The Evolution of Cercopithecoid Locomotion: A Morphometric, Phylogenetic, and Character Mapping Approach

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Abstract of the Dissertation

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Cercopithecoidea is the superfamily within the order Primates representing Old World Monkeys. Cercopithecoids are relatively rare in the fossil record prior to the middle Miocene. However, since the PlioPleistocene, cercopithecoids have undergone a diversification making them one of most ecological diverse groups of primates today. Although cercopithecoids are ecologically and behaviorally diverse, their locomotor behavior is not considered specialized and their postcrania reflect a generalized quadrupedal locomotor repertoire. Many cercopithecoids today are considered “semi-terrestrial” meaning that they are efficient on the ground and in the trees. However, the colobines are almost exclusively arboreal and committed terrestriality is thought to have evolved at least twice in the papionins.

Based primarily on interpretations of the mid-Miocene fossil monkey *Victoriapithecus*, it has been argued that the last common ancestor (LCA) of cercopithecoids engaged in terrestrial behavior and that arboreality has been secondarily evolved in the colobines, some guenons and various macaques. *Victoriapithecus*, the proposed sister taxon to crown Cercopithecoidea, has been reconstructed as semi-terrestrial. In 2010, a skeleton of *Microcolobus*, a proposed stem colobine was described as primarily arboreal, suggesting that the earliest colobines were not terrestrial and the arboreality in the clade was inherited from the LCA of crown colobines. This work also challenges the hypothesis that the ancestral cercopithecoid was semi-terrestrial.

Lack of resolution on the pattern of locomotor evolution in cercopithecoids is compounded by the absence of taxonomically comprehensive, quantitative assessments of form-function relationships and conflicting perspectives generated by a multitude of more restrictive studies. This dissertation seeks to examine the associations between morphology and locomotor behavior in cercopithecoids with the ultimate goal of improving resolution on the pattern of locomotor transitions throughout the evolution of Cercopithecoidea.

Chapter 2 summarizes a morphometric study of the humerus, femur, astragalus, and calcaneus of a sample of 52 anthropoid primates using recently developed phylogenetic comparative methods. The results from this chapter document several associations between morphology and behavior supporting previous research on the functional morphology of cercopithecoids. The major findings from this chapter are that "primarily arboreal" and "primarily terrestrial" cercopithecoids are well separated by many morphometric features but "semi-terrestrial" cercopithecoids overlap in their morphology with each of the more specialized groups. The lack of consistently "intermediate" trait values for "semi-terrestrial" cercopithecoids leads to the conclusion that they are not united by a consistent set of "intermediate" functional demands. Instead the pattern suggests that different "semi-terrestrial" taxa may differ in the degree to which functional demands of terrestriality versus arboreality have influenced the morphology of any given feature. Therefore it is unlikely that the extent of terrestrial behavior can be reliably determined in fossil taxa that lack extreme and/or consistent specialization for either terrestriality or arboreality throughout the skeleton. Although this chapter suggests that locomotor reconstructions of fossil cercopithecoids may not be highly specific in the exact amount of time a species spent in the ground or in the trees, the morphological associations can still inform us of a fossil species general locomotor behavior. First, given the separation between primarily arboreal and primarily terrestrial extant cercopithecoids, it should be possible to determine if a fossil species was highly arboreal or terrestrial. Second, if a fossil species falls into the intermediate space between primarily arboreal and primarily terrestrial cercopithecoids, or if this taxon has a pattern of morphology that suggests arboreality in some features but terrestriality in others, then this species should be considered as flexible in its locomotor behavior as many "semi-terrestrial" cercopithecoids are today. The associations between morphology and behavior and the locomotor diversity of extant cercopithecoids presented in this chapter, form the basis for the fossil reconstruction in Chapter 3.

Seventeen fossil stem and crown cercopithecoids are studied in Chapter 3 and their most likely locomotor reconstructions are presented. *Victoriapithecus* is reconstructed as considerably more arboreal than previous work has suggested. Nonetheless, the data also suggest that *Victoirpaithecus* would likely have engaged in a limited amount terrestrial behavior. Most elements from *Victoriapithecus* are classified as arboreal, but the distal humerus is consistently classified as semi-terrestrial due to a relatively dorsally projecting medial epicondyle. *Micrcolobus* is classified consistently to the arboreal group supporting previous work on this species. Given that *Victoriapithecus* probably engaged in a substantial amount of arboreal behavior and that *Microcolobus* was probably primarily arboreal, this chapter suggests that the LCA of crown cercopithecoid was arboreal, with a limited amount of terrestrial behavior possible. Importantly, this implies that in most respects, the LCA of crown colobines inherited arboreality from the LCA of crown cercopithecoids, with a possible increase in commitment to an arboreal lifestyle (i.e., colobines did not "re-evolve" arboreality).

Of the other fossil cercopithecoids studied, species that have been previously interpreted as arboreal, such as *Paracolobus* and *Rhinocolobus* are also reconstructed as arboreal in this study. Similarly, this study's reconstructions of *Theropithecus oswaldi* support previous work suggesting that this species was committed to terrestriality. However, many species previously interpreted as terrestrial, such as *Cercopithecoides*, *Dolichopithecus*, and *Theropithecus brumpti* are found to have included some arboreal behavior in their locomotor repertoire. Extensive previous work has consistently suggested "semi-terrestriality" in *Mesopithecus* and this study supports a reconstruction of *Mesopithecus* as arboreal with some limited amount of terrestrial behavior. Although this chapter suggests that the LCA of crown cercopithecoids was arboreal and presents reconstructions for fossil cercopithecoids, the pattern of locomotor transitions throughout cercopithecoid evolution can only be loosely hypothesized from the fossil record. Chapter 4 uses ancestral state reconstruction (ASR) methods to more rigorously test hypotheses concerning the timing and number of transitions to terrestriality in cercopithecoids.

Chapter 4 presents the results from ASR analyses that reconstruct 30 nodes along an anthropoid phylogeny. Crown Anthropoidea, crown Catarrhini, crown Cercopithecoidea, and crown Colobinae are consistently reconstructed as arboreal by all analyses. However, the other nodes, including crown Cercopithecinae, crown Cercopithecini, crown Papionini, crown Papionina, and crown *Macaca* are classified inconsistently to different locomotor groups across different analyses. Examining the character evolution of morphological features provides information to be considered in conjunction with classification analyses from Chapter 3. ASR suggests that the morphology of crown Cercopithecoidea is associated with arboreal behavior and that this morphology is retained in crown Colobinae. The morphology of crown Cercopithecinae shows a shift from the state of crown Cercopithecoidea to more terrestrial behavior with this shift continuing in crown Papionini. Relative to crown Cercopithecinae, the morphology of crown Cercopithecini is shifted more towards increasing arboreality. Overall, the results of Chapter 4 support an arboreal LCA for crown Cercopithecoidea and crown Colobinae with the evolution of committed terrestrial behavior first appearing in crown Cercopithecinae.

This dissertation documents the morphological diversity in the cercopithecoid postcranium and presents several features that exhibit a morphological continuum with respect to substrate preference. Using this morphometric dataset, the locomotor behavior of fossil stem and crown cercopithecoids and hypothetical ancestors are reconstructed. The findings of this dissertation suggest that early cercopithecoids were arboreal with committed terrestriality evolving in the late Miocene during cercopithecine evolution. The transition to increased use of terrestrial behavior at around 10 million years ago coincides with global cooling that began in the late Miocene.

Dedication

For my parents, Colette and Hassan, and my brother, Max, who have made me who I am today

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List of Institutional Abbreviations

AMNH – American Museum of Natural History, New York

AIZ – Anthropological Institute, Zurich

BNHM – The Natural History Museum, London

CPRC – Caribbean Primate Research Center, San Juan

FM – Field Museum, Chicago

KNM – Kenya National Museum, Nairobi

MCZ – Museum of Comparative Zoology, Cambridge

MHNL – Muséum d’Histoire Naturelle, Lyon

MNHN-P – Muséum National d’Histoire Naturelle, Laboratoire de Paléontologie, Paris

NME – National Museum of Ethiopia, Addis Ababa

NMNH – National Museum of Natural History, Washington, DC

NMNH-S – National Museum of Natural History, Sofia

PCM – Powell-Cottom Museum, Birchington-on-Sea

RMCA – Royal Museum of Central Africa, Tervuren

UCB – University of California, Berkeley (personal collection of Tim White)

UTA – University of Texas at Austin

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Chapter 1
Introduction

Section 1.1: Introduction

Morphologists have long sought to identify musculoskeletal adaptations to locomotion in order to understand the functional significance of morphological features (Ashton and Oxnard 1964; Jenkins 1973; Taylor 1974; Fleagle 1976; Taylor 1976; Fleagle 1977; Manaster 1979; Rodman 1979; Ward and Sussman 1979; Van Valkenburgh 1987; Fleagle and Meldrum 1988; Kappelman 1988; Rose 1988; Strasser 1988; White 1993; Gebo and Sargis 1994; Larson 1995). Studies that have combined field observations with morphological analyses of closely related species with different locomotor modes have established an association between musculoskeletal anatomy and positional behavior, and an adaptive basis for morphological variation (Fleagle 1976; Fleagle 1977; Ward and Sussman 1979; Fleagle and Meldrum 1988). Broad morphological studies have demonstrated that some aspects of skeletal anatomy may be associated with phylogenetic relatedness in addition to functional demands in groups whose various members exhibit some level of uniformity in positional behaviors (e.g., Ashton and Oxnard 1964; Jenkins 1973; Rose 1988; Larson 1995). Although this work has been influential in finding associations between anatomical structures and locomotor behavior, most primatological studies have not addressed functional adaptations within a phylogenetic context. The next step is to incorporate this information into the study of character evolution where phylogenetic and functional information will be integrated to assess the evolutionary history of locomotion. Therefore, I plan to address the evolution of locomotor adaptations in cercopithecoids within a taxonomically broad, and explicitly phylogenetic, framework (e.g. Ciochon 1993; Jones 2008).

Cercopithecoidea is an interesting group in which to study the evolution of skeletal adaptation to locomotor behavior because it is arguably one of the most taxonomically diverse but functionally constrained groups of primates. Previous studies have documented difficulty in discriminating between arboreal, semi-terrestrial, and terrestrial species because the differences between these locomotor groups are subtle (Ripley 1975; Gebo and Sargis 1994). The reason for this subtly is likely because of the fluidity with which many cercopithecoids transition between terrestrial and arboreal activity. Even some of the most terrestrial species engage in arboreal foraging or have sleeping sites in trees while some arboreal species may travel on the ground.

Within primates, Cercopithecoidea includes the largest number of terrestrial species and possibly several evolutionary transitions between arboreality and terrestriality (Strasser 1988; Ciochon 1993; Benefit 1999b; Benefit and McCrossin 2002; Jablonski 2002; Leakey et al. 2003; Sargis et al. 2008; Nakatsukasa et al. 2010). Although several studies have examined the locomotor diversity and evolutionary history of cercopithecoids, many issues remain unresolved (Etter 1973; Manaster 1979; Rodman 1979; Kingdon 1988; Strasser 1988; Harrison 1989; McCrossin and Benefit 1992; Ciochon 1993; Gebo and Sargis 1994; Nakatsukasa 1994; McCrossin et al. 1998; Elton 2002; Sargis et al. 2008; Su and Jablonski 2009). Questions that have arisen from previous work include 1) how clear is the separation of locomotor groups (i.e. arboreal, terrestrial, semi-terrestrial) given the behavioral flexibility of species within cercopithecoids (Manaster 1979; Gebo and Sargis 1994; Nakatsukasa 1994; Elton 2002; Youlatos 2003), 2) how many locomotor transitions occurred in the evolution of cercopithecoids (Ciochon 1993; Sargis et al. 2008; Nakatsukasa et al. 2010), and 3) what is the most likely locomotor mode at important divergences along the cercopithecoid lineage (Ciochon, 1993;

Sargis et al. 2008; Nakatsukasa et al. 2010)? These questions have been difficult to assess because, until recently, the phylogeny of the group was poorly resolved. However, in the last several years molecular phylogenetic studies have resolved relationships across the clade and provided detailed phylogenies for previously understudied groups, such as the langurs (Karanth et al. 2008; Osterholz et al. 2008). Additionally, large species-level studies that provide divergence estimates have become available for the clade (Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012). The new phylogenetic information now available allows for the application of recently developed approaches for the study of associations between morphology and behavior using a phylogenetically-informed approach and the study of character evolution and ancestral state reconstructions that require both well-resolved phylogenies and branch lengths. An important component of this dissertation will be to understand postcranial diversity of cercopithecoids in an explicitly phylogenetic framework and reassess associations between morphology and behavior.

Section 1.2: Background

Section 1.2.1: Functional Morphology of Cercopithecoidea

In order to understand the locomotor evolution of cercopithecoids, several studies have attempted to determine which morphological features are indicative of arboreal, terrestrial, and semi-terrestrial behaviors (Etter 1973; Manaster 1979; Rodman 1979; Kingdon 1988; Strasser 1988; Harrison 1989; Strasser 1992; Ciochon 1993; Larson 1993; Gebo and Sargis 1994; Larson 1995; Elton 2002; Patel 2010). Features such as relatively short digits (Etter 1973; Kingdon 1988; Strasser 1992; Patel 2010), a greater tubercle that projects above the humeral head (Harrison 1989; Ciochon 1993; Larson 1993), a posteriorly directed humeral medial epicondyle (Harrison 1989; Ciochon 1993), a short and posteriorly directed ulnar olecranon process (Ciochon 1993), low femoral neck angle (Fleagle 1983; Fleagle and Meldrum 1988), a wedge shaped and asymmetrical astragalar trochea (Strasser 1988), a strongly curved ectal facet (Strasser 1988), and a reduced articular surface areas (Gebo and Sargis 1994) have been shown previously to be associated with terrestriality. Semi-terrestrial species are often categorized as "intermediate" by either falling in between arboreal and terrestrial species along a morphological continuum (Manaster 1979; Nakatsukasa 1994) or, as in the same case of some fossil cercopithecoids, exhibiting both arboreal and terrestrial features within the same element (Birchette 1982; Elton 2002; Youlatos 2003). For example, Nakatsukasa (1994) found a continuum in some postcranial features, such as femoral shaft robustness, with *Cercocebus galeritus* positioned between the more terrestrial *Cercocebus torquatus* and the more arboreal *Lophocebus albigena*. On the other hand, Birchette (1982) found that *Paracolobus chemeroni* resembled arboreal taxa in having a more medially projecting medial epicondyle, but was similar to terrestrial taxa in having a projecting greater tubercle. Since the publication of most this work, biologists have come to understand that standard statistical methods may inflate differences between species due to their shared evolutionary history (Felsenstein 1985). Felsenstein (1985) was one of the first biologists to argue that due to the hierarchical structure of phylogenies, species cannot be considered independent data points in comparative biology. Since then, several approaches have been developed to account for phylogeny in statistical approaches examining.

In addition to studying extant morphological diversity, some studies have attempted to identify the order in which particular adaptations evolved or reconstruct the most likely suite of morphological characters of an ancestral node (Strasser 1988; Ciochon 1993; Gebo and Sargis 1994). Strasser (1988) identified 12 pedal features of cercopithecoids derived from the catarrhine morphotype that she suggests emphasized a more terrestrial lifestyle and a continuation of the specialization among the cercopithecines. She also documents nine derived features of colobines relative to the cercopithecoid morphotype that she suggests are associated with a reversal to a more arboreal lifestyle.

Ciochon (1993) studied characters of the scapula, humerus, radius, and ulna in 13 cercopithecoid species and determined character polarities by comparing the extant dataset to three outgroup taxa, *Victoriapithecus*, *Aegyptopithecus*, and *Apidium*. He found that cercopithecoids and *Victoriapithecus* share features that are derived relative to the ancestral catarrhine morphotype, such as an elongated humeral head, a posteriorly directed medial epicondyle, an expanded and more posteriorly oriented radial notch, and a narrow trochlea. He also concluded that arboreality was secondarily evolved in colobines based on five reversals from the ancestral crown cercopithecoid state to the primitive crown catarrhine state, including a rounded humeral head, a medially oriented medial epicondyle, a narrow and anteriorly positioned radial notch, and a wide trochlea (Ciochon, 1993; Fig 56, pp 210).

Gebo and Sargis (1994) studied postcranial adaptations in guenons and suggested that terrestrial behavior evolved three times during guenon evolution. Based on phylogenies from that time, they suggested that terrestriality evolved in the ancestor of *Allochrocebus lhoesti*, *C. preussi*, and *C. solatus* and that terrestriality evolved separatly in both *C. aethiops* and *Erythrocebus patas*. Using more recent molecular phylogenies of guenons, Sargis et al. (2008) re-examined the evolution of locomotor adaptations in guenons. They concluded that terrestriality evolved only once in guenons, because molecular data suggest that *C. aethiops* and *E. patas* are the sister group to the *A. lhoesti* group.

These studies used either a presence/absence criterion or a standard parsimony based character mapping approach to reconstruct transitions in locomotor behavior among cercopithecoids. More sophisticated methods of study character state evolution and ancestral state reconstruction have been developed (Hansen and Martins 1996; Martins and Hansen 1997; Pagel 1997; Schluter et al. 1997; Pagel 1999a; Pagel 1999b; Freckleton et al. 2002; Nunn 2011). These methods use maximum likelihood or Bayesian approaches to model character state evolution along a dated molecular phylegny using multiple models of evolution. Therefore, an important aspect of this dissertation will be the reconstruction of the sequence of evolutionary changes that resulted in the diverse postcranial morphology exhibited by extant cercopithecoids. Reconstructions based on information from extant taxa will then be compared to the evidence that is available from the early fossil record documenting cercopithecoid evolution.

