 | 1.84 | 1.93 |
| FEM_AP_MID | | | | | | |
| N of cases | 22 | 58 | 10 | 13 | 63 | 13 |
| Minimum | 19.18 | 19.09 | 19.43 | 18.04 | 18.28 | 18.51 |
| Maximum | 24.43 | 26.56 | 23.17 | 24.79 | 27.90 | 21.99 |
| Mean | 22.39 | 22.98 | 21.08 | 22.01 | 22.37 | 20.40 |
| SD | 1.37 | 1.51 | 1.23 | 2.16 | 1.89 | 1.05 |
| FEM_HEAD_HT | | | | | | |
| N of cases | 23 | 59 | 10 | 13 | 63 | 12 |
| Minimum | 28.85 | 30.25 | 30.30 | 28.55 | 26.34 | 28.75 |
| Maximum | 37.83 | 38.91 | 34.08 | 35.65 | 37.11 | 32.96 |
| Mean | 33.47 | 34.23 | 31.82 | 31.77 | 31.93 | 30.35 |
| SD | 2.12 | 1.87 | 1.18 | 2.53 | 2.10 | 1.38 |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| FEM_BICON_WD | | | | | | |
| N of cases | 23 | 58 | 10 | 13 | 63 | 13 |
| Minimum | 51.54 | 52.00 | 53.54 | 48.41 | 47.63 | 51.55 |
| Maximum | 59.33 | 64.62 | 62.13 | 56.94 | 65.20 | 57.01 |
| Mean | 55.88 | 58.79 | 57.26 | 53.17 | 54.67 | 53.48 |
| SD | 2.25 | 2.95 | 2.50 | 3.08 | 3.28 | 1.56 |
| *Tibia* | | | | | | |
| TIB_LENGTH | | | | | | |
| N of cases | 23 | 57 | 10 | 12 | 61 | 12 |
| Minimum | 221.41 | 233.83 | 233.64 | 213.02 | 215.60 | 227.53 |
| Maximum | 275.75 | 288.16 | 265.47 | 270.16 | 273.06 | 250.96 |
| Mean | 251.70 | 254.86 | 243.03 | 243.53 | 244.94 | 237.15 |
| SD | 15.21 | 12.57 | 8.93 | 19.16 | 13.14 | 7.88 |
| TIB_ML_MID | | | | | | |
| N of cases | 22 | 57 | 10 | 12 | 61 | 12 |
| Minimum | 12.35 | 13.19 | 13.46 | 13.05 | 12.17 | 13.39 |
| Maximum | 17.46 | 19.03 | 16.97 | 17.69 | 19.47 | 15.41 |
| Mean | 14.71 | 15.74 | 14.95 | 14.90 | 15.00 | 14.42 |
| SD | 1.28 | 1.20 | 1.07 | 1.68 | 1.56 | 0.70 |
| TIB_AP_MID | | | | | | |
| N of cases | 22 | 57 | 10 | 12 | 61 | 12 |
| Minimum | 20.31 | 19.32 | 19.86 | 17.54 | 18.68 | 18.49 |
| Maximum | 27.19 | 27.88 | 23.99 | 25.63 | 28.11 | 22.04 |
| Mean | 22.78 | 23.69 | 22.25 | 21.20 | 22.27 | 20.38 |
| SD | 1.61 | 1.55 | 1.40 | 2.39 | 1.87 | 1.12 |
| TIB_PLATEAU | | | | | | |
| N of cases | 23 | 57 | 10 | 12 | 62 | 12 |
| Minimum | 53.31 | 54.13 | 55.02 | 50.57 | 48.50 | 45.42 |
| Maximum | 61.26 | 68.07 | 66.48 | 59.64 | 64.82 | 58.36 |
| Mean | 58.04 | 60.60 | 59.27 | 55.30 | 56.42 | 54.40 |
| SD | 2.13 | 3.12 | 3.23 | 2.72 | 3.21 | 3.42 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| *Calcaneus* | | | | | | |
| C_LENGTH | | | | | | |
| N of cases | 23 | 67 | 10 | 14 | 87 | 11 |
| Minimum | 46.38 | 49.52 | 48.82 | 47.82 | 45.87 | 48.13 |
| Maximum | 64.98 | 61.51 | 56.82 | 58.08 | 62.44 | 58.04 |
| Mean | 54.51 | 55.09 | 53.49 | 53.63 | 52.57 | 51.74 |
| SD | 4.76 | 2.66 | 2.67 | 3.60 | 3.41 | 3.09 |
| C_TUB_LENGTH | | | | | | |
| N of cases | 23 | 67 | 8 | 14 | 86 | 11 |
| Minimum | 15.90 | 14.43 | 16.63 | 16.17 | 13.74 | 15.05 |