Section 1.2.2: The fossil record of Cercopithecoidea

Several fossil stem and crown cercopithecoids have associated postcrania or postcrania assigned based on size and/or the presence or absence of other cercopithecoids at a given locality. *Victoriapithecus macinnesi* is considered by many to be the sister taxon to crown cercopithecoids (von Koenigswald 1969; Benefit and McCrossin 1991; Benefit 1993; Benefit and McCrossin 1997; Benefit 1999b; Benefit 1999a; Benefit 2000; Benefit and McCrossin 2002; Miller et al. 2009) and a substantial amount of postcrania is attributed to this species, with almost every postcranial bone represented (Benefit and McCrossin 2002). *Microcolobus tugenensis*, a likely colobine (Benefit and Pickford 1986), was recently placed as a stem colobine by Rossie et al. (2013) and Nakatsukasa et al. (2010) described a fairly complete postcranium of *Microcolobus*. Several crown colobines have well preserved postcrania but a comprehensive study of the phylogenetic position of these fossils is lacking. These colobines include *Mesopithecus* (Delson 1973; Szalay and Delson 1979), *Dolichopithecus* (Delson 1973; Szalay and Delson 1979), and *Parapresbytis* (Egi et al. 2007) from the Miocene and Pliocene of Eurasia and *Kuseracolobus* (Hlusko 2006), *Paracolobus* (Birchette 1982; Leakey 1982), *Cercopithecoides* (Leakey 1982; Frost and Delson 2002; Jablonski et al. 2008b), and *Rhinocolobus* (Leakey 1982; Frost and Delson 2002; Jablonski et al. 2008b) from the Pliocene and Pleistocene of Africa. *Mesopithecus* has been hypothesized to have affinities with Asian colobines (Delson 1975; Jablonski and Peng 1993; Jablonski 1998; Pan et al. 2004) while *Paracolobus* and *Cercopithecoides* have been suggested as a sister group to extant African colobines (Delson 1975).

Currently, little fossil material has been suggested to be a possible stem cercopithecine or a possible stem or crown guenon (but see Cooke 2006). However, the papionins are well represented in the fossil record and many species have associated or assigned postcrania. *Parapapio*, a stem papionin with several known species (Gilbert 2013), has two species, *P. jonesi* and *P. lothagamensis* with assigned postcrania (Frost and Delson 2002; Leakey et al. 2003). *Paradolichopithecus* and *Procynocephalus* are considered to be within the crown macaque group (Delson 1973; Szalay and Delson 1979; Strasser and Delson 1987; Jablonski 2002), although their relationship to extant macaques is unknown. *Paradolichopithecus* is represented by a limited amount of postcrania and unfortunately the *Procynocephalus* material (including the only postcrania) from the Zhoukoudian, Kutitsun, and Yüshe study areas have been missing from the Beijing (Peking) museum since at least the 1970's (Szalay and Delson 1979, pp. 363). Finally, *Theropithecus* is well represented by both associated and assigned postcrania (Krentz 1993; Jablonski 2002; Jablonski et al. 2002; Jablonski et al. 2008a; Gilbert et al. 2011; Guthrie 2011).

The evolutionary history of cercopithecoids is complicated and likely involves several locomotor transitions along different lineages. Based on mutiple lines of fossil evidence, many studies have interpreted the last common ancestor (LCA) of crown cercopithecoids as having been at least partly terrestrial (Leakey 1982; Strasser 1988; Harrison 1989; McCrossin and Benefit 1992; Ciochon 1993; McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003; Youlatos et al. 2012). Under this evolutionary scenario, if terrestriality evolved early in cercopithecoid evolution (i.e., along the cercopithecoid stem lineage), then arboreal taxa -- such as most extant colobines and guenons, *Lophocebus*, and several extant macaques -- evolved this locomotor mode secondarily. Previous work has reconstructed *Victoriapithecus* as semi-terrestrial and given its position as a stem cercopithecoid, some authors suggest that the last common ancestor of cercopithecoids inherited semi-terrestriality from *Victoriapithecus* (Harrison 1989; McCrossin and Benefit 1992; McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003). Additional evidence for this hypothesis came from a fossil record that was largely interpreted as being dominated by semi-terrestrial and terrestrial species from both the cercopithecine and colobine lineages, including *Mesopithecus* (Delson 1973; Birchette 1982; Ciochon 1993; Youlatos 2003; Ingicco 2008; Youlatos and Koufos 2010; Youlatos et al. 2012), *Dolichopithecus* (Ignaccio, 2008; Ciochon 1993; Delson 1973), *Cercopithecoides* (Birchette 1982; Leakey 1982; Frost and Delson 2002; Jablonski et al. 2008b), *Parapapio* (Frost and Delson 2002; Leakey et al. 2003), and multiple species of *Theropithecus* (Krentz 1993; Jablonski 2002; Jablonski et al. 2002; Jablonski et al. 2008a; Gilbert et al. 2011; Guthrie 2011). Finally, Leakey et al. (2003) recontruct colobine material of indeterminate genus and species from Lothagam as terrestrial. They argue that this material, which is dated to between 7.44 – 5.0 mya (McDougall and Feibel 1999), and the late Pliocene genera of *Rhinocolobus* and *Paracolobus* support the hypothesis that arboreality evolved late in colobine evolution and independently in the African and Asian radiations.

The recently described postcranium of *Microcolobus*, which is interpreted as primarily arboreal, does not support the hypothesis that colobines evolved arboreality independently (Nakatsukasa et al. 2010). Given the position of *Microcolobus* as a stem colobine (Rossie et al. 2013), the LCA of crown colobines was likely to have been arboreal as well (Nakatsukasa et al. 2010). In addition to the postctanium of *Microcolobus*, other recently described early fossil colobines are suggested to be arboreal and add to an increasingly growing body of evidence that suggests some early colobines were arboreal (Hlusko 2006; Hlusko 2007; Gilbert et al. 2010). Hlusko (2007; 2006) described postcranial material of *Kuseracolobus* (dated to 4.4 ma) from Asa Issie, Ethiopia and of colobines of genus indeterminate from Lemundong'o, Kenya (dated to 6 ma) as primarily arboreal. Gilbert et al. (2010) described a Pliocene colobine astragalus of indeterminate species from the Tugen Hills (dated to 6.1 – 5.88 ma) as arboreal. The work by Gilbert et al. (2010) and Hlusko (2007; 2006) document the presence arboreal colobines in the late Miocene, which interpreted a colobine astragalus as arboreal based on a strongly curved ectal facet. Hlusko (2007; 2006) and Gilbert et al. (2010) suggest that the earliest Pliocene colobines were primarily arboreal, and suggest that terrestriality may have been independently evolved in colobines.

Thus, numerous evolutionary scenarios for locomotor transitions are possible within cercopithecoids. First, the LCA of crown cercopithecoids engaged in terrestrial behavior with the LCA of crown cercopithecines retaining this locomotor behavior and the LCA of crown colobines undergoing a reversal to a primarily arboreal lifestyle. Following this scenario, terrestriality is evolved independently and multiple times in colobine evolution. Additionally, arboreality is secondarily revolved in guenons since the LCA of crown Cercopithecinae is hypothesized to be partly terrestrial.

Alternatively, the LCA of crown cercopithecoids could have been arboreal with the LCA of colobines retaining the ancestral condition. The LCA of crown cercopithecinae could also have retained this lifestyle, which would suggest independent acquisitions of terrestriality in guenons and papionins. Alternatively, the LCA of crown cercopithecinae could have evolved a lifestyle including terrestrial behavior, which would make the acquisition of arboreality in guenons a reversal, as discussed above.

Finally, under wither scenario, extreme adaptations to a committed terrestrial lifestyle are seen among the papionins, including *Papio*, *Theropithecus*, and *Mandrillus*. The evolution a more committed terrestrial lifestyle evolved up to three times given the well-supported separation of a *Cercocebus-Mandrillus* clade and *Papio-Theropithecus-Lophocebus* clade (Cronin and Sarich 1976; Disotell et al. 1992; Harris and Disotell 1998; Page et al. 1999; Harris 2000; Tosi et al. 2003; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012; Guevara and Steiper in press). The position of *Lophocebus* is still debated (Disotell et al. 1992; Harris and Disotell 1998; Page et al. 1999; Harris 2000; Tosi et al. 2003; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012; Guevara and Steiper in press), but if *Lophocebus* is more closely related to either *Papio* or *Theropithecus*, then a committed terrestrial lifestyle would have evolved twice in this clade.

Section 1.2.3: Phylogenetics of Cercopithecoidea

The comparative and character mapping approaches used in this dissertation require a well-resolved phylogeny with known branch lengths, and therefore cannot be applied to groups with unresolved relationships. Cercopithecoidea is an excellent group for character mapping because it has been well studied and the extant phylogeny is now fairly resolved. Molecular studies of primate phylogenies have consistently recovered monophyletic groupings of Cercopithecinae and Colobinae (Bigoni et al. 2004; Xing et al. 2005; Chattarjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012). Within the Cercopithecinae two monophyletic tribes are supported, the Papionini and the Cercopithecini (Tosi et al. 2005; Xing et al. 2005; Chattarjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012).

The Papionini have a well-established phylogeny with *Macaca* as the most basal member followed by the divergence of a *Cercocebus*-*Mandrillus* clade and a *Lophocebus*-*Theropithecus*-*Papio* clade (Cronin and Sarich 1976; Disotell et al. 1992; Harris and Disotell 1998; Page et al. 1999; Harris 2000; Tosi et al. 2003; Davenport et al. 2006; Olson et al. 2008; Fabre et al. 2009; Zinner et al. 2009; Roberts et al. 2010; Perelman et al. 2011; Springer et al. 2012; Guevara and Steiper in press), although as mentioned previously the position of *Lophocebus* vis-à-vis *Theropithecus* and *Papio* is still debated. Some studies place *Papio* as the sister-taxon to *Theropithecus* to the exclusion of *Lophocebus* (Disotell et al. 1992; Page et al. 1999; Fabre et al. 2009). However, the most recent molecular studies and the other eariler studies place *Lophocebus* as the sister taxon to *Papio* to the exclusion of *Theropithecus* (Harris and Disotell 1998; Harris 2000; Perelman et al. 2011; Springer et al. 2012; Guevara and Steiper in press). Only one study has placed *Lophocebus* as the sister taxon to *Theropithecus* (Tosi et al. 2003). Guevara and Steiper (in press) suggest that although they recovered *Lophocebus* and *Papio* as sister taxa, there was likely hybridization among the *Lophocebus*, *Papio,* and *Theropithecus* lineages early in their evolution, make the resolution of this clade difficult. Finally, the recently described species, *Rungwecebus kipunji*, has been placed as the sister taxon to *Papio* by multiple studies (Davenport et al. 2006; Olson et al. 2008; Zinner et al. 2009; Roberts et al. 2010; Springer et al. 2012) and has been suggested to have experienced hybridization during its evolutionary history (Burrell et al. 2009; Zinner et al. 2009; Roberts et al. 2010).

Most studies recognize the only African macaque, *Macaca sylvanus*, as basal in the *Macaca* clade, with subsequent divergences into the *silenus*, *sinica*, and *fascicularis* groups (Morales and Melnick 1998; Ziegler et al. 2007; Chattarjee et al. 2009; Fabre et al. 2009; Li et al. 2009; Perelman et al. 2011; Springer et al. 2012). However most studies do not agree on the placement of *M. arctoides* with several different phylogenetic positions possible (Hoelzer et al. 1992; Morales and Melnick 1998; Chattarjee et al. 2009; Fabre et al. 2009; Li et al. 2009; Perelman et al. 2011; Springer et al. 2012).

In the cercopithecin clade, *Allenopithecus* has been found to be the sister taxon to all other genera (Xing et al. 2007; Fabre et al. 2009). Although recently Guschanski et al. (2013) have suggested that *Miopithecus* is the sister taxon to all other guenons and Springer et al. (2012) found *Allenopithecus* and *Miopithecus* to be sister taxa and form an outgroup to all other guenons. Additionally, multiple studies have found *Cercopithecus* to be paraphyletic and a new genus name has been given to the l'hoesti monkey – *Allochrocebus lhoesti* – which will be used throughout the dissertation (Tosi et al. 2003; Tosi et al. 2004; Tosi et al. 2005; Xing et al. 2007; Moulin et al. 2008; Chattarjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012; Guschanski et al. 2013). Perelman et al., (2011) found *Allenopithecus* to be the sister taxon to the “terrestrial” guenon clade including *Chlorocebus*, *Erythrocebus*, and *Allochrocebus*. Finally, although multiple studies have suggested that the “terrestrial” guenons – *Chlorocebus*, *Erythrocebus*, and *Allochrocebus* form a clade (Tosi et al. 2004; Tosi et al. 2005; Xing et al. 2007; Moulin et al. 2008; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012), results from Guschanski et al. (2013) do not support this topology.

Within the Colobinae, most studies find langurs grouping with the odd-nosed monkeys to the exclusion of African colobines (Xing et al. 2005; Chattarjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012). Most studies recover a polytomy relationship between the odd-nosed monkeys, the langurs and *Presbytis* (Osterholz et al. 2008; Fabre et al. 2009) and also recover a paraphyletic *Trachypithecus* (Karanth et al. 2008; Osterholz et al. 2008; Chattarjee et al. 2009; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012). Recently, Md-Zain et al. (2008) document that the genus *Presbytis* is monophyletic and *Trachypithecus* species on the Indian subcontinent have been found to be more closely related to sympatric *Semnopithecus* than they are to Southeast Asian *Trachypithecus* (Karanth et al. 2008). Finally, *Colobus* has been found by recent studies to be the sister taxon to the clade containing *Procolobus* and *Piliocolobus* (Fabre et al. 2009; Springer et al. 2012).

Section 1.3: Goals of the dissertation

The goals of this dissertation are to 1) gain a better understanding of postcranial diversity in cercopithecoids by examining a broad taxonomic sample by this clade, 2) determine associations between morphology and behavior within a phylogenetic context, 3) determine the utility of a “semi-terrestrial” locomotor category, 4) provide improved reconstructions for stem and crown cercopithecoid fossils, 5) study the character state evolution of morphological features that are associated with locomotor behavior, and 6) reconstruct ancestral states for important divergences and crown nodes within Cercopithecoidea. Chapter 2 investigates associations between morphology and behavior using a combination of phylogenetically-informed and standard univariate analyses and multivariate analyses. This chapter seeks to find morphological features that separate arboreal, semi-terrestrial, and terrestrial groups. In addition, this chapter discusses the utility of a semi-terrestrial locomotor category and if such a category can be defined morphologically. Chapter 3 tests the ability of morphological features that have associations with behavior to discriminate and correctly classify individuals to their *a priori* locomotor mode. This chapter also provides fossil reconstructions using a combination of isolated elements and composite or associated specimens. Finally, Chapter 4 presents results from ancestral state reconstructions (ASR). ASR analyses were run across multiple phylogenies that included and excluded fossil taxa and varied in the timing of the divergences of major primate clades. Reconstructions for crown nodes and other important divergences are suggested and the character state evolution of morphological features is discussed. The chapters combined provide a new, phylogenetically informed framework to study postcranial diversity and locomotor evolution in cercopithecoids, clarifies the extent to which features of the postcranium can be reliably used to track locomotor transitions in the fossil record, and suggest new hypotheses for locomotor transitions in cercopithecoid evolution.

Chapter 2
The Validity of Semi-terrestriality as a Locomotor Category

Section 2.1: Introduction

Molecular and fossil evidence suggests that Cercopithecoidea diverged from Hominoidea in the late Oligocene, around 25 million years ago (mya) (Springer et al. 2012; Steiper and Seiffert 2012; Stevens et al. 2013). Stevens et al. (2013) recently described the earliest stem cercopithecoid, *Nsungwepithecus gunnelli*, represented by a lower third molar from the Rukwa Rift Basin of Tanzania, dated to 25.2 mya. All other published fossil evidence of cercopithecoid evolution comes from the Miocene, after ~ 20 mya (Benefit and McCrossin 2002; Jablonski 2002; Jablonski and Frost 2010). The earliest cercopithecoids, including the genera *Prohylobates*, *Victoriapithecus*, *Zaltanpithecus*, and *Noropithecus*, are generally accepted to be from the extinct group Victoriapithecidae, a group of stem cercopithecoids that may be paraphyletic (Jablonski and Frost 2010; Miller et al. 2009; Benefit and McCrossin 2002). Of these four genera, only middle Miocene *Victoriapithecus* is represented by both cranial and postcranial material (Benefit and McCrossin 2002).

Victoriapithecus is considered to be the most derived victoriapithecid and is thought to be the sister-taxon to crown Cercopithecoidea based on craniodental characters, such as expanded bilophodont lower molars, expansion of the hypocone on the upper molars, absence of the maxillary sinus, a narrow interorbital septum, and long nasal bones (for a complete review see (von Koenigswald 1969; Benefit and McCrossin 1991; Benefit 1993; Benefit and McCrossin 1993; Benefit and McCrossin 1997; Benefit 1999b; Benefit 2000; Benefit and McCrossin 2002; Miller et al. 2009). Based on the vast assemblage of postcranial material attributed to *Victoriapithecus*, previous work has suggested that this species was "semi-terrestrial" (Harrison 1989). Anatomical features of *Victoriapithecus* that are suggestive of terrestrial behavior include a greater tubercle that projects proximal to the humeral head, a dorsally oriented humeral medial epicondyle, a humeral trochlear flange, a dorsally directed olecranon process on the ulna, a low femoral neck angle, and relatively short phalanges (Harrison 1989; McCrossin et al. 1998). Based on this morphology, students of early cercopithecoid evolution generally consider it likely that the ancestral crown cercopithecoid engaged in at least some terrestrial behavior, and that the highly arboreal behavior seen in many guenons and colobines represent evolutionary reversals (Senut 1986, Birchette 1982; Harrison 1989; Ciochon 1993; McCrossin et al. 1998; Benefit 1999b; Benefit 1999a). It should be noted that since other victoriapithecid genera are not represented by postcrania, there is no evidence to suggest that all victoriapithecids shared these adaptations for efficient terrestrial locomotion.

Although *Victoriapithecus* is generally considered to have been "semi-terrestrial," this category has neither a well-defined behavioral or morphological definition. Almost all cercopithecoids are adept at both arboreal and terrestrial locomotion. Although some cercopithecoids have strong preferences for travel in the trees or on the ground (such as small-bodied guenons and geladas, respectively; for substrate preferences of cercopithecoid species see Appendix A), most cercopithecoid species are adept at traveling and foraging in both the trees and on the ground. This flexibility has led to a generalized body plan, and previous morphological studies demonstrate subtle differences in morphology between arboreal, semi-terrestrial, and terrestrial cercopithecoids (Manaster 1979; Rodman 1979; Birchette 1982; Strasser 1988; Ciochon 1993; Gebo and Sargis 1994; Nakatsukasa 1994; Elton 2002).

Without a clear definition of what "semi-terrestriality" is, it is difficult to discuss locomotor evolution within Cercopithecoidea. Given that *Victoriapithecus* is considered by most specialists to be "semi-terrestrial", and if this pattern is accordingly ancestral for crown Cercopithecoidea, the next logical step in studying the evolution of this clade would be to determine when (and how many times) dedicated arboreality evolved, and when dedicated terrestriality evolved (notably within Papionina). It would be of interest to determine how many times these transitions took place, and examine morphological evidence for convergence. However, these questions are difficult to address when previous morphological work suggests that "semi-terrestrial" groups have morphological features that overlap with those of both primarily arboreal and terrestrial species (Gebo and Sargis 1994; Nakatsukasa 1994; Elton 2002).

The goal of this study is to examine the validity of a "semi-terrestrial" morphology by examining four skeletal elements in a broad taxonomic sample of cercopithecoid primates. Cercopithecoids are a highly diverse clade and differing degrees of "arboreal" and "terrestrial" behaviors are exhibited in all of the major cercopithecoid clades. For instance, while most colobines are arboreal, with some species engaging in leaping behaviors, the genera *Rhinopithecus* and *Semnopithecus* regularly travel on the ground. Terrestrial travel is also well documented in cercopithecine guenons and some of these "terrestrial" species have recently been shown to form a monophyletic group (Tosi et al. 2004; Tosi et al. 2005; Sargis et al. 2008). Papionina includes the most terrestrial cercopithecoid species, but it is also a diverse group that contains some highly arboreal macaques. Finally, the fossil record suggests that in some cases locomotor diversity was greater in the past than it is today. This is especially true of the colobines, which had several large bodied forms in the PlioPleistocene, such as *Cercopithecoides* and *Paracolobus*. *Cercopithecoides* has been reconstructed as terrestrial (Birchette 1982; Frost and Delson 2002; Jablonski et al. 2008b) and *Paracolobus* has been reconstructed as arboreal with the capacity for terrestrial behavior (Birchette 1982; Ciochon 1993). Clearly, transitions between primarily arboreal and primarily terrestrial habits have occurred multiple times throughout cercopithecoid evolution, and an accurate understanding of locomotor evolution within the clade requires a better understanding of their extant diversity.

Section 2.2: Methods

Section 2.2.1: Data Collection

The humerus, femur, astragalus, and calcaneus were considered in this study. These elements were chosen based on previous work that has demonstrated that anatomical features of these elements are associated with substrate preference (Manaster 1979; Rodman 1979; Birchette 1982; Strasser 1988; Ciochon 1993; Gebo and Sargis 1994; Nakatsukasa 1994; Elton 2002), and also based their prevalence in the fossil record. Appendix B lists the measurements taken for each element, subsequent indices created from these measurements, and the abbreviations that will be used to identify variables throughout the study. Measurements were adapted from previous morphological studies of cercopithecoids (Strasser 1988; Harrison 1989; Ciochon 1993; Gebo and Sargis 1994; Elton 2002). Although previous work has suggested that ulnar morphology is associated with locomotor behavior in cercopithecoids (Fleagle 1983; Rose 1988; Harrison 1989; Ciochon 1993; Gebo and Sargis 1994; Richmond et al. 1998; Ruff 2002), the articular surfaces of the proximal ulna for the distal humerus and proxial radius are probably better studied using computed tomography (CT), which allow for measures of surface area and curvature. Because one major goal of the disseration was to obtain the most comprehensive taxonomic sampling to date, the large sample size collected prohibited the use of CT and the ulna was excluded from the scope of this study.

A total of 608 specimens of 52 primate species were studied (Table 2.1; Appendix C). Whenever possible, six male and six female skeletons were measured for each species, and all four elements were studied for each individual. Elements were excluded when epiphyses were not fully fused, although specimens with modest epiphyseal lines present were included. Specimens were also excuded if they showed any signs of injury or pathology. Priority was given to measuring wild-caught specimens, however in some cases, captive individuals had to be included in order to meet sample size goals. Appendix D lists the species means for all measurements included in the study.

To determine whether captive individuals might express different morphologies than their wild-caught counterparts, a series of one-way analyses of variance (ANOVAs) was performed on a captive and wild-caught sample of *Theropithecus gelada*. Most species in the sample do not have any captive individuals included. For species in which captive individuals were included, the number of captive individuals is usually less than three. *Theropithecus gelada* was the only species for which an approximately equal sample of wild caught (9) and captive (11) individuals was available (Table 2.1). Although captive geladas probably engage in similar behavior to wild geladas (i.e., sitting and terrestrial travel) and thus may not be the most appropriate species for this analysis, previous work has not documented differences between wild-caught and captive populations in other species (e.g., (Bello-Hellegouarch et al. 2013). Of 65 variables measured, the only feature that shows a significant difference between wild-caught and captive specimens in *T. gelada* is the width of the medial epicondyle of the femur (F = 4.75; df = 14; p = 0.047). Because the results otherwise suggest no morphological differences between wild-caught and captive specimens, captive specimens (or specimens of unknown origin) were not removed from the dataset.

All measurements, aside from angular measurements and ratios, were converted to Mosimann shape variables using the geometric mean (Jungers et al. 1995). Angular measurements were converted to radians before analysis. In order to assess whether shape conversion of variables eliminated size differences between males and females in sexually dimorphic taxa, a series of one-way ANOVAs was run between males and females of *Papio cynocephalus* and *Papio anubis* (species were analyzed separately). Of 65 variables total, seven variables were found to be significantly different between males and females in either *P. cynocephalus* or *P. anubis*. No significant differences were found between males and females in humeral or calcaneal variables of either species. In the femur, males and females of *P. cynocephalus* differed in the height of the patellar groove (F = 7.63; df = 10; p = 0.02). Males and females of *P. anubis* differed in the width of the femoral head (F = 7.27; df = 9; p = 0.025), the height of the femoral head (F = 9.88; df = 9; p = 0.012), and the proximodistal height of the lateral condyle (F = 7.99; df = 9; 0.02). In the astragalus, males and females of *P. cynocephalus* differed in the height of the tibial facet (F = 7.16; df = 10; p = 0.023) and the height of the fibular facet (F = 6.21; df = 10; p = 0.032). Males and females of *P. anubis* trended towards a significant difference in total length of the astragalus (F = 5.3; df = 8; p = 0.0503). Males and females also differed significantly in the angle of the astragalar head (F = 6.15; df = 8; p = 0.038), but this variable did not undergo a size adjustment. Given that only seven of 65 variables shows significant differences between males and females of a sexually dimorphic species, shape conversion of variables appears to remove the effect of dimorphism well and sexes can be pooled when creating species means.

To determine the most repeatable method for separating locomotor groups, multiple measurements were taken for the height of the greater tubercle and angle of the medial epicondyle of the humerus, using digital photographs of these anatomical features. The greater tubercle was measured as a length and also as an index, and the angle of the medial epicondyle was measured by two lengths, an index of these two lengths, and as an angle (see Appendix B). Length of the greater tubercle (GTH) and the angular measurement for angle of the medial epicondyle (AME) are presented here to reduce redundancy in results as all measures tended to have similar separation of locomotor groups. These features are chosen because they were, in most cases, normally distributed and are also most similar to measures presented in previous studies and therefore may be more intuitive to the reader. The geometric mean used to create Mosimann shape variables included all length variables measured from these two features, in addition to all other length measurements on the humerus, in order to maximize the number of variables from different regions of humerus and increase the number of relatively large measurements contributing to the geometric mean (Coleman 2008).

Section 2.2.2: Locomotor Assignments

In order to test for associations between morphology and locomotor behavior, an accurate assessment of substrate preference for cercopithecoid species is required. Data for substrate preference were culled from the literature, the All the World's Primates database (Rowe and Myers 2013), the Mammals of Africa Volume 2 (Butynski et al. 2013), and through a Terrestriality Assessment Survey that received 20 responses from primatologists. These data can be seen in Appendix A and the Terrestriality Assessment Survey can be seen in Appendix E. When percentage data were available, species were considered arboreal if they spent less than 15% of their time on the ground, or if they were described qualitatively as having rarely descended to the ground. Species were considered semi-terrestrial when they spent between 16% and 79% of their time on the ground. Species were considered terrestrial when they spent more than 80% of their time on the ground, or were described qualitatively as having rarely ascended trees. When data were provided for the percent of time on the ground during traveling, this percentage was used instead of the percentage of time on the ground from the entire activity budget. When seasonality data were provided, the percentage of time on ground was taken from the season in which the species was more terrestrial. As many sources as possible were collected for each species (68 sources total) and the locomotor codings reflect the best possible assignment based on activity budgets and qualitative assessments (Appendix A).

The only species for which no primary sources on locomotor bevahior could be found were *Chlorocebus pygerythrus*, *Piliocolobus foai*, *Presbytis melalophos*, and *Presbystis rubicunda*. These species have either been recently elevated to the species level from the subspecies level or belong to genera that have undergone reclassification (Groves 2001; Brandon-Jones et al. 2004). *Chlorocebus pygerthrus* is assigned the semi-terrestrial group based on the sources for *Chlorocebus aethiops*. *Piliocolobus foai* is assigned to the arboreal group based on the sources for *Piliocobus badius* and *P. kirkii*. *Presbytis melalophos* and *Presbytis rubicunda* are the only species of *Presbytis* included in this study, but they are assigned to the arboreal group based on sources from other species of *Presbytis* not included in the dissertation (i.e. *Presbytis comata*) and species that used to be included in the genus *Presbytis* but now belong to the *Tracypithecus* genus (i.e., *Trachypithecus obscurus*).

Two locomotor codings schemes were created (Table 2.2). In Coding 1, cercopithecoid species were placed into one of three categories (arboreal, semi-terrestrial, and terrestrial). Using Coding 2, cercopithecoids were split into one of two locomotor categories -- arboreal and terrestrial. Coding 1 is based on Appendix A and follows the locomotor assignments listed according to the literature review and the survey. Coding 2 recodes species according to their amount of terrestrial behavior *relative* to other species in their clade. For example, *Cercopithecus neglectus* is coded as semi-terrestrial in Coding 1 based on McGraw (1994) and the All the World's Primates database, but as terrestrial in Coding 2. The removal of the semi-terrestrial category was created to determine whether functional demands on *any* amount of terrestrial behavior were strong enough to select for the same functional adaptations across a highly diverse clade. If so, such features could aid in the identification of convergent acquisitions of terrestriality. Analyses that examined associations between morphology and behavior in cercopithecoids used both Coding 1 and 2. Analyses that incorporated the entire anthropoid dataset used Coding 2, with platyrrhines added to the arboreal group and a suspensory category added for the hominoid species.

Although chimpanzees do spend a substantial amount of time engaged in terrestrial travel (Doran 1992; Hunt 1992; Doran 1993), they engage in climbing and unimanual arm hanging (Hunt 1992), large males engage in suspensory behavior during feeing on small diameter branches (Doran 1993), and infants engage frequently in suspensory behavior (Doran 1992). The placement of chimpanzees into a locomotor group poses a problem because although chimpanzees are terrestrial, adult individuals can engage in suspension, a locomotor behavior not exhibited by adult cercopithecoids. Additionally, the behavioral groupings of arboreal, semi-terrestrial, and terrestrial created for cercopithecoid species represent substrate preferences for a generalized quadruped, but chimpanzees are highly specialized in their morphology. Thus, chimpanzees are placed in the suspensory group rather than the terrestrial group to reflect their use of a specialized behavior not exhibited in the cercopithecoid clade.

Section 2.2.3: Univariate Statistical Analyses

A series of one-way ANOVAs was run to determine which anatomical features are consistently associated with substrate preference. One assumption of ANOVA is that data points are statistically independent (Sokal and Rolhf 1995). Species along a phylogeny form a hierarchy of ancestor-descendent relationships and therefore cannot be considered statistically independent (Felsenstein 1985) because the covariance between any two taxa is proportional to their evolutionary history (Pagel 1997; Pagel 1999b). In addition to violating the assumption of independence, degrees of freedom may be inflated and lead to an increase in Type I errors (Garland et al. 1993; Freckleton et al. 2002; Revell 2009). Degrees of freedom for standard ANOVAs are calculated based on the number of groups being compared and the total number of observations. Again, because observations (or species) are not independent, the standard calculation of degrees of freedom is inappropriate. Phylogenetic generalized least squares (PGLS) regression accounts for the interdependence of comparative data by incorporating an error term into the regression equation that represents the variance-covariance matrix scaled by the phylogenetic relationships among species (Martins and Hansen 1997; Pagel 1997; Pagel 1999b; Nunn 2011). One commonly used term to scale the variance-covariance matrix is Pagel's lambda (λ), which can vary between 0 and 1 (Pagel 1997; Pagel 1999b; Freckleton et al. 2002; Nunn 2011). A lambda of 0 indicates that there is no correlation between the data and the phylogeny, suggestive of a star phylogeny. A lambda of 1 means that the data covary exactly with the phylogeny as might be expected under a Brownian motion model of evolution (Pagel 1997; Pagel 1999b; Freckleton et al. 2002; Nunn 2011). Using a phylogenetic transformation, such as lambda, in standard statistical approaches incorporates phylogenetic signal (i.e., variation in morphology related to phylogenetic relatedness) into analyses and lessens the problems associated with violating the assumption of independence.

Phylogenetic ANOVAs were run using the *caper* (Comparative Analyses of Phylogenetic and Evolution in R) package in R (Orme 2012). Since most previous morphometric work on cercopithecoid postcrania used standard statistical approaches, standard ANOVAs were also run in R to determine whether results from phylogenetically informed analyses are dramatically different from those that do not take into account phylogeny. All variables were log10 transformed prior to analysis, and a species mean dataset was created, because phylogenetic ANOVAs do not currently take intraspecific variation into consideration.

Phylogenetic principal components analyses (PCA) (Revell 2009) were first run for each element using both the cercopithecoid-only dataset, and the entire anthropoid dataset, to examine the overall variance in the dataset. Analyses were examined to determine whether any principal components group taxa by either locomotor group or phylogenetic group *a priori* of group assignment.

The phylogenies used in the phylogenetic PCAs and ANOVAs were downloaded from the 10kTrees Project [(Arnold et al. 2010); version 3] and included one tree with all of the species in the dataset, and a second tree that included only the cercopithecoid species in the dataset. Both trees were consensus trees, based on a tree block containing 100 trees. *Presbytis rubicunda* was the only species included in the dataset that is not available on the 10kTrees Project. Version 3 of 10KTrees Project includes only two species of *Presbytis – P. melalophos* and *P. comata* (Arnold et al. 2010). Since the only two species of *Presbytis* included in this study are *P. melalophos* and *P. rubicunda* and Zain et al. (2011) has documented that the genus *Presbytis* is monophyletic, *Presbytis comata* was used in place of *Presbytis rubincunda* when trees were downloaded from the 10KTrees Project. These trees are available in Appendix F.

Four sets of phylogenetic ANOVAs were run to examine associations between morphology and behavior. The first set of analyses used the cercopithecoid-only dataset with species assigned to locomotor groupings based on Coding 1 (i.e., arboreal vs. semi-terrestrial vs. terrestrial). The second set of analyses used the cercopithecoid-only dataset with species assigned to locomotor groupings based on Coding 2 (i.e., arboreal vs. terrestrial). The third set of analyses used the entire dataset (i.e., including platyrrhines and hominoids) with species assigned to locomotor groupings based on Coding 2 (i.e., arboreal vs. terrestrial vs. suspensory). The final set of analyses examined difference between arboreal and terrestrial guenons, colobines, and papionins separately using Coding 2 (i.e., arboreal vs. terrestrial).

The first three sets of analyses were also repeated using standard ANOVAs to determine if results from phylogenetically-informed and standard methods are similar. Species mean data were also used for these ANOVAs, in order to maintain an equivalent level of power between the phylogenetic and standard ANOVAs. When comparing the consistencies of both sets of analyses, post-hoc tests were considered significant at the 0.05 level, rather than at an adjusted critical level for multiple comparisons, as is done when examining associations between morphology and behavior (see below).