| Maximum | 24.15 | 27.09 | 21.65 | 23.05 | 27.26 | 23.18 |
| Mean | 19.97 | 20.27 | 19.26 | 20.13 | 19.07 | 19.51 |
| SD | 2.27 | 2.36 | 1.73 | 2.15 | 2.48 | 2.53 |
| C_TUB_HTADJ | | | | | | |
| N of cases | 23 | 67 | 10 | 14 | 87 | 11 |
| Minimum | 29.65 | 28.71 | 29.50 | 27.79 | 25.58 | 29.13 |
| Maximum | 38.44 | 41.48 | 37.83 | 37.17 | 39.52 | 34.03 |
| Mean | 33.34 | 33.59 | 33.24 | 31.34 | 31.49 | 31.00 |
| SD | 2.66 | 2.51 | 2.69 | 2.34 | 2.67 | 1.35 |
| C_TENDON_WD | | | | | | |
| N of cases | 23 | 67 | 10 | 14 | 87 | 11 |
| Minimum | 14.73 | 15.29 | 15.83 | 12.57 | 13.71 | 15.85 |
| Maximum | 22.45 | 22.19 | 20.83 | 19.66 | 21.07 | 18.70 |
| Mean | 17.62 | 18.61 | 18.45 | 16.44 | 17.15 | 17.36 |
| SD | 2.02 | 1.41 | 1.57 | 1.81 | 1.39 | 0.93 |
| C_CUB_WD | | | | | | |
| N of cases | 23 | 67 | 9 | 14 | 86 | 12 |
| Minimum | 18.81 | 17.95 | 19.67 | 17.98 | 17.23 | 19.28 |
| Maximum | 25.16 | 24.81 | 24.76 | 23.97 | 24.71 | 22.44 |
| Mean | 21.65 | 21.53 | 21.31 | 20.50 | 20.14 | 20.79 |
| SD | 1.96 | 1.47 | 1.53 | 1.84 | 1.46 | 1.01 |
| | | | | | | |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| C_CUB_DPADJ | | | | | | |
| N of cases | 23 | 65 | 9 | 14 | 84 | 12 |
| Minimum | 2.51 | 1.71 | 1.64 | 2.06 | 2.40 | 2.16 |
| Maximum | 7.05 | 7.11 | 5.76 | 5.32 | 6.94 | 4.40 |
| Mean | 4.35 | 4.38 | 4.07 | 4.03 | 3.90 | 3.38 |
| SD | 1.04 | 0.83 | 1.20 | 0.96 | 0.85 | 0.58 |
| *Metatarsal 1* | | | | | | |
| MT1_LENGTH | | | | | | |
| N of cases | 22 | 64 | 9 | 16 | 87 | 11 |
| Minimum | 49.03 | 48.15 | 49.63 | 47.24 | 46.71 | 49.77 |
| Maximum | 63.62 | 62.85 | 60.84 | 59.34 | 64.80 | 58.83 |
| Mean | 55.58 | 56.25 | 55.83 | 53.58 | 55.07 | 53.30 |
| SD | 4.31 | 3.15 | 3.23 | 3.99 | 3.65 | 2.79 |
| *Metatarsal 3* | | | | | | |
| MT3_LENGTH | | | | | | |
| N of cases | 25 | 65 | 9 | 15 | 85 | 12 |
| Minimum | 57.40 | 64.33 | 66.18 | 59.36 | 56.54 | 60.40 |
| Maximum | 79.25 | 80.72 | 75.42 | 75.60 | 77.70 | 72.37 |
| Mean | 68.27 | 70.57 | 69.98 | 66.66 | 68.76 | 66.95 |
| SD | 6.27 | 3.71 | 3.33 | 5.42 | 4.47 | 3.29 |
| MT3_ML_HEAD | | | | | | |
| N of cases | 25 | 65 | 9 | 15 | 85 | 12 |
| Minimum | 8.08 | 9.14 | 8.87 | 8.35 | 8.15 | 8.89 |
| Maximum | 11.95 | 12.41 | 11.50 | 11.62 | 11.77 | 10.56 |
| Mean | 10.35 | 10.65 | 10.18 | 9.96 | 9.95 | 9.98 |
| SD | 0.98 | 0.80 | 0.88 | 0.94 | 0.82 | 0.44 |
| MT3_BIEPI | | | | | | |
| N of cases | 25 | 65 | 9 | 15 | 85 | 12 |
| Minimum | 7.90 | 8.37 | 9.09 | 7.74 | 7.81 | 8.52 |
| Maximum | 11.41 | 11.56 | 11.36 | 11.05 | 13.23 | 10.15 |
| Mean | 9.44 | 9.80 | 9.77 | 9.04 | 9.41 | 9.28 |
| SD | 0.93 | 0.72 | 0.70 | 0.88 | 0.87 | 0.52 |
| | | | | | | |
| | | | | | | |