Two sets of phylogenetic ANOVAs were run to investigate if any morphologies were associated with any particular sub-clades within the dataset and/or if any morphologies found to be highly associated with behavior were also associated with phylogenetic group. The first set of analyses used the cercopithecoid-only dataset and species were categorized as colobine, guenon, or papionin. The second set of analyses examined the entire dataset and species were categorized as cercopithecine, colobine, hominoid, or platyrrhine.

Residuals from analyses were checked for normality and outliers were removed when data did not meet the assumption of normality. In a few cases residuals were not normally distributed even after outliers had been removed, or if there were no outliers to remove. Currently, there are no phylogenetically informed non-parametric statistics, so analyses were run even though the assumption of normality was not met. Analyses that did not meet this assumption are noted in their respective tables.

After phylogenetic and standard ANOVAs were completed, a series of planned comparisons between locomotor groups were performed. Critical p-values were adjusted for the planned comparisons using the Sequential Dunn-Sidák method for planned comparisons (Sokal and Rolhf 1995). The Sequential Dunn-Sidák method should be used when planned comparisons are not orthogonal. Non-orthogonality occurs when planned comparisons outnumber the number the degrees of freedom (i.e., number groups - 1). In this method, the adjusted critical value is computed as:

$\alpha' = 1 - (1 - 0.05)^{1/k}$ (where k = the number of groups in the analysis)

If one of the comparisons between two groups meets α', then the critical value is adjusted again:

$\alpha' = 1 - (1 - 0.05)^{1/k-1}$

This sequential adjustment of the critical value can be completed as many times as is necessary in order to assess all comparisons between groups in a given set of planned comparisons. The following critical values are used when appropriate in assessing the significance of planned comparisons.

$\alpha' = 1 - (1 - 0.05)^{1/4} = 0.0127$

$\alpha'' = 1 - (1 - 0.05)^{1/3} = 0.0169$

$\alpha''' = 1 - (1 - 0.05)^{1/2} = 0.0253$

$\alpha'''' = 1 - (1 - 0.05)^{1/1} = 0.05$

Section 2.2.4: Multivariate Statistical Analyses

Linear discriminant analysis (LDA) and canonical variates analysis (CVA) are commonly used in morphometric studies to find linear combinations of variables that can discriminate between groups better than one variable alone. LDA and CVA are also predictive, and an observation with an unknown group membership can be given a probability of group assignment based on its discriminant function score (Mitteroecker and Bookstein 2011; Rencher and

Christensen 2012). LDA and CVA find linear combinations by maximizing the ratio of between-group sum of squares to within-group sums of squares (Fisher 1936; Mitteroecker and Bookstein 2011; Rencher and Christensen 2012). An important assumption of linear discriminant analysis is that the number of observations (*n*) per group is greater than the number of variables (*p*) (Boulesteix 2005; Rencher and Christensen 2012). However, meeting the assumption of $n > p$ is often difficult in morphometrics when samples are limited. In the present study, the terrestrial category in Coding 1 has four species and the suspensory category in Coding 2 has three species. Thus, to meet the assumption of $n < p$ in a linear discriminant analysis, only three or two variables could be added to analyses considering those groups, respectively.

Between-group principal component analysis (PCA) is a good alternative to LDA and CVA when the number of observations per group is close to or less than the number of variables (Boulesteix 2005; Mitteroecker and Bookstein 2011). As in a classical PCA, between-group PCA seeks to create new variables as linear combinations of the original input variables. However, the linear combinations created by between-group PCA are based on group means, rather than on the total dataset (Boulesteix 2005). Between-group PCA and LDA are collinear (Boulesteix 2005), but between-group PCA is not restricted by assumption of $n > p$ (Boulesteix 2005; Mitteroecker and Bookstein 2011). The distribution of the groups can be visualized in a similar manner as LDA by projecting the observations onto the principal components of the group means. This can be accomplished by transforming the observations into PC-scores based on the eigenvectors calculated by the PCA on the group means (Mitteroecker and Bookstein 2011).

Given the limited number of species (observations) per locomotor group in this study, between-group PCA is preferable to LDA or CVA. Three between-group PCAs were run for each element based on corresponding phylogenetic ANOVAs: a) cercopithecoid-only analysis using Coding 1, b) a cercopithecoid-only analysis using Coding 2, and c) an analysis of the entire dataset using Coding 2. Three between-group PCAs were also run using all the elements combined. Variables that showed significant associations between morphology and behavior in the phylogenetic ANOVAs were selected for the analysis. When possible, variables were chosen for multivariate analyses when at least one post-hoc comparison met the adjusted critical value. In the femur and calcaneus, some analyses produced results that were significant only at the standard 0.05 level. In these cases, the standard for variable selection was lowered to include variables that were significant at any level. Table 2.3 lists the variables that were included in the between-group PCA analyses, and their level of significance.

Section 2.3: Results

Section 2.3.1: Humerus

Phylogenetic Principal Components Analysis

Phylogenetic PCA was run on the cercopithecoid-only sample (Table 2.4a) and the entire anthropoid sample (Table 2.4b). In the cercopithecoid-only sample, PC 1 accounts for 24.3% of the variation and the variables with the highest loadings are height of the olecranon fossa (0.84), width of the lesser tubercle (-0.71), and height of greater tubercle (-0.7409). PC 2 accounts for 14.6% of the variation and the variables with the highest loadings are the humeral head index (0.74) and width of the distal articular surface (-0.61). Figure 2.1a shows that terrestrial cercopithecoids are separated from arboreal cercopithecoids on PC 1. Arboreal and semi-terrestrial cercopithecoids overlap, but arboreal taxa tend to have higher scores on PC 1 and lower scores on PC 2. Figure 2.1b shows substantial overlap when cercopithecoids are labeled as colobine, guenon, or papionin.

In the entire anthropoid sample, PC 1 accounts for 22.9% of the variation and the variables with highest loadings are height of the olecranon fossa (0.86), height of the greater tubercle (-0.64), and depth of the trochlea (-0.62). PC 2 accounts for 16.8% of the variation and the variables with the highest loadings are total length of the humerus (-0.82) and the width of the greater tubercle (0.67). Figure 2.1c shows that most taxa appear to have low scores on PC 1 and high scores on PC 2, with terrestrial and suspensory anthropoids separating well along PC 2. Figure 2.1d shows substantial overlap between colobines, cercopithecines, and platyrrhines.

Phylogenetic ANOVAs by Locomotor Grouping

Phylogenetic ANOVAs showed significant differences among arboreal, semi-terrestrial and terrestrial cercopithecoids in ten variables (Table 2.5a; Figure 2.2a). Height of the greater tubercle and angle of the medial epicondyle show significant differences across all three locomotor groups. Terrestrial cercopithecoids are significantly different from arboreal and semi-terrestrial cercopithecoids in width of the lesser tubercle. Arboreal and semi-terrestrial taxa are not significantly different ($p = 0.074$) in this trait. Arboreal cercopithecoids are significantly different from semi-terrestrial cercopithecoids in humeral head index. Arboreal and terrestrial taxa differ in humeral head index at the 0.05 level but do not achieve significance at the adjusted critical level ($p = 0.034$). Semi-terrestrial and terrestrial cercopithecoids are not significantly different in this trait. Five additional variables (mediolateral width of the humeral head, width of the greater tubercle, height and width of the olecranon fossa, and proximodistal height of the capitulum) show significant differences between locomotor groups at the $\alpha = 0.05$ level but not at the adjusted α levels.

Significant differences between arboreal and terrestrial taxa were found in seven variables when the semi-terrestrial locomotor group was combined with the terrestrial group (Table 2.5b; Figure 2.2b). Of these seven variables, humeral head index, width of the lesser tubercle, height of the greater tubercle, and angle of the medial epicondyle were also found to show significant differences in the previous set of analyses. Although semi-terrestrial and arboreal taxa were not found to be significantly different in the width of the lesser tubercle, this trait does differ when examining only two locomotor groups. Width of the greater tubercle and height of the capitulum are significantly different in arboreal and terrestrial taxa. Although these variables did not reach significance at the adjusted critical value in the previous analyses, both variables showed significant differences between arboreal and semi-terrestrial taxa and between arboreal and terrestrial taxa at the 0.05 level. Humeral length is also significantly different between arboreal and terrestrial taxa.

Significant differences were found between suspensory, arboreal, and terrestrial anthropoids in nine variables (Table 2.5c; Figure 2.2c). Width of the humeral head and angle of the medial epicondyle showed significant differences across all three locomotor groups. Suspensory taxa are significantly different from arboreal and terrestrial taxa in height of the humeral head, width of the lesser tubercle, and width of the bicipital groove. Arboreal and terrestrial taxa are not significantly different in these three traits. Height of the greater tubercle is significantly different only among arboreal and terrestrial taxa, and suspensory taxa overlap with arboreal taxa in this feature (Figure 2.2c). The humeral head index was also different between arboreal and terrestrial taxa at the 0.05 level. Three additional variables (width of the trochlea, width of the distal epiphysis, and biepicondylar breadth) show significant differences between suspensory taxa and arboreal and terrestrial taxa at the $\alpha = 0.05$ level, but not at the adjusted α levels.

Arboreal and terrestrial guenons are significantly different in height of the humeral head, the humeral head index, and width of the greater tubercle (Table 2.5d). Additional differences in width of the biciptal groove and biepicondylar breadth trended towards significance with p-values of 0.069 and 0.066, respectively. Arboreal and terrestrial colobines are significantly different in height of the greater tubercle, biepicondylar breadth, and angle of the medial epicondyle (Table 2.5e). Overall length of the humerus and depth of the trochlea trended towards significance with p-values of 0.059 and 0.072, respectively. Arboreal and terrestrial papionins differ significantly in height and width of the olecranon fossa, height of the capitulum, and angle of the medial epicondyle (Table 2.5f). Width of the humeral head (0.056), height of the greater tubercle (0.069), and width of the lesser tubercle (0.076) trend towards significance.

Standard ANOVAs by Locomotor Group

Of all the elements, the humerus shows the most inconsistencies between standard and phylogenetic ANOVA (Tables 2.6a-c). Height of the humeral head and width of the trochlea is significantly different between arboreal and semi-terrestrial cercopithecoids in the standard ANOVA but not in the phylogenetic ANOVA. In the standard ANOVAs, arboreal cercopithecoids are significantly different in the width of the lesser tubercle from both semi-terrestrial and terrestrial cercopithecoids, and furthermore the comparison between semi-terrestrial and terrestrial cercopithecoids approaches significance ($p = 0.059$). In the phylogenetic ANOVA, terrestrial cercopithecoids are significantly different from arboreal and semi-terrestrial cercopithecoids. The comparison between arboreal and semi-terrestrial cercopithecoids approaches significance ($p = 0.074$). No difference is found between arboreal and semi-terrestrial cercopithecoids in height of capitulum in the standard ANOVA, but this comparison is significant in the phylogenetic ANOVA. Depth of the trochlea is significantly different between arboreal and semi-terrestrial cercopithecoids in the standard ANOVA, but this comparison only trends towards significance in the phylogenetic ANOVA ($p = 0.059$).

Width of the bicipital groove, depth and width of the trochlea, width of the distal articular surface, and biepicondylar breadth are significantly different in standard ANOVAs using the cercopithecoid-only sample and Coding 2, but these variables are not different in the phylogenetic ANOVA. Width of the greater tubercle and height of the capitulum are significantly different in phylogenetic ANOVA but not in the standard ANOVA.

Using the entire anthropoid sample, arboreal and terrestrial anthropoids are significantly different in the height of the humeral head, the width of the lesser tubercle, the height of the capitulum, and the depth of the trochlea in the standard ANOVA. These variables are not significant in the phylogenetic ANOVA, although width of the lesser tubercle approaches significance ($p = 0.061$). Significant differences are found between suspensory and terrestrial anthropoids in biepicondylar breadth and the humeral head index in standard ANOVAs, but these comparisons are not significant in the phylogenetic ANOVA.

Phylogenetic ANOVAs by Phylogenetic Grouping

Phylogenetic ANOVAs showed significant differences between colobines, guenons, and papionins in seven variables (Table 2.7a; Figure 2.3a). All three groups differed significantly in the width of the bicipital groove, width of the distal articular surface, biepicondylar breadth, and angle of the medial epicondyle. Papionins are significantly different from colobines and guenons in humeral length. Guenons are significantly different from papionins and colobines in the width of the capitulum. Colobines are significantly different from papionins and guenons in the depth of the trochlea. Of these seven variables, only the angle of the medial epicondyle also showed a significant association with substrate preferences of cercopithecoids.

Nine variables show significant differences across cercopithecines, colobines, platyrrhines, and hominoids (Table 2.7b; Figure 2.3b). Width of the bicipital groove differs significantly across all groups, except for the comparison of cercopithecines to platyrrhines. Hominoids significantly differ from other groups in width of the lesser tubercle and width of the humeral head. Hominoids are also significantly different from cercopithecines and colobines in height of the humeral head, but do not differ from platyrrhines. Platyrrhines differ from all other groups in depth of the trochlea, and cercopithecines and colobines also differ significantly in this trait. Width of the distal articular surface differs significantly between cercopithecines and colobines, between cercopithecines and hominoids, and between hominoids and platyrrhines. Biepicondylar breadth differs significantly between cercopithecines and colobines, and between cercopithecines and hominoids. This trait approaches significance at the adjusted critical level of 0.0253 between cercopithecines and platyrrhines (0.0278) and between colobines and hominoids (0.026). Width of the olecranon fossa differs significantly only between hominoids and platyrrhines, while angle of the medial epicondyle differs significantly only between cercopithecines and hominoids. Width and height of the humeral head, width of the lesser tubercle, width of the bicipital groove, and angle of the medial epicondyle are also associated with substrate preference. Given that the species that make up the “hominoid” group are the same as those in the “suspensory” group in previous analyses, it is not surprising that there is? overlap in association between substrate preference and phylogenetic relatedness.

Between-group Principal Components Analysis

Four variables were included in the between-group PCA on cercopithecoids using three locomotor codings - humeral head index, height of the greater tubercle, width of the lesser tubercle, and angle of the medial epicondyle (Table 2.8a). PC 1 accounts for 96.8% of the variation with PC 2 accounting for the remaining 3.2% of the variation. The variables with the highest loadings on PC 1 are angle of the medial epicondyle (-0.605) and height of the greater tubercle (-0.581). Humeral head index has the highest loading on PC 2 (0.725). Figure 2.4a shows that arboreal cercopithecoids are separated from semi-terrestrial and terrestrial cercopithecoids on PC 1, indicating that arboreal taxa are best distinguished from relatively terrestrial species by differences in the height of the greater tubercle and the angle of the medial epicondyle. PC 2 does not separate locomotor groups well, with arboreal and terrestrial taxa occupying spaces with both low and high PC 2 scores.

Six variables were included in the between-group PCA of cercopithecoids using only two locomotor codings - humeral head index, height of the greater tubercle, width of the greater tubercle, width of the lesser tubercle, height of the capitulum, and angle of the medial epicondyle (Table 2.8b). PC 1 accounts for 100% of the variation, and the variables with the highest loadings are the angle of the medial epicondyle (0.6133) and the height of the greater tubercle (0.4842). Figure 2.4b shows the separation of arboreal and terrestrial taxa along PC 1.

Six variables were included in the between-group PCA of anthropoids with three locomotor groups – width of the humeral head, height of the humeral head, height of the greater tubercle, width of the lesser tubercle, width of the bicipital groove, and angle of the medial epicondyle (Table 2.8c). PC 1 accounts for 95.7% of the variation and PC 2 accounts for the remaining 4.3% of the variation. Width of the lesser tubercle loads highest on PC 1 (-0.5412) with height of the humeral head (0.4614), width of the bicipital groove (0.4382), and width of the humeral head (0.429) contributing to PC 1 about equally. Height of the greater tubercle has the highest loading on PC 2 (0.683). Figure 2.4c shows that suspensory taxa are well-separated from both arboreal and terrestrial taxa along PC 1. Arboreal and terrestrial taxa are separated along PC 2.

Section 2.3.2: Femur

Phylogenetic Principal Components Analysis

Results for the phylogenetic PCA of femoral variables using the cercopithecoid-only sample, and the entire anthropoid sample, are listed in Tables 2.9a and 2.9b, respectively. For the cercopithecoid-only sample, PC accounts for 26.8% of the variation, and the variables with the highest loadings are width of the femoral head (-0.90) and height of the femoral head (-0.86). PC 2 accounts for 14.4% of the variation, and the variables with the highest loadings are proximodistal height (0.77), anteroposterior depth (0.62), and mediolateral width (-0.60) of the medial condyle. These variables do not separate cercopithecoids either by locomotor or phylogenetic group, as can be seen in Figures 2.5a and 2.5b.

For the entire anthropoid sample, PC 1 accounts for 29.2% of the variation and variables with the highest loadings are width and height of the femoral head (-0.86 and -0.82, respectively). PC 2 accounts for 16.5% of the variation, and the anteroposterior depth of the medial condyle (0.78) has the highest loading. Hominoids fall outside the clustering of all other anthropoids when coded either according to locomotor or phylogenetic grouping (Figures 2.5c and 2.5d).

Phylogenetic ANOVAs by Locomotor Group

No variables showed significant differences between arboreal, semi-terrestrial, and terrestrial cercopithecoids at the adjusted critical level, but arboreal and terrestrial cercopithecoids differed in the overall length of the femur and the height of the patellar groove at the 0.05 level (Table 2.10a; Figure 2.6a). When cercopithecoids were analyzed using only the arboreal and terrestrial locomotor categories, these variables remained significant (Table 2.10b; Figure 2.6b). Suspensory anthropoids were significantly different from arboreal and terrestrial anthropoids in height and width of the femoral head, anteroposterior depth and proximodistal height of the lateral condyle, proximodistal condylar height index, width of the patellar groove, femoral neck angle, and asymmetry of the femoral condyles (Table 2.10c; Figure 2.6c).

Arboreal and terrestrial guenons different significantly in height of the femoral head and trended towards significance in depth of the lateral condyle (0.07) and width of the lateral condyle (0.072) (Table 2.10d). Arboreal and terrestrial colobines are not significantly different in any femoral variables (Table 2.10e). Arboreal and terrestrial papionins are significantly different in height of the patellar groove (Table 2.10f).

Standard ANOVAs by Locomotor Group

Overall, results from phylogenetic and standard ANOVAs were highly consistent for the femur. All results for analyses using the cercopithecoid-only sample and Coding 1 are consistent, except for a minor difference in the height of the patellar groove (Table 2.11a). In the standard ANOVA, arboreal cercopithecoids are significantly different from semi-terrestrial ($p = 0.006$)

cercopithecoids but this comparison only trends towards significance in the phylogenetic ANOVA (p =0.052). All results are consistent between both sets of analyses for the cercopithecoid-only sample using Coding 2 (Table 2.11b).

Five variables found to have significant comparisons in the standard ANOVAs for the entire anthropoid sample are found to be not significant in the phylogenetic ANOVAs (Table 2.11c). These variables are length of the femur, width of the medial condyle, bicondylar breadth, height of the patellar groove, and the anteroposterior breadth condylar index.

Phylogenetic ANOVAs by Phylogenetic Group

Twelve variables showed significant differences between papionins, guenons, and colobines (Table 2.12a; Figure 2.7a). Papionins were significantly different from guenons and colobines in overall length of the femur, proximodistal height of the lateral condyle, and height of the patellar groove. Papionins differed significantly from colobines in the proximodistal condylar height index but were only significantly different from guenons at the 0.05 level. Papionins also significantly differed from guenons in height of the femoral head. Guenons differed significantly from papionins and colobines in width of the femoral head, anteroposterior depth of the lateral condyle, and femoral neck angle. Colobines differed significantly from papionins and guenons in height of the lesser trochanter, anteroposterior depth of the medial condyle, mediolateral width of the lateral condyle, and condylar asymmetry.

Ten variables showed significant differenced between cercopithecines, colobines, hominoids, and platyrrhines (Table 2.12b; Figure 2.7b). All groups were significantly different in femoral neck angle and proximodistal height of the lateral condyle. Hominoids are significantly different from other phylogenetic groups in the height and width of the femoral head, and anteroposterior depth of the lateral condyle. These results are not surprising given that suspensory (i.e., hominoid) primates are significantly different from arboreal and terrestrial anthropoids in these traits. Condylar asymmetry was significantly different across all groups except in the cercopithecine-platyrrhine comparison. Cercopithecines and colobines differed significantly from platyrhines and hominoids in the proximodistal condylar height index and also differed from hominoids in width of the patellar groove. Colobines were significantly different from cercopithecines, hominoids, and platyrrhines in the height of the lesser trochanter. Cercopithecines were significantly different from colobines and hominoids in anteroposterior depth of the medial condyle. Hominoids and platyrrhines also differed in this variable, but only at the 0.05 level.

Between-group Principal Components Analysis

The overall length of the femur and the height of the patellar groove were included in the between-group PCAs on cercopithecoids using both three locomotor categories (Table 2.13a) and two locomotor categories (Table 2.13b). PC 1 accounts for 99.4% of the variation with PC 2 accounting for the remaining 0.6% in the analysis using three locomotor codings. Height of the patellar groove is loaded highest on PC 1 (-0.727) and length of the femur is loaded highest on PC 2 (-0.727). PC 1 accounts for 100% of the variation and height of the patellar groove loads highest (-0.742). Arboreal and terrestrial cercopithecoids separate along PC 1 but semi-terrestrial cercopithecoids overlap with both groups (Figure 2.8a). No clear separation exists between arboreal and terrestrial cercopithecoids when examining only two locomotor codings (Figure 2.8b).

Seven variables were included in the between-group PCA of all anthropoids – width and height of the femoral head, anteroposterior depth of the lateral condyle, patellar groove width, proximodistal height index of the femoral condyles, femoral neck angle, and condylar asymmetry (Table 2.13c). PC 1 accounts for 99.5% of the variation and PC 2 accounts for the remaining 0.5%. Femoral neck angle and anteroposterior depth of the lateral condyle and have the highest loadings on PC 1 (0.479 and -0.419, respectively). Condylar asymmetry and femoral neck angle loaded highest on PC 2 (-0.535 and -0.478, respectively). Suspensory anthropoids are well-separated from arboreal and terrestrial anthropoids along PC 1. Considerable overlap exists between arboreal and terrestrial anthropoids, as was discussed above (Figure 2.8c).

Section 2.3.3: Astragalus

Phylogenetic Principal Components Analysis

Tables 2.14a and 2.14b list the results for phylogenetic PCAs of the astragalus using the cercopithecoid-only sample and entire anthropoid sample, respectively. For the cercopithecoid-only sample, PC 1 accounts for 18.4% of the variation and the variables with the highest loadings are height of the medial ridge (-0.72) and length of the body (0.63). PC 2 accounts for 15.7% of the variation and the variables with the highest loadings are height of the tibial facet (0.75) and height of the fibular facet (-0.65). Figure 2.9a shows substantial overlap between arboreal, semi-terrestrial, and terrestrial anthropoids and Figure 2.9b shows similar overlap when cercopithecoids are grouped by clade.

For the entire anthropoid sample, PC 1 accounts for 22.9% of the variation and the variables with the highest loadings on PC 1 are distal width of the trochlea (0.86) and trochlear width at the midpoint (0.82). PC 2 accounts for 15.3% of the variation and the variables with the highest loadings are ectal facet with (0.54), proximal width of the trochlea (-0.53), and height of the lateral trochlear ridge (0.53). Figure 2.9c shows that arboreal and terrestrial anthropoids overlap in their PC 1 and PC 2 scores. Suspensory anthropoids have high scores along PC 2 but still overlap with arboreal and terrestrial anthropoids. Figure 2.9d shows that platyrrhines and hominoids separate along PC 2, but both groups overlap with colobines and cercopithecines.

Phylogenetic ANOVAs by Locomotor Grouping

Four variables show significant differences across arboreal, semi-terrestrial, and terrestrial cercopithecoids (Table 2.15a; 2.10a) Arboreal cercopithecoids differ significantly from semi-terrestrial and terrestrial cercopithecoids in the length of the astragalus. Semi-terrestrial cercopithecoids are significantly different from arboreal cercopithecoids in ectal facet length, but arboreal and terrestrial cercopithecoids do not differ significantly in this trait. Terrestrial cercopithecoids do overlap in ectal facet length with semi-terrestrial cercopithecoids. A lack of significance between arboreal and terrestrial cercopithecoids in the feature may be related to a lack of power, since only four species are assigned to the terrestrial group. Angle of the astragalar head and width of the astragalar head both show differences among locomotor groups at the 0.05 level but are not significantly different at the adjusted critical level. Terrestrial cercopithecoids differ from arboreal ($p = 0.05$) and semi-terrestrial cercopithecoids ($p = 0.034$) in angle of the astragalar head, and from arboreal cercopithecoids in width of the talar head ($p = 0.023$). Arboreal and terrestrial taxa differ in the width of the astragalar head at the 0.05 level but not at the adjusted critical level.

When comparing cercopithecoids in arboreal and terrestrial groupings, total astragalar length, width of the astragalar head, and ectal facet length show significant differences between groups as in the above set of analyses, but the angle of the astragalar head does not (Table 2.15b; Figure 2.10b). Astragalar wedging is also significantly different between arboreal and terrestrial cercopithecoids.

Eight variables show significant differences between suspensory, arboreal, and terrestrial taxa (Table 2.15c; Figure 2.10c). Ectal facet length shows significant differences between all three locomotor groups. Width of the astragalar head shows significant differences between arboreal anthropoids and terrestrial and suspensory anthropoids and a trend towards significance between suspensory and terrestrial anthropoids ($p = 0.076$). Suspensory anthropoids are significantly different from arboreal and terrestrial anthropoids in the length of the astragalar head and neck. Height of the fibular facet also shows suspensory anthropoids to be different from arboreal and terrestrial anthropoids, but only at the 0.05 level. Total length of the astragalus differs significantly between arboreal and terrestrial taxa, but suspensory taxa cannot be distinguished from either group. Distal width of the trochlea and astragalar wedging both show a difference between suspensory and terrestrial anthropoids but only at the 0.05 level. These two variables are also inter-related given that distal width of the trochlea is used to create the index that describes trochlear wedging. Angle of the astragalar head shows a difference between arboreal and suspensory anthropoids but only at the 0.05 level. This trait trends towards significance between suspensory and terrestrial anthropoids ($p = 0.052$).

No significant difference exists between arboreal and terrestrial guenons but height of the lateral trochlear ridge and ectal facet length trend towards significance (Table 2.15d). Aboreal and terrestrial colobines are significantly different in width of the trochlea distally and trend towards significance in trochlear width (0.091) (Table 2.15e). Arboreal and terrestrial papionins are significantly different in overall length of the astragalus and trend towards significance in width of the astragalar head (0.6) (Table 2.15f).

Standard ANOVAs by Locomotor Grouping

Standard and phylogenetic ANOVAs are generally consistent for the astragalus. All comparisons for the cercopithecoid-only sample are consistent with the phylogenetic ANOVAs except for differences in length of the astragalus (Table 2.16a). In the standard ANOVA, the comparison between arboreal and semi-terrestrial cercopithecoids only approaches significance ($p = 0.067$) but the other comparisons are significant. In the phylogenetic ANOVA, arboreal cercopithecoids are significantly different from semi-terrestrial and terrestrial cercopithecoids but semi-terrestrial and terrestrial cercopithecoid do not differ.

Only two variables differ between standard and phylogenetic ANOVAs using the cercopithecoid-only sample with Coding 2 (Table 2.16b). Width of the astragalar head is not significant in the standard ANOVA but is significant in the phylogenetic ANOVA. Trochlear asymmetry is significant in the standard ANOVA but not in the phylogenetic ANOVA.

Five variables that show significant post-hoc comparisons in the standard ANOVAs are not significant in the phylogenetic ANOVA (Table 2.16c). Arboreal and terrestrial anthropoids are significantly different in length of the astragalar head and neck in the standard ANOVA but not in the phylogenetic ANOVA. Arboreal and suspensory anthropoids are significantly different in the length of the astragalus in the standard ANOVA, but this comparison only trends towards significance in the phylogenetic ANOVA ($p = 0.079$). Suspensory anthropoids differ significantly from arboreal and terrestrial anthropoids in the width of the ectal facet in the standard ANOVA. In the phylogenetic ANOVA, no significant difference is found between suspensory and terrestrial anthropoids, and the comparison between suspensory and arboreal anthropoids trends towards significance (p = 0.06). Suspensory anthropoids are found to be significantly different from terrestrial anthropoids in the width and angle of the astragalar head in the standard ANOVA, but in the phylogenetic ANOVA these comparisons trend towards significance (width: p = 0.076; angle: 0.052).

Phylogenetic ANOVAs by Phylogenetic Grouping

Nine variables show significant differences between colobines, guenons, and papionins (Table 2.17a; Figure 2.11a). Guenons differ significantly from colobines and papionins in total length of the astragalus and height of the lateral trochlear ridge. Colobines differ from guenons and papionins in the length of the body of the astragalus, the height of the medial trochlear ridge, the height and width of the fibular facet, ectal facet width, and trochlear asymmetry. Papionins differ from colobines and guenons only in the angle of the astragalar head. Total length of the astragalus is also associated with substrate preference across cercopithecoids. Angle of the astragalar head differs across cercopithecoids when categorized according to locomotor preference, but is not significant at the adjusted critical levels.

Eleven variables show significant differences across cercopithecines, colobines, platyrrhines, and hominoids (Table 2.17b; Figure 2.11b). Length of the head and neck differed significantly across all groups. Height of fibular facet differed across all groups except for the comparison between cercopithecines and platyrhines. Ectal facet width differed across all groups except for the comparison between colobines and hominoids. Trochlear asymmetry and angle of the astragalar head differed across all groups except for the comparison between hominoids and platyrrhines. Cercopithecines and colobines differed from hominoids and platyrrhines in ectal facet length. Cercopithecines and colobines differed from hominoids in trochlear width. Colobines differed from all other groups in overall length of the astragalus and the width of the fibular facet. Finally, width of the astragalar head differed between cercopithecines and hominoids, and between hominoids and platyrrhines. Total length of the astragalus, length of the head and neck, and ectal facet length are also associated with substrate preferences.

Between-group Principal Components Analysis

Four variables were included in the between-group PCA on cercopithecoids using three locomotor groups – total length, ectal facet length, width of the astragalar head, and angle of the astragalar head (Table 2.18a). PC 1 accounts for 92.3% of the variation and PC 2 accounts for 7.7% of the variation. Total astragalar length has the highest loading on PC 1 (-0.657) and ectal facet length has the highest loading on PC 2 (-0.896). Terrestrial cercopithecoids are mostly separated from arboreal cercopithecoids along PC 1, but semi-terrestrial cercopithecoids overlap with both arboreal and terrestrial groups (Figure 2.12a).

Four variables were included in the between-group PCA on cercopithecoids using only two locomotor groups – total length, ectal facet length, width of the astragalar head, and trochlear wedging (Table 2.18b). PC 1 accounts for 100% of the variation, and ectal facet length has the highest loading (-0.61). Arboreal and terrestrial cercopithecoids are separated along PC 1 but there is substantial overlap between the two groups (Figure 2.12b).

Four variables were included in the between-group PCA on all anthropoids using three locomotor groups – total length, length of the head and neck, ectal facet length, and width of the astragalar head (Table 2.18c). PC 1 accounts for 90.9% of the variation and PC 2 accounts for

9.1% of the variation. Legnth of the head and neck (-0.587), ectal facet length (0.557), and width of the astragalar head (0.519) all have high loadings on PC 1. Ectal facet length (0.764) and total length (0.54) have the highest loadings on PC 2. Suspensory taxa are separated from arboreal and terrestrial individuals on PC 1 (Figure 2.12c). PC 2 separates arboreal and terrestrial taxa but there is overlap between the two groups.

Section 2.3.4: Calcaneus

Phylogenetic Principal Components Analysis

Results of phylogenetic PCAs of calcaneal variables across the cercopithecoid-only, and the entire anthropoid, samples are presented in Tables 2.19a and 2.19b, respectively. For the cercopithecoid-only sample, PC 1 accounts for 25.1% of the variation and the variables with the highest loadings are the width of the sustentaculum tali (-0.76), length of the body of the calcaneus (-0.63), and width of the tuber (0.63). PC 2 accounts for 22.4% of the variation and the variables with the highest loadings are total length of the calcaneus (-0.74) and length of the astragalar facet (-0.65) (Table 9a). Figure 2.13a shows that generally, arboreal species have PC 1 scores below zero while terrestrial and semi-terrestrial species have PC 1 scores above zero. Figure 2.13b shows that colobines have low scores on PC 1 and papionins have high scores on PC 1, with guenons occupying an intermediate space.

For the entire anthropoid sample, PC 1 accounts for 26.9% of the variation and the variables with the highest loading are width of the sustentaculum (-0.77) and width of the tuber (0.69). PC 2 accounts for 22.4% of the variation and variables with the highest loadings are overall length of the calcaneus (-0.76) and height of the cuboid facet (0.54). Figure 2.13c shows that arboreal and terrestrial species separate along PC 1 although there is considerable overlap between the groups. Suspensory anthropoids have high PC 2 scores that separate them from the arboreal and terrestrial group. Figure 2.13d shows that platyrrhines and cercopithecines are separated along PC 1 and colobines occupy an intermediate space. Hominoids have high PC 2 scores and are separated from the other clades.

Phylogenetic ANOVA by Locomotor Grouping

No significant differences were found between arboreal, semi-terrestrial, and terrestrial cercopithecoids when using the adjusted α levels of 0.0169 and 0.0253 (Table 2.20a; Figure 2.14a). Arboreal cercopithecoids were different from semi-terrestrial and terrestrial cercopithecoids in the length of the body of the calcaneus, the length of the tuber, and the width of the sustentaculum tali. Arboreal cercopithecoids were also different from terrestrial cercopithecoids in the height of cuboid facet at the 0.05 level (Table 2.20a). When cercopithecoids are placed into only two locomotor groupings, arboreal and terrestrial taxa differ significantly in the total length of the calcaneus, the length of the body, and the height of the cuboid facet (Table 2.20b; Figure 2.14b).

Total length of the calcaneus and width of the sustentaculum show significant differences between suspensory, arboreal, and terrestrial groups (Table 2.20c; Figure 2.14c). Suspensory anthropoids are significantly different from terrestrial and arboreal anthropoids in proximodistal length of the astragalar facet. Suspensory anthropoids are also different from terrestrial and arboreal anthropoids in the length of the tuber and the mediolateral length of the astragalar facet, but only at the 0.05 level. Terrestrial anthropoids are different from arboreal and suspensory anthropoids in width of the tuber, but only at the 0.05 level. Length of the body of the astragalus and height of the cuboid facet show significant differences between arboreal and terrestrial anthropoids as above, but suspensory groups are not significantly different from either group.