| **Variables**[1] | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | *schwein.* | *troglod.* | *verus* | *schwein.* | *troglod.* | *verus* |
| *Proximal foot phalanx 3* | | | | | | |
| FP_LENGTH | | | | | | |
| N of cases | 17 | 64 | 7 | 10 | 85 | 8 |
| Minimum | 35.85 | 38.91 | 38.99 | 35.33 | 36.65 | 37.54 |
| Maximum | 46.48 | 48.96 | 44.33 | 45.05 | 50.22 | 42.09 |
| Mean | 41.04 | 43.40 | 41.87 | 41.11 | 42.80 | 39.92 |
| SD | 3.27 | 2.44 | 1.91 | 3.57 | 2.85 | 1.32 |
| FP_MAXSHAFT | | | | | | |
| N of cases | 17 | 64 | 7 | 10 | 85 | 8 |
| Minimum | 7.06 | 7.11 | 7.52 | 6.72 | 6.03 | 6.36 |
| Maximum | 9.36 | 9.89 | 9.55 | 8.48 | 10.44 | 8.23 |
| Mean | 8.24 | 8.48 | 8.46 | 7.75 | 7.90 | 7.55 |
| SD | 0.70 | 0.64 | 0.69 | 0.49 | 0.70 | 0.56 |
| FP_MINSHAFT | | | | | | |
| N of cases | 17 | 64 | 7 | 10 | 85 | 8 |
| Minimum | 6.15 | 6.29 | 6.07 | 6.10 | 5.34 | 6.01 |
| Maximum | 8.50 | 9.09 | 7.61 | 7.74 | 9.37 | 7.18 |
| Mean | 7.19 | 7.60 | 6.88 | 6.86 | 6.79 | 6.56 |
| SD | 0.78 | 0.55 | 0.55 | 0.55 | 0.68 | 0.42 |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