Arboreal and terrestrial guenons are significant different in any calcaneal variable (Table 2.20d). Arboreal and terrestrial colobines are significantly different in overall length of the calcaneus and trend towards to significance in length of the body of the calcaneus (0.086) (Table 2.20e). Arboreal and terrestrial papionins are significantly different in height of the cuboid facet and trend towards significance in length of the calcaneal body (0.053) (Table 2.20f)

Standard ANOVAs by Locomotor Grouping

Three variables that were found to have significant post-hoc comparisons in the standard ANOVAs for the cercopithecoid-only sample using Coding 1 are not significant in the phylogenetic ANOVAs (Table 2.21a). All three post-hoc comparisons are significant for length of the body of the calcaneus but in the phylogenetic ANOVA the comparison between semi-terrestrial and terrestrial cercopithecoid is not significant. Arboreal and semi-terrestrial cercopithecoids are significantly different in width of the astragalar facet for the standard ANOVA but are not significant in the phylogenetic ANOVA. Arboreal cercopithecoids are significantly different in the height of cuboid facet from semi-terrestrial and terrestrial cercopithecoids in the standard ANOVA, but the comparison between arboreal and semi-terrestrial cercopithecoids was not significant in the standard ANOVA.

In the standard ANOVAs using the cercopithecoid-only sample with Coding 2 (Table 2.21b), length and width of the tuber are significantly different between arboreal and terrestrial cercopithecoids. In the phylogenetic ANOVA, these variables only trend towards significance. Width of the distal astragalar facet (abbreviation: MLF) is significant in the standard ANOVA but not in the phylogenetic ANOVA.

Arboreal and suspensory anthropoids are significantly different in the length of the body of the calcaneus and length of the tuber (Table 2.21c), but these comparisons are not significant in the phylogenetic ANOVA. Arboreal and terrestrial anthropoids are also significantly different in the length of the astragalar facet in the standard ANOVA but not in the phylogenetic ANOVA.

Phylogenetic ANOVAs by Phylogenetic Grouping

Seven variables show significant differences between colobines, guenons, and papionins (Table 2.22a; Figure 2.15a). Colobines differ significantly from guenons and papionins in the width of the astragalar facet and the width of the calcaneal tuber. Papionins differ significantly from colobines and guenons in the height of the cuboid facet. Papionins also differ significantly from guenons in the overall length of the calcaneus and the length of the body. Finally, papionins differ from colobines in the length of the tuber. Colobines and guenons differ in the length of the astragalar facet. Overall length of the calcaneus, length of the body, and height of the cuboid facet are also associated with substrate preference in cercopithecoids.

Six variables show significant differences across cercopithecines, colobines, platyrrhines, and hominoids (Table 2.22b; Figure 2.15b). Length of the tuber and length of the astragalar facet differ across all groups, except for the comparison between hominoids and platyrrhines. Width of the astragalar facet also differs across all groups except for the comparison between colobines and hominoids. Hominoids differ from all other groups in overall length of the calcaneus. Cercopithecines differ from all other groups in width of the sustentaculum and width of the tuber (the cercopithecine-platyrrhine comparison for width of the tuber approaches the Bonferroni adjusted critical value at 0.0172). Colobines and hominoids also differ significantly in width of the tuber. Overall length of the calcaneus, length of the astragalar facet, width of the sustentaculum, and width of the tuber are also associated with substrate preference across anthropoids.

Between-group Principal Components Analysis

Four variables were included in the between-group PCA on cercopithecoids using three locomotor codings – length of the calcaneal body, length of the tuber, width of the sustentaculum, and height of the cuboid facet (Table 2.23a). PC 1 accounts for 98% of the variation and PC 2 accounts of the remaining 2% of the variation. The variables with the highest loadings on PC 1 are length of the calcaneal body (-0.5934) and height of the cuboid facet (0.5119). The variable with the highest loadings on PC 2 is length of the calcaneal body (-0.7316). Figure 2.16a shows that locomotor groups are not well-separated on either PC 1 or PC 2.

Three variables were included in the between-group PCA on cercopithecoids when using only two locomotor codings – total length of the calcaneus, length of the calcaneal body, and height of the cuboid facet (Table 2.23b). PC 1 explains 100% of the variation and the variable with the highest loading is height of the cuboid facet (0.6829). Similar to the between-group PCA on three locomotor groups previously discussed, arboreal and terrestrial cercopithecoids are not well separated by PC 1 (Figure 2.16b).

Five variables were included in the between-group PCA examining all anthropoids with three locomotor groups - total length of the calcaneus, length of the calcaneal body, length of the astragalar facet, width of the sustentaculum, and height of the cuboid facet (Table 2.23c). PC 1 accounts for 89.9% of the variation and PC 2 accounts for 10.1% of the variation. Length of the astragalar facet (0.678) and width of the sustentaculum (0.556) have the highest loadings on PC 1. Length of the calcaneal body (-0.763) and height of cuboid facet (0.445) have the highest loadings on PC 2. Figure 2.16c shows that suspensory taxa are well-separated from arboreal and terrestrial taxa on PC 1. Arboreal and terrestrial taxa are separated along PC 2 although there is overlap between the two groups. The variables with the highest loadings on PC 2 (length of the calcaneal body and height of the cuboid facet) are the same variables that have the highest loadings on PC 1 in the first between-group PCA that examines cercopithecoids coded into three locomotor groups.

Section 2.3.5: All elements combined

Between-group Principal Components Analysis

Fourteen variables were included in the between-group PCA on cercopithecoids using three locomotor codings (Table 2.24a). PC 1 accounts for 95.8% of the variation and PC 2 accounts of the remaining 4.2% of the variation. The variables with the highest loadings on PC 1 are angle of the medial epicondyle (0.372) and height of the greater tubercle (0.363). The variables with the highest loadings on PC 2 are the humeral head index (-0.476) and length of the ectal facet on the astragalus (0.46). Figure 2.17a shows that locomotor groups are well separated along PC 1 with semi-terrestrial species occupying an intermediate space between arboreal and terrestrial species.

Fifteen variables were included in the between-group PCA on cercopithecoids using two locomotor codings (Table 2.24b). PC 1 accounts for 100% of the variation and the variables with the highest loadings are angle of the medial epicondyle (0.41), height of the greater tubercle

(0.326), and height of the cuboid facet on the calcaneus (0.317). Figure 2.14b shows that arboreal and terrestrial species are separated along PC 1 with some overlap between the two groups.

Twenty-two variables were included in the between-group PCA on the entire anthropoid sample (Table 2.24c). PC 1 accounts for 95.2% of the variation and PC 2 accounts for 4.8% of the variation. The variables with the highest loadings on PC 1 are width of the lesser tubercle (0.32) and femoral neck angle (0.3). The variables with the highest loadings on PC 2 are height of the greater tubercle (0.4), angle of the medial epicondyle (0.353), and length of the distal segment of the calcaneus (-0.346). Figure 2.17c shows that suspensory species are well separated from arboreal and terrestrial species on PC 1. Arboreal and terrestrial species are separated on PC 2 although overlap exists between the two groups.

Section 2.4: Functional Explanations

Several features of the cercopithecoid postcranium support a graded continuum of morphological variation that is functionally related to substrate preference. The articular surface of the humeral head becomes increasingly elliptical in shape with increasing levels of terrestrial behavior. An elliptical articular surface of the humeral head helps restrict the glenohumeral joint to movements in the sagittal plane when the humerus is fully flexed (i.e., in a weight-bearing position) (Harrison 1989; Rose 1989; Larson 1993). The width of the greater and lesser tubercles also increase in size with increasing terrestriality. Given that the greater and lesser tubercles are the attachment sites for the rotator cuff muscles (supraspinatus, infraspinatus, teres minor, and subscapularis), an increasing size of these bony protuberances may reflect larger rotator cuff muscle bodies, for better stabilization of the glenohumeral joint during the rapid and successive arm extension required by terrestrial locomotion. Anapol and Gray (2003) found that the semi-terrestrial *Chlorocebus aethiops* have absolutely and relatively larger rotator cuff muscles than the arboreal *Cercopithecus ascanius*, lending support to this functional explanation. As has been documented previously, height (or projection) of the greater tubercle increases with increasing terrestriality (Jolly 1967; Birchette 1982; Gebo et al. 1988; Harrison 1989; Ciochon 1993; Larson 1993; Elton 2002). Because the glenohumeral joint moves mostly in the sagittal plane during terrestrial locomotion, an increase in the height of the greater tubercle (i.e., a longer lever arm for supraspinatus) does not impede range of motion of the humerus. The force required to stabilize the glenohumeral joint during the support phase of walking is reduced in species with a projecting greater tubercle. Thus, this musculoskeletal arrangement is less energetically costly, making it advantageous for species that engage in terrestrial behavior to increase the height of the greater tubercle (Larson and Stern 1989; Larson and Stern 1992; Larson 1993).

The proximodistal height of the olecranon fossa decreases as terrestrial behavior increases. This may reflect the different orientation of the olecranon process of the ulna in arboreal and terrestrial cercopithecoids. Arboreal cercopithecoids have a tall olecranon process that projects proximally while terrestrial cercopithecoids have an olecranon process that projects dorsally and is short in the proximodistal direction. This orientation is related to the relatively extended elbow posture of terrestrial cercopithecoids, and increases the moment arm of the triceps muscle that acts to extend the forearm. Because the olecranon process of terrestrial cercopithecoids is not tall proximodistally, then the olecranon fossa does not need to be expanded in that direction. The depth of the capitulum (i.e., the proximodistal height) increases in semi-terrestrial and terrestrial cercopithecoids relative to those or primarily arboreal cercopithecoids. Rose (1988) previously demonstrated that *Cercopithecus* has a more anteroposteriorly flattened, but proximodistally longer, capitulum than those of hominoids or platyrrhines. He suggests that this configuration of the capitulum allows for greater contact with the radial head during partial flexion at the elbow, although this explanation is speculative and requires more investigation.

The medial epicondyle becomes more dorsally oriented with increasing amounts of terrestriality. This feature is well documented (Jolly 1967; Jenkins 1973; Harrison 1989; Nakatsukasa 1994; Elton 2002) and this morphological arrangement reorients the digital flexor musculature such that the force created results in flexion and does not create the medial torque that results in supination, as occurs with a more medial orientation of the medial epicondyle (Jenkins 1973). Arboreal cercopithecoids have a medial epicondyle that projects more medially, which increases the mechanical advantage of the forearm flexors when the arm and forearm are in flexed postures. The angle of the medial epicondyle also differs among colobines, guenons, and papionins, reflecting the primary locomotor mode of most species in each group. However, this relationship between medial epicondyle angle and phylogeny may also reflect the evolutionary history of each clade. For example, if the last common ancestor (LCA) of papionins engaged in frequent terrestrial behavior, then even arboreal papionins may have a medial epicondyle more indicative of a semi-terrestrial or terrestrial lifestyle. Although arboreal and terrestrial papionins differ significantly in the angle of the medial epicondyle (Table 2.5f), papionins overall have a much more dorsally oriented medial epicondyle than colobines (Figure 2.3a). Therefore, although some papionins are arboreal, the orientation of their medial epicondyle is not similar to that of the predominately arboreal colobines, which most likely reflects different evolutionary histories of these clades. Interestingly, *Semnopithecus entellus*, a colobine that engages in terrestrial behavior seasonally (see Appendix A), is an outlier among colobines in the angle of the medial epicondyle (Fig 2.3a) and overlaps in this morphology with papionins. Therefore, the mechanical advantage afforded by a dorsally projecting medial epicondyle is highly beneficial to species that engage in any regular amount of terrestrial behavior. Since arboreal guenons and papionins do not approach the relative medial projection seen in colobines, this suggests that a dorsally projecting medial epicondyle may not compromise the ability of these species to engage in arboreal behaviors.

The femoral neck angle has long been cited as a feature that differentiates arboreal, terrestrial, and suspensory primates (Fleagle 1983). This study supports previous work documenting a highly obtuse femoral neck angle among suspensory anthropoids, which increases mobility at the hip joint. However, no difference between arboreal and terrestrial cercopithecoids (or arboreal and terrestrial anthropoids) was found. The relationship between relative amount of terrestrial behavior and femoral neck angle is clearer across the entire anthropoid sample. Figure 2.7b demonstrates that while hominoids have the highest neck angle among anthropoids, platyrrhines also have a higher neck angle than do cercopithecoids, especially cercopithecines. Among cercopithecoids, guenons have the lowest neck angles, while papionins and colobines overlap mostly with colobines. Therefore, although cercopithecoids do differ from other anthropoids in having relatively low neck angles, this trait should not be used to reconstruct substrate preference within Cercopithecoidea.

Elton (2002) found that ratios describing the relative length, depth, and breadth of the femoral condyles reflected substrate preference in a group of nine cercopithecoids (see also (Gebo and Sargis 1994) for similar indices in guenons). Her indices were modified in this study, but were not found to be associated with locomotor behavior of cercopithecoids in a much broader taxonomic sample. However, Elton's (2002) results are consistent with results from this study when examining cercopithecoids by clades. Elton (2002) found that arboreal cercopithecoids have tall and broad lateral condyles. In this study, colobines have a tall (as measured by the condylar asymmetry [ACON] variable) and a broad lateral condyle. Given that the arboreal group in Elton (2002) was composed of one species each of colobine, guenon, and papionin, and no colobines were included in the semi-terrestrial or terrestrial group, her results may have been reflecting phylogenetic differences rather than locomotor differences. Additionally, she found her terrestrial group (comprised of two papionin species) to have a longer medial condyle relative to the lateral condyle. This study found that a relatively long medial condyle (as measured by the proximodistal condylar index [PID]) is a feature of *all* papionins, regardless of their substrate preference. Although this feature may reflect an adaptation to terrestriality, members of the colobine and guenon clades that engage in terrestrial behavior do not exhibit this trait. These results illustrate the problem of examining functional adaptations in relation to substrate preference without a broad sample of "known" phylogeny. As discussed previously in relation to the medial epicondyle, the behavior and morphology of the LCA of papionins was probably considerably different from that of the colobine LCA. A tall and broad lateral condyle, as exhibited by colobines, may be functionally related to their primarily arboreal lifestyle, but this feature does not discriminate arboreal papionins and guenons from terrestrial ones (Tables 2.10d and 2.10f). Given the high degree of variation in the distal femur among the major cercopithecoid clades, the distal femur does not appear to be a reliable region for determining substrate preferences of fossil specimens.

Several features of the astragalus and calcaneus also exhibit a graded morphological continuum across arboreal, semi-terrestrial, and terrestrial cercopithecoids. Total length of the astragalus and total length of the body of the calcaneus (i.e., not including the tuber) decrease as terrestriality increases. Several previous studies have documented shortened pedal elements in terrestrial cercopithecoids relative to arboreal cercopithecoids (Kingdon 1988; Strasser 1988; Gebo and Sargis 1994). Most terrestrial cercopithecoids utilize a digitigrade posture, which increases the effective limb length, allowing for longer but fewer strides during terrestrial travel (Hildebrand 1985; Schmitt and Larson 1995; Hildebrand and Goslow 2001; Patel 2009). This functional complex involves a shortening of the proximal pedal elements and lengthing of the metapodials. A reduction in the proximal pes both lightens the limb and moves the center of mass of the limb closer to the pelvic girdle, allowing the limb to move more slowly (and increase the stride length) (Hildebrand 1985). Thus, a decrease in overall astraglar and calcaneal length, and the digitigrade posture, in terrestrial cercopithecoids is convergent on the highly specialized pedal morphology of cusorial artiodactyls.

The length of the calcaneal tuber exhibits the opposite trend in which the tuber becomes more elongate with increasing terrestrial behavior. The calcaneal tuber serves as the insertion for the triceps surae, which plantarflex the foot. A longer tuber increases the mechanical advantage of the triceps surae, which contribute to propulsion during walking. This feature also distinguishes clades within cercopithecoids, with colobines having the shortest tubers, papionins having the longest tubers, and guenons occupying an intermediate space. Again, this relationship may be related to the predominant mode of locomotion exhibited by the species within each clade or more reflective of the evolutionary history of each clade.

In the astragalus, semi-terrestrial and terrestrial cercopithecoids have a shorter ectal facet than arboreal cercopithecoids. Strasser (1988) noted that colobines have a more tightly curved ectal facet than cercopithecines, but her conclusion may be more related to the fact that as a clade colobines are more arboreal than cercopithicines. No differences between ectal facet length is found between colobines, guenons, and papionins in this study. Strasser (1988) suggests that a longer ectal facet provides the flexor fibularis with more leverage by moving the attachment site for the muscle more plantarly (see Figure 6 in Strasser, 1988, pp. 237). Given that the flexor fibularis is a plantarflexor of the foot and digital flexor, increasing the lever arm of this muscle would beneficial in arboreal species that utilize more dorsiflexed foot postures. Strasser (1988) also suggests that an elongate ectal facet increases the surface area of the subtalar joint and may provide more stability against substrate reaction forces.

Arboreal and semi-terrestrial cercopithecoids have a more highly angled astragalar head than terrestrial cercopithecoids, which Strasser (1988) also noted to be a difference between colobines and cercopithecines. In this study papionins were found to have a less angled astragalar head than colobines and guenons (Figure 2.11a), which partly supports Strasser's (1988) findings. Papionins as a clade include some of the most terrestrial cercopithecoids, and the terrestrial locomotor category includes only papionin species. Given that the angle of the astragalar head is found to be significant in both ANOVAs by locomotor group and phylogenetic group, it seems that this feature may be specific to the papionin clade. Strasser (1988) suggests that an angled astragalar head (as seen in guenons and colobines) prevents proximal displacement of the astragalus by stabilizing the distal articulation between the astragalus and calcaneus during inversion.

Strasser (1988) found that cercopithecoids have a wedge-shaped (distal end wider than proximal end) and asymmetrical (lateral ridge higher than medial ridge) astragalar trochlea in comparison to platyrrhines and hominoids (see Figure 1 in Strasser, 1988, pp 230). Differences in trochlear wedging were found between arboreal and terrestrial cercopithecoids but only when the "terrestrial" group included both terrestrial and semi-terrestrial species (i.e., Coding 2), and the level of significance is not very high ($p = 0.043$). Additionally terrestrial species have a more wedge-shaped trochlea in comparison to suspensory anthropoids, but arboreal cercopithecoids do not differ from suspensory anthropoids or platyrrhines. Contrary to Strasser (1988), this trait does not discriminate cercopithecoids from platyrrhines or hominoids.

Cercopithecoids do have greater trochlear asymmetry than hominoids and platyrrhines, which supports Strasser (1988) (see also, Boyer and Seiffert 2013). Additionally, guenons and papionins have more trochlear asymmetry than colobines (Figure 2.11a). Strasser (1988) suggests that trochlear asymmetry may be related to increasing range of abduction during a dorsiflexed foot posture, but Boyer and Seiffert (2013) suggest an alternate view that asymmetry is related to a wider foot stance on larger substrates (including the ground) where the ankle is lateral to the knee putting the tibia and fibula in an abducted posture relative to the ankle (see also see Fleagle 1976 for discussion of trochlear asymmetry in relation to leaping). However, both these hypotheses need to be evaluated using a kinematic study of tarsal articulation and mobility (e.g Orr et al. 2010).

Arboreal cercopithecoids have a relatively narrow astragalar head when compared to terrestrial cercopithecoids. Figure 2.10a shows that semi-terrestrial cercopithecoids have a very similar distribution to arboreal cercopithecoids in this variable. Semi-terrestrial cercopithecoids may not differ from terrestrial cercopithecoids due to a lack of power in this analysis (the standard ANOVA only approaches significance in this comparison). Gebo and Sargis also (1994) found *Chlorocebus aethiops* to have a wide astragalar head while *Cercopithecus lhoesti* had a narrow astragalar head. Given the wide distribution of this feature in semi-terrestrial and arboreal cercopithecoids, the variation found by Gebo and Sargis (1994) is not surprising.

In the calcaneus, terrestrial cercopithecoids have a narrower sustentaculum tali and a taller cuboid facet than arboreal cercopithecoids. A narrower sustentaculum may restrict mobility and inversion at the subtalar joint. A taller cuboid facet may help stabilize the transverse tarsal joint during sagittal movements when loading on the joint is high.

Section 2.5: Discussion

Overall, standard ANOVAs returned more significant results across all sets of analyses than phylogenetic ANOVAs. This result is expected given the increase in Type I error seen when using standard ANOVAs on data that does not meet the assumption of normality (Garland et al. 1993; Freckleton et al. 2002; Revell 2009). Therefore, results from comparative work using standard statistical model should be interpreted with caution. Generally, adaptations previously suggested to be associated with terrestriality in cercopithecoids are found significant by both standard and phylogenetic ANOVA in the present study, suggesting that previous work on cercopithecoid postcranial morphology is not inaccurate despite the use of standard statistical models (e.g., Ciochon 1993; Elton 2002).

While many of the post-hoc comparisons between arboreal, semi-terrestrial, and terrestrial species are not significant at adjusted p-value levels, Figures 2.2a, 2.6a, 2.10a, and 2.14a demonstrate that these features generally show semi-terrestrial cercopithecoids as intermediate to arboreal and terrestrial cercopithecoids. Arboreal and terrestrial species are well-differentiated from each other, although either group may overlap in the morphospace with semi-terrestrial species. Although many of the same features show significant differences when cercopithecoids are sorted using either Coding 1 or Coding 2, information appears to be lost in comparisons that categorize cercopithecoids using only two locomotor categories (i.e., arboreal and terrestrial). As can be seen in Figures 2.2b, 2.6b, 2.10b, and 2.14b substantial overlap exists between arboreal and “terrestrial” (i.e., terrestrial and semi-terrestrial) cercopithecoids. Although overlap also exists in Figures 2.2a, 2.6a, 2.10a, 2.14a, most of the overlap concerns the semi-terrestrial species and does not obscure relationships between highly arboreal and highly terrestrial species. The same pattern occurs in multivariate analyses. Figures 2.4a, 2.8a, 2.12a, 2.16a, and 2.17a show that in multivariate space arboreal and terrestrial species occupying distinct non-overlapping morphospaces with semi-terrestrial species occupying intermediate space that overlaps with both other groups. Figures 2.4b, 2.8b, 2.12b, 2.16b, and 2.17b show that when only examining two locomotor groups (arboreal and terrestrial), substantial overlap exists between the two groups. Therefore, a “semi-terrestrial” category is useful when examining postcranial variation in cercopithecoids as it often allows better differentiation between the arboreal and terrestrial extremes.

However, the biological basis for a semi-terrestrial locomotor mode as a catch-all category for all species that can engage in both arboreal or terrestrial behavior is debatable. Semi-terrestrialists can be understood as “uncommitted” to either the ground or an arboreal substrate and theoretically might be identified through an “intermediate” morphology relative to the morphologies of more committed arborealists and terrestrialists. Morphological studies (Elton, 2002; Nakatsukasa, 1994), including the present study, have found associations between morphological features and the amount of terrestrial behavior in which a species engages. But the morphological continua presented here are subtle compared to the high differentiation that can be seen when examining morphological differences between arboreal, terrestrial, and suspensory anthropoids (see Figures 2.2c, 2.6c, 2.10c and 2.14c), which would be expected for a more functionally restricted clade. Additionally, not all features that differentiate highly arboreal from highly terrestrial cercopithecoids show consistently intermediate morphologies in semi-terrestrial species. This is especially the case for the astragalus, an element in which semi-terrestrial cercopithecoids are morphologically similar to arboreal cercopithecoids in the width and angle of the astragalar head but are morphologically similar to terrestrial anthropoids in length of the ectal facet. This finding may mean that even within an individual element, some features may respond to selective pressures from arboreal demands while other features respond to terrestrial demands, suggesting that selection can act quite differently on specific regions within an element that may be experiencing "opposing" functional demands.

Several features exhibit a morphological continuum between "arboreal", "semi-terrestrial", and "terrestrial" cercopithecoids and this pattern indicates that morphology does not clearly separate locomotor groups into disjointed and unique morphospaces. Morphological continuums exist in other locomotor modes such as the variable length of the navicular and calcaneus in leaping primates (Gebo 1988; Gebo and Dagosto 1988; Boyer et al. 2013). As in the present study, extreme calcaneal elongation as exhibited by *Tarsius* and *Galago* is indicative of species that are highly committed to leaping, but overall variation in elongation does not accurately predict the amount of leaping behavior in which a species engages (Gebo 1988; Gebo and Dagosto 1988; Boyer et al. 2013). Thus, many morphological features documented in this study as exhibiting a "morphological continuum" probably reflect subtle *variation* in functional demands that are not reflective of separation between locomotor modes defined simply by percentage of time in arboreal versus terrestrial settings. As discussed by Anapol et al. (2005), the frequent transitions from the ground to above-ground substrates (and the requisite climbing involved in such transitions) is just as important to the definition of semi-terrestriality as the actual ground and above-ground locomotion. Finally, this study shows that phylogeny also has an effect on the morphological adaptations exhibited by different clades. For example, the medial epicondyle of papionins is more dorsally directed than that of guenons or colobines (Figure 2.3a) even though the papionin clade includes some arboreal members and the guenon and colobine clade include some semit-terresttrial members (see Appendix A). It is likely that the angle of the medial epicondyle (or any morphology associated with behavior) exhibited by extant taxa is not only reflection of their locomotor behavior but also conveys information about evolutionary history. Given the relatively dorsally oriented medial epicondyle of all papionins, it seems probably that this feature was inherited from an ancestor that engaged in terrestrial behavior. This hypothesis will be tested in Chapter 4, which examine character trait evolution throughout the cercopithecoid clade.

Thus, anatomical features such as the orientation of the medial epicondyle, relative size of the femoral condyles, and the relative length of the calcaneal tuber illustrate the difficulty in ascribing an "arboreal," "semi-terrestrial," and "terrestrial" morphology across a phylogenetic group that underwent a rapid diversification (Jablonski and Frost 2010) and contains species with differing evolutionary histories. Clear examples of morphological features that are highly associated with substrate preference across cercopithecoids are rare. The angle of the medial epicondyle is one example, with *Semnopithecus entellus* exhibiting a morphology overlapping with papionins. However, other features, such at the length of calcaneal tuber, exhibit a morphological continuum across *both* locomotor group and phylogenetic group.

Given the difficulty of defining a "semi-terrestrial" morphology across the entire cercopithecoid clade, one alternative would be to determine adaptations to terrestrial behavior within each major clade of cercopithecoids. However, the overall findings from this study show that the morphology of arboreal and terrestrial species within the guenons, colobines, and papionins is highly similar with few variables exhibiting significant differences. Additionally, the features that do differentiate arboreal and terrestrial species are different across each clade, suggesting that adaptations to terrestriality can be achieved in different ways (Sargis et al. 2008). The overall similarity of arboreal and terrestrial individuals within each clade may be another indicator that the generalized body plan of cercopithecoids allows for frequent transitions between arboreal and terrestrial behavior.

Section 3.6: Conclusions

Despite the high level of phylogenetic diversity in cercopithecoids, the body plan of this group is relatively generalized. Overall the findings from morphological and myological studies are consistent in demonstrating the subtle differences that allow sympatric cercopithecoids to occupy specific niches within a single habitat (Thomas 1991; McGraw 1994; Gebo and Chapman 1995b; Gebo and Chapman 1995a; Anapol and Barry 1996; McGraw 1996; Anapol and Gray 2003; Anapol et al. 2005; Hadi et al. 2012). Although much work has focused on determining the exact suite of features that define semi-terrestriality, I suggest here that cercopithecoids, relative to other mammalian specialists, are all "semi-terrestrial" to varying degrees and that attempts to unite "semi-terrestrialists" using either behavioral data or morphological features obscures the unique flexibility that cercopithecoids have to utilize the microhabitats within their home range, as well unique history of selection and adaptive change that has lead various taxa to arrive in their particular "semi-terrestrial" niche. Obviously, no cercopithecoid primate has become so highly specialized for terrestrial locomotion as to converge on the morphology of a curosiral artiodactyl. But, the general quadrupedal morphology of cercopithecoids is adaptive and has allowed cercopithecoids to coexist sympatrically through niche separation. Additionally, the capacity of all cercopithecoids to enter trees possibly provides advantages in predation avoidance.

Primatologists can discuss the relative amount of time a primate engages in a certain mode of locomotion, but it is difficult to assess the selective pressures placed on a given species based on the proportion of time it spends on the ground or in the trees. There are examples of predominately arboreal (e.g. *Cercopithecus diana*) and predominantly terrestrial (e.g. *Theropithecus gelada*) cercopithecoid primates, but using these two extremes as a dichotomy to bookend a "semi-terrestrial" mode of locomotion does not necessarily provide information on the functional demands influencing "semi-terrestrial" species. The subtle adaptations that cercopithecoids have made to their bony and muscular anatomy is influenced by their preferred habitat, which in turn is influenced by their dietary specializations and competitive environment. Cercopithecoids should be recognized as a phylogenetically diverse clade that has evolved a body plan adapted to not only arboreal and terrestrial travel but also climbing and leaping (Anapol et al. 2005). This body plan can be fine-tuned to accommodate the challenges of a specific microhabitat or range of habitats.

Although this conclusion may seem unsatisfactory to paleoanthropologists interested in reconstructing the specific locomotor mode of fossil cercopithecoids, the important findings of this study suggest that bony structures can inform us of differing functional demands in relatively "extreme" behaviors and environments. Primarily arboreal and primarily terrestrial cercopithecoids are differentiated from one another in several features of the postcranium, which will allow paleoanthroplogists to determine if fossil cercopithecoids fall into one of these two categories as might be the case for *Microcolobus tugenensis,* an early, and probable arboreal colobine (Nakatsukasa et al. 2010) and *Parapapio jonesi*, a probable terrestrial papionin (Frost and Delson 2002). Finally, although many fossil cercopithecoids will fall into the middle "semi-terrestrial" morphospace, this finding tells us that many fossil cercopithecoids were adapted to do what extant cercopithecoids do today – that is, engage in locomotor, social, and dietary behaviors in both the tree canopy, understory, and ground.

Table 2.1. List of extant specimens collected for study. Total number of specimens provided and broken down by sex. The number of captive specimens is listed when included in the sample. See Appendix C for specimen numbers.

Species	**Total**	**Males**	**Females**	**Unknown Sex**	**Captive**	**Collection**
Allenopithecus nigroviridis	2	1	1		1	AMNH (1); NMNH (1)
Allochrocebus lhoesti	8	3	4	1	2	RMCA (8)
Alouatta palliata	9	5	4			NMNH (9)
Aotus azarae	12	6	6			AMNH (12)
Cebus apella	12	6	6			AMNH (12)
Cercocebus torquatus	14	9	5			PCM (11); BMNH (3)
Cercopithecus ascanius	15	6	5	4	1	RMCA (13); BMNH (2)
Cercopithecus cephus	10	6	4			PCM (10)
Cercopithecus diana	6	2	4		5	NMNH (4); FMNH (2)
Cercopithecus hamlyni	6	1	3	2	1	RMCA (6)
Cercopithecus mitis	14	8	6			NMNH (10); AMNH (4)
Cercopithecus mona	14	9	4	1		PCM (5); BMNH (3); NMNH (2); AMNH (4)
Cercopithecus neglectus	14	7	5	2	1	AMNH (2); RMCA (5); PCM (2); BMNH (5)
Cercopithecus nictitans	13	6	7			PCM (10); BMNH (3)
Cercopithecus pogonias	12	6	6			PCM (12)
Chlorocebus aethiops	9	4	5			AMNH (4); BMNH (4); MCZ (1)
Chlorocebus pygerythrus	15	7	8			AMNH (6); RMCA (4); BMNH (5)
Colobus guereza	15	9	6		2	RMCA (7); PCM (8)
Erythrocebus patas	12	6	6		12	CPRC (12)
Hylobates lar	12	6	6			MCZ (12)
Lophocebus albigena	14	6	8			PCM (12); NMNH (1); AMNH (1)
Macaca arctoides	15	8	7		11	AMNH (1); BMNH (1); CPRC (10); FMNH (3)
Macaca assamensis	11	7	4			FMNH (3); MCZ (8)
Macaca fascicularis	12	6	6			MCZ (12)
Macaca mulatta	12	6	6			CPRC (12)
Macaca nemestrina	16	4	12		5	NMNH (3); CPRC (5); MCZ (8)
Macaca nigra	17	7	8	2	9	AIM (3); AMNH (1); BMNH (1); NMNH (7); FMNH (5)
Macaca sinica	9	9	0		7	AIM (7); FMNH (2)
Macaca sylvanus	9	4	4	1	2	AIM (2); NMNH (3); FMNH (2); MCZ (2)
Macaca thibetana	10	6	4			NMNH (7); FMNH (3)
Macaca tonkeana	4	3	1			AMNH (4)

Mandrillus sphinx	14	9	4	1		AIM (2); AMNH (7): PCM (1); BMNH (2); MCZ (2)
Miopithecus talapoin	19	11	8		4	AIM (9); PCM (2); BMNH (6); NMNH (2)
Nasalis larvatus	14	8	6			MCZ (14)
Pan troglodytes	12	6	6			AMNH (12)
Papio anubis	13	7	6			NMNH (12); AMNH (1)
Papio cynocephalus	12	6	6			UTA (12)
Piliocolobus badius	13	7	6			PCM (13)
Piliocolobus foai	9	3	5	1		RMCA (9)
Piliocolobus kirkii	3	1	2		3	RMCA (3)
Pongo pygmeaus	12	6	6			NMNH (11); AMNH (1)
Presbytis melalophos	4	2	2			BMNH (3); NMNH (1)
Presbytis rubicunda	13	6	7			MCZ (13)
Pygathrix nemaeus	15	10	6		3	AIM (3); NMNH (4); FMNH (5); MCZ (2); AMNH (2)
Rhinopithecus roxellana	13	5	6	2		AMNH (2); NMNH (10); FMNH (1)
Saguinus oedipus	10	5	5			NMNH (10)
Saimiri sciureus	10	5	5			NMNH (10)
Semnopithecus entellus	10	4	6		3	AIM (2); BMNH (1); NMNH (1); FMNH (6)
Theropithecus gelada	20	7	12	1	11	AIM (9); AMNH (1); UCB (5); NMNH (2); FMNH (1); NME (2)
Trachypithecus cristatus	12	6	6			MCZ (12)
Trachypithecus obscurus	15	6	8	1		BMNH (13); FMNH (2)
Trachypithecus phayrei	12	5	7			FMNH (2); MCZ (10)

Table 2.2. Locomotor codings used for phylogenetic ANOVAs. Coding 1 is used to compare arboreal, semi-terrestrial, and terrestrial cercopithecoids. Coding 2 is used to compare a) arboreal and terrestrial (semi-terrestrial + terrestrial) cercopithecoids and b) arboreal, terrestrial, and suspensory anthropoids.