Table 6. Descriptive statistics for raw measurements in *P. t. vellerosus*

| **Variables**[1] | Females only (no males in sample) |
|---|---|
| ***Forelimb*** | |
| *Humerus* | |
| HUM_LENGTH | |
| N of cases | 6 |
| Minimum | 276.48 |
| Maximum | 307.77 |
| Mean | 291.91 |
| SD | 11.40 |
| HUM_ML_MID | |
| N of cases | 6 |
| Minimum | 19.69 |
| Maximum | 24.97 |
| Mean | 21.31 |
| SD | 1.92 |
| HUM_AP_MID | |
| N of cases | 6 |
| Minimum | 18.27 |
| Maximum | 22.13 |
| Mean | 20.36 |
| SD | 1.75 |
| HUM_SI_HEAD | |
| N of cases | 6 |
| Minimum | 32.16 |
| Maximum | 39.14 |
| Mean | 36.24 |
| SD | 2.74 |
| HUM_DISTARTWD | |
| N of cases | 6 |
| Minimum | 38.81 |
| Maximum | 46.60 |
| Mean | 41.72 |
| SD | 3.01 |
| HUM_BIEPI | |
| N of cases | 6 |
| Minimum | 53.98 |
| Maximum | 60.84 |
| Mean | 57.66 |
| SD | 2.85 |
| | |
| | |
| | |
| | |

| | |
|---|---|
| *Radius* | |
| RAD_LENGTH | |
| N of cases | 6 |
| Minimum | 258.09 |
| Maximum | 276.79 |
| Mean | 267.49 |
| SD | 7.92 |
| RAD_ML_MID | |
| N of cases | 6 |
| Minimum | 13.28 |
| Maximum | 17.43 |
| Mean | 14.80 |
| SD | 1.62 |
| RAD_AP_MID | |
| N of cases | 6 |
| Minimum | 12.48 |
| Maximum | 13.85 |
| Mean | 13.19 |
| SD | 0.54 |
| RAD_ML_HEAD | |
| N of cases | 6 |
| Minimum | 19.87 |
| Maximum | 24.55 |
| Mean | 22.65 |
| SD | 1.81 |
| RAD_DISTALWD | |
| N of cases | 6 |
| Minimum | 27.47 |
| Maximum | 31.26 |
| Mean | 29.32 |
| SD | 1.61 |
| *Metacarpal 3* | |
| MC_LENGTH | |
| N of cases | 6 |
| Minimum | 78.61 |
| Maximum | 93.71 |
| Mean | 84.79 |
| SD | 5.61 |
| MC_RU_MID | |
| N of cases | 6 |
| Minimum | 6.98 |
| Maximum | 8.81 |
| Mean | 7.87 |
| SD | 0.76 |
| | |

| MC_DP_MID | |
|---|---|
| N of cases | 6 |
| Minimum | 8.03 |
| Maximum | 10.10 |
| Mean | 8.91 |
| SD | 0.77 |
| MC_RU_HEAD | |
| N of cases | 6 |
| Minimum | 11.51 |
| Maximum | 14.83 |
| Mean | 13.14 |
| SD | 1.23 |
| MC_BIEPI | |
| N of cases | 6 |
| Minimum | 13.58 |
| Maximum | 17.12 |
| Mean | 15.12 |
| SD | 1.27 |
| *Proximal hand phalanx 3* | |
| HP_LENGTH | |
| N of cases | 6 |
| Minimum | 56.73 |
| Maximum | 62.25 |
| Mean | 59.41 |
| SD | 1.77 |
| HP_RU_MAX | |
| N of cases | 6 |
| Minimum | 11.69 |
| Maximum | 14.17 |
| Mean | 12.58 |
| SD | 0.90 |
| HP_RU_MIN | |
| N of cases | 6 |
| Minimum | 8.94 |
| Maximum | 12.03 |
| Mean | 10.29 |
| SD | 1.10 |
| HP_RU_BASE | |
| N of cases | 6 |
| Minimum | 14.48 |
| Maximum | 17.32 |
| Mean | 15.75 |
| SD | 0.99 |
| | |
| | |

| HP_RU_TROCH | |
|---|---|
| N of cases | 6 |
| Minimum | 11.27 |
| Maximum | 12.96 |
| Mean | 12.17 |
| SD | 0.69 |
| ***Hindlimb*** | |
| *Femur* | |
| FEM_LENGTH | |
| N of cases | 4 |
| Minimum | 274.71 |
| Maximum | 292.26 |
| Mean | 284.34 |
| SD | 7.33 |
| FEM_ML_MID | |
| N of cases | 4 |
| Minimum | 23.09 |
| Maximum | 25.79 |
| Mean | 24.15 |
| SD | 1.17 |
| FEM_AP_MID | |
| N of cases | 4 |
| Minimum | 19.24 |
| Maximum | 24.06 |
| Mean | 21.83 |
| SD | 2.01 |
| FEM_HEAD_HT | |
| N of cases | 4 |
| Minimum | 27.90 |
| Maximum | 31.84 |
| Mean | 30.40 |
| SD | 1.77 |
| FEM_BICON_WD | |
| N of cases | 4 |
| Minimum | 51.04 |
| Maximum | 55.05 |
| Mean | 53.31 |
| SD | 1.67 |
| *Tibia* | |
| TIB_LENGTH | |
| N of cases | 3 |
| Minimum | 243.94 |
| Maximum | 250.96 |
| Mean | 247.21 |
| SD | 3.53 |

| TIB_ML_MID | |
|---|---|
| N of cases | 3 |
| Minimum | 12.64 |
| Maximum | 15.67 |
| Mean | 14.07 |
| SD | 1.52 |
| TIB_AP_MID | |
| N of cases | 3 |
| Minimum | 21.07 |
| Maximum | 22.46 |
| Mean | 21.87 |
| SD | 0.72 |
| TIB_PLATEAU | |
| N of cases | 3 |
| Minimum | 55.66 |
| Maximum | 56.79 |
| Mean | 56.13 |
| SD | 0.59 |
| *Calcaneus* | |
| C_LENGTH | |
| N of cases | 6 |
| Minimum | 49.19 |
| Maximum | 59.81 |
| Mean | 53.12 |
| SD | 4.02 |
| C_TUB_LENGTH | |
| N of cases | 6 |
| Minimum | 19.53 |
| Maximum | 21.68 |
| Mean | 20.24 |
| SD | 0.94 |
| C_TUB_HTADJ | |
| N of cases | 6 |
| Minimum | 28.60 |
| Maximum | 35.35 |
| Mean | 31.12 |
| SD | 2.64 |
| C_TENDON_WD | |
| N of cases | 6 |
| Minimum | 15.59 |
| Maximum | 18.89 |
| Mean | 16.84 |
| SD | 1.24 |
| | |
| | |

| C_CUB_WD | |
|---|---|
| N of cases | 6 |
| Minimum | 18.63 |
| Maximum | 22.90 |
| Mean | 20.40 |
| SD | 1.64 |
| C_CUB_DPADJ | |
| N of cases | 6 |
| Minimum | 3.24 |
| Maximum | 5.42 |
| Mean | 4.64 |
| SD | 0.82 |
| *Metatarsal 1* | |
| MT1_LENGTH | |
| N of cases | 6 |
| Minimum | 52.10 |
| Maximum | 57.85 |
| Mean | 55.32 |
| SD | 2.38 |
| *Metatarsal 3* | |
| MT3_LENGTH | |
| N of cases | 6 |
| Minimum | 64.83 |
| Maximum | 74.39 |
| Mean | 68.16 |
| SD | 3.50 |
| MT3_ML_HEAD | |
| N of cases | 6 |
| Minimum | 9.13 |
| Maximum | 10.94 |
| Mean | 10.03 |
| SD | 0.67 |
| MT3_BIEPI | |
| N of cases | 6 |
| Minimum | 8.28 |
| Maximum | 10.20 |
| Mean | 9.16 |
| SD | 0.79 |
| *Proximal foot phalanx 3* | |
| FP_LENGTH | |
| N of cases | 6 |
| Minimum | 41.36 |
| Maximum | 44.21 |
| Mean | 42.54 |
| SD | 1.07 |

| FP_MAXSHAFT | |
|---|---|
| N of cases | 6 |
| Minimum | 6.62 |
| Maximum | 8.52 |
| Mean | 7.49 |
| SD | 0.71 |
| FP_MINSHAFT | |
| N of cases | 6 |
| Minimum | 5.84 |
| Maximum | 7.31 |
| Mean | 6.51 |
| SD | 0.56 |

[1] Variables are organized anatomically within each element, as follows: length(s), shaft diameters, other shaft measurements, measurements of proximal end, and measurements of distal end.

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