Species	Coding 1	Coding 2
Allenopithecus_nigroviridis	semi	ter
Alouatta_palliata	n/a	bor
Aotus_azarae	n/a	bor
Cebus_apella	n/a	bor
Cercocebus_torquatus	semi	ter
Cercopithecus_ascanius	bor	bor
Cercopithecus_cephus	bor	bor
Cercopithecus_diana	bor	bor
Cercopithecus_hamlyni	semi	ter
Cercopithecus_lhoesti	semi	ter
Cercopithecus_mitis	bor	bor
Cercopithecus_mona	bor	bor
Cercopithecus_neglectus	semi	ter
Cercopithecus_nictitans	bor	bor
Cercopithecus_pogonias	bor	bor
Chlorocebus_aethiops	semi	ter
Chlorocebus_pygerythrus	semi	ter
Colobus_guereza	bor	bor
Erythrocebus_patas	semi	ter
Hylobates_lar	n/a	sus
Lophocebus_albigena	bor	bor
Macaca_arctoides	semi	ter
Macaca_assamensis	bor	bor
Macaca_fascicularis	bor	bor
Macaca_mulatta	semi	ter
Macaca_nemestrina	semi	ter
Macaca_nigra	semi	ter
Macaca_sinica	bor	bor
Macaca_sylvanus	semi	ter
Macaca_thibetana	ter	ter
Macaca_tonkeana	semi	ter
Mandrillus_sphinx	ter	ter
Miopithecus_talapoin	bor	bor
Nasalis_larvatus	bor	bor
Pan_troglodytes	n/a	sus
Papio_anubis	semi	ter
Papio_cynocephalus	ter	ter
Piliocolobus_badius	bor	bor
Piliocolobus_foai	bor	bor
Piliocolobus_kirkii	bor	bor
Pongo_pygmaeus	n/a	sus
Presbytis_comata	bor	bor
Presbytis_melalophos	bor	bor
Pygathrix_nemaeus	bor	bor
Rhinopithecus_roxellana	bor	ter
Saguinus_oedipus	n/a	bor
Saimiri_sciureus	n/a	bor
Semnopithecus_entellus	semi	ter
Theropithecus_gelada	ter	ter
Trachypithecus_cristatus	bor	bor
Trachypithecus_obscurus	bor	bor
Trachypithecus_phayrei	bor	bor

Table 2.3. Variables from humerus, femur, astragalus, and calcaneus selected for multivariate analyses. Asterisk (*) notes when variables are significant at then adjusted critical value based on the Sequential Bonferroni method. Variables without asterisk are significant only at 0.05 level.

	Cercopithecoid only - 3 locomotor categories	**Cercopithecoid only - 2 locomotor categories**	**All anthropoids**
Humerus	Humeral head index (HHI)*	Humeral head index (HHI)*	Width of humeral head (MLHH)*
	Width of lesser tubercle (MLT)*	Width of greater tubercle (MGT)*	Height of humeral head (SIHH)*
	Height of greater tubercle (GTH)*	Width of lesser tubercle (MLT)*	Width of lesser tubercle (MLT)*
	Angle of medial epicondyle (AME)*	Height of greater tubercle (GTH)*	Width of biciptal groove (BGW)*
		Height of capitulum (PDC)*	Height of greater tubercle (GTH)*
		Angle of medial epicondyle (AME)*	Angle of medial epicondyle (AME)*
Femur	Length of femur (FL)	Length of femur (FL)*	Width of femoral head (APFH)*
	Patellar groove height (PH)	Patellar groove height (PH)*	Height of femoral head (PDFH)*
			Anteroposterior breadth of lateral condyle (APLC)*
			Patellar groove width (PW)*
			Proximodistal height condylar index (PDI)*
			Femoral neck angle (FNA)*
			Condylar asymmetry (ACON)*
Astragalus	Total length (AL)*	Total length (AL)*	Total length (AL)*
	Ectal facet length (EL)*	Ectal facet length (EL)*	Length of head and neck (HNPD)*
	Width of astragalar head (WTH)	Width of astragalar head (WTH)*	Ectal facet length (EL)*
	Angle of astragalar head (ATH)	Trochlear wedging (WED)*	Width of astragalar head (WTH)*
Calcaneus	Total length (CL)	Total length (CL)*	Total length (CL)*
	Length of tuber (CTL)	Length of body (PDA)*	Length of body (PDA)*
	Width of sustentaculum (MLS)	Height of cuboid facet (HCF)	Length of astragalar facet (PDF)
	Height of cuboid facet (HCF)		Width of sustentaculum (MLS)
			Height of cuboid facet (HCF)

Table 2.4a. Results for phylogenetic PCA of the humerus using cercopithecoid-only sample. Lambda = 0.71

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**
Proportion of Variance	24.3074	14.5971	13.6401	11.5930	7.1786	6.5988	5.2264	4.0194	3.5546	2.7856	2.5398	1.6970	1.3071	0.5984	0.3566
Loadings															
HL	0.2023	-0.1801	0.7401	-0.0117	0.3668	0.1676	0.0581	0.3242	0.2933	-0.0666	0.0410	0.0132	-0.1175	0.0404	-0.0050
MGT	-0.4848	0.3123	-0.3603	-0.1061	0.5518	0.3137	-0.2511	-0.0262	-0.1669	-0.1174	0.0815	-0.0807	-0.0685	-0.0004	-0.0151
MLT	-0.7091	-0.0763	0.1568	-0.0407	0.0081	0.1961	-0.2782	-0.0701	0.3221	0.0508	-0.4181	-0.1828	0.1627	-0.0314	0.0477
BGW	-0.1564	0.0345	0.1301	0.6994	-0.2529	0.1274	0.3401	-0.0382	0.0059	-0.2982	0.1907	-0.3729	-0.0192	-0.0678	0.0407
MLOF	0.2782	-0.4049	-0.5682	0.3434	0.3570	-0.3876	0.0640	0.0115	0.0980	-0.0659	-0.1274	-0.0315	-0.0422	0.0461	0.0305
PDOF	0.8386	0.0591	0.2134	0.1106	-0.0068	0.0571	-0.1795	0.1231	-0.3064	0.1670	-0.1767	-0.1424	-0.0976	-0.0266	0.0348
PDC	-0.5799	-0.4399	0.2714	0.2131	0.1487	-0.3448	-0.2479	0.0947	-0.0763	0.2516	0.2395	-0.0735	0.0733	-0.0492	-0.0069
MLC	-0.2361	-0.3119	0.5670	-0.4337	0.2654	-0.1318	0.2520	-0.2917	-0.2694	-0.1151	-0.0417	0.0157	0.0376	0.0337	0.1032
PDT	-0.6483	0.1339	-0.1294	0.3212	0.1170	0.2387	0.4452	-0.0483	0.0043	0.3759	-0.0723	0.0652	-0.1365	-0.0186	0.0292
MLTR	-0.1631	-0.4571	-0.4834	-0.3540	-0.1431	0.2764	0.1568	0.4914	-0.1287	0.0104	0.0501	-0.0300	0.1250	0.0444	0.0694
MLTC	-0.3340	-0.6071	-0.0202	-0.5514	-0.0831	-0.0925	0.2558	-0.0189	-0.1007	0.0123	-0.1608	-0.2230	-0.1186	0.0118	-0.1846
BB	-0.2560	0.3446	-0.1999	-0.6470	-0.2667	-0.3268	-0.1346	-0.0011	0.2228	0.0767	0.1258	-0.1443	-0.2430	0.0313	0.0947
GTH	-0.6994	-0.3959	0.0519	0.2076	-0.2639	-0.0432	-0.1970	0.1417	-0.1330	-0.2368	-0.1431	0.1918	-0.1895	-0.1026	0.0217
HHI	-0.3535	0.7434	0.1294	-0.0174	0.1004	-0.3857	0.1720	0.2891	-0.0979	-0.0635	-0.1210	-0.0081	0.0664	-0.0176	-0.0179
AME	-0.6227	0.0963	0.2467	0.5244	-0.3032	0.0151	-0.1982	-0.0022	-0.1649	-0.0084	-0.0431	-0.0188	-0.0353	0.3236	-0.0149

Table 2.4b. Results for phylogenetic PCA of the humerus using the entire anthropoid sample. Lambda = 0.94

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**	**PC16**
Proportion of Variance	22.8794	16.8133	11.9587	9.8915	8.9621	6.2911	5.3116	4.2680	3.7557	2.7002	2.3356	1.8236	1.3098	0.8170	0.5219	0.3605
Loadings																
HL	-0.0317	-0.8208	-0.1053	0.1315	0.1639	-0.0416	0.3958	-0.0057	-0.0549	0.1200	-0.2058	0.1962	0.0789	-0.0077	0.3077	0.0599
MLHH	-0.3606	-0.1151	0.4744	0.0995	0.3564	0.5964	-0.0802	-0.0610	0.3249	0.0472	-0.0979	-0.0107	-0.0517	-0.0927	-0.0549	-0.0141
SIHH	-0.1624	-0.3270	0.3303	-0.3747	0.0320	0.1711	0.2434	0.1979	-0.2314	0.2195	0.5680	-0.1271	0.0127	-0.1663	0.3168	0.1863
MGT	-0.3507	0.6706	0.0356	0.3772	-0.2973	0.2212	0.3078	0.0748	-0.1535	0.0816	-0.0894	-0.0649	0.0584	-0.0059	0.0462	-0.0581
MLT	-0.2609	0.3736	-0.5848	0.2266	-0.0589	-0.0845	-0.1733	-0.0128	-0.2398	-0.1046	-0.0679	0.3053	-0.2718	-0.3317	-0.0668	0.2436
BGW	0.0115	0.3254	-0.4269	-0.0449	0.4416	-0.4215	-0.1115	0.1570	0.2271	0.2993	-0.1867	-0.2778	0.1596	-0.1357	0.0171	0.1849
MLOF	0.5039	0.3755	-0.2130	-0.5545	-0.3062	0.1791	0.1568	-0.2131	0.2073	0.0552	-0.0363	0.0770	0.0258	-0.0124	0.1448	0.1749
PDOF	0.8593	-0.1936	-0.0529	0.0650	0.0015	0.2831	-0.0525	0.1944	-0.1368	-0.2186	-0.0640	-0.0664	0.1288	-0.0531	-0.1068	0.1870
PDC	-0.5590	-0.3252	-0.4834	-0.2181	0.1270	0.1261	0.2126	-0.3287	-0.1318	-0.1906	-0.0353	-0.2409	-0.0399	-0.0119	-0.0963	-0.0053
MLC	-0.3067	-0.5266	-0.3341	0.2727	-0.5798	0.1086	-0.1585	0.1053	0.2053	0.0707	0.0360	-0.0601	-0.0183	0.0368	-0.0267	0.3369
PDT	-0.6150	0.2780	-0.0963	0.1114	0.1776	-0.1692	0.2971	0.1447	0.3605	-0.3722	0.1934	0.1328	0.1657	-0.0089	-0.0610	0.1665
MLTR	-0.4117	0.0202	0.5087	-0.5568	-0.0720	-0.1191	0.1324	0.3458	-0.0728	-0.0887	-0.2318	-0.0530	-0.1376	0.0627	-0.0742	0.4297
MLTC	-0.5429	-0.2452	0.1467	-0.4135	-0.5233	-0.1144	-0.1865	0.1615	0.0433	-0.1472	-0.1333	-0.0126	0.1113	-0.1543	0.2139	-0.5464
BB	-0.3741	0.0625	0.5920	0.1329	-0.1446	-0.1448	-0.3391	-0.4864	-0.1709	-0.0654	-0.0548	0.0164	0.2030	-0.0141	0.1831	0.4162
GTH	-0.6353	0.0644	-0.3631	-0.3863	0.1771	0.2922	-0.2384	0.1263	-0.2000	0.1452	0.0242	0.1603	0.1554	0.0636	-0.2880	0.0126
AME	-0.1902	0.4471	-0.4981	0.0639	0.3645	0.2524	-0.3484	0.1802	-0.0078	-0.1873	-0.0574	-0.0222	-0.0912	0.1325	0.7625	0.0355

Table 2.5a. Results for phylogenetic ANOVAs for humerus by locomotor group using cercopithecoid-only dataset and Coding 1

Variable	**Lambda**	**df**	**F**	**model p**	**arboreal mean**	**semi-t mean**	**terrestrial mean**	**arb-semi**	**arb-ter**	**semi-ter**
HL	0.97	41	1.88	ns	1.025±0.013	1.0127± 0.0069	1.0104±0.01	ns	ns	ns
MLHH	0.59	41	2.35	ns	0.0582 ± 0.0056	0.0633±0.0044	0.073±0.007	ns	0.04	ns
SIHH	0.75	41	1.15	ns	0.0203± 0.0054	0.0148±0.0037	0.0181±0.006	ns	ns	ns
MGT	0.9	41	3.49	<0.05	0.0227 ± 0.008	0.0329±0.0043	0.0369±0.00647	0.0254	0.0344	ns
MLT	1	41	6.2	<0.01	-0.1362 ± 0.012	-0.125± 0.006	-0.106± 0.009	0.0743	0.0011	0.016
BGW	0.84	41	0.268	ns	-0.4724±0.021	-0.475±0.013	-0.462±0.019	ns	ns	ns
MLOF	0	40	2.21	0.05434	-0.10127±0.004	-0.1088±0.006	-0.1215±0.01	ns	0.05653	ns
PDOF	0.69	41	3.13	<0.05	-0.229±0.018	-0.245±0.013	-0.28±0.02	ns	0.017	0.073
PDC	1	41	3.69	<0.05	-0.123±0.009	-0.1117±0.0048	-0.1083±0.0066	0.019	0.028	ns
MLC	0.6	41	0.018	ns	-0.2398± 0.011	-0.241±0.008	-0.2401±0.013	ns	ns	ns
PDT	0.58	41	1.89	ns	-0.0721± 0.008	-0.0604±0.006	-0.715±0.01	0.059	0.059	ns
MLTR	0.63	41	1.24	ns	-0.1148±0.007	-0.123±0.005	0.1195±0.008	ns	ns	ns
MLCT	0.79	41	0.178	ns	0.127±0.006	0.125±0.004	0.124±0.006	ns	ns	ns
BB	0.86	41	1.52	ns	0.2702±0.007	0.2779±0.004	0.275±0.007	ns	ns	ns
GTH	0.75	41	6.33	<0.01	0.141±0.007	0.152±0.007	0.1667±0.007	0.0238	0.0015	0.049
HHI	0	41	6.16	<0.01	0.0382±0.003	0.0518±0.004	0.0539±0.007	0.0027	0.0342	ns
AME	0.82	41	11.2	<0.0001	-0.2035±0.017	-0.1673±0.01	-0.1341±0.016	0.0012	<0.0001	0.0288

Table 2.5b. Results for phylogenetic ANOVAs for humerus by locomotor group using cercopithecoid-only dataset and Coding 2

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
HL	0.98	42	4.24	<0.05	1.0258±0.013	1.013±0.0064	0.046
MLHH	0.41	42	2.11	ns	0.0583±0.0047	0.0642±0.0041	ns
SIHH	0.86	42	0.376	ns	0.0195±0.0062	0.0174±0.0035	ns
MGT	0.9	42	4.34	<0.05	0.0232±0.0077	0.032±0.0042	0.0433
MLT	0.94	42	4.55	<0.05	-0.1357±0.012	-0.1226±0.0062	0.039
BGW	0.82	42	0.002	ns	-0.4718±0.02	-0.4724±0.012	ns
MLOF	0	42	1.88	ns	-0.1251±0.0041	-0.1332±0.006	ns
PDOF	0.68	42	2.09	ns	-0.2304±0.019	-0.249±0.013	ns
PDC	1	42	4.86	<0.05	-0.1229±0.01	-0.1128±0.005	0.033
MLC	0.6	42	0.069	ns	-0.2394±0.011	0.2414±0.008	ns
PDT	0.67	42	2.15	ns	-0.0717±0.0084	-0.0634±0.0057	ns
MLTR	0.66	42	1.4	ns	-0.1152±0.007	-0.1208±0.0048	ns
MLCT	0.8	42	0.042	ns	0.1268±0.0062	0.126±0.0037	ns
BB	0.83	42	1.63	ns	0.2706±0.007	0.2759±0.004	ns
GTH	0.87	42	11.7	<0.0001	0.1399±0.008	0.1554±0.0045	0.0014
HHI	0	42	7.72	<0.01	0.0391±0.003	0.0506±0.004	0.0081
AME	0.83	42	13.9	<0.0001	-0.2033±0.018	-0.1647±0.01	0.00057

Table 2.5c. Results for phylogenetic ANOVAs for humerus by locomotor group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
HL	1	49	2.61	0.0621	1.03996±0.033	1.112±0.045	1.0266±0.009	ns	ns	0.065
MLHH §	0	49	26.3	<0.0001	0.0789±0.002	0.1329±0.007	0.0864±0.004	<0.0001	0.042	<0.0001
SIHH	0.98	49	7.82	<0.001	0.0603±0.011	0.0119±0.016	0.0576±0.003	0.00041	ns	0.00026
MGT §	0.95	49	2.25	ns	0.0471±0.014	0.0322±0.019	0.0553±0.004	ns	0.0625	0.24
MLT	0.95	49	19.8	<0.0001	-0.131±0.022	-0.308±0.03	-0.1182±0.007	<0.0001	0.061	<0.0001
BGW	0.9	49	6.53	<0.001	-0.4248 ±0.038	-0.6143±0.052	-0.4274±0.013	0.00071	ns	0.00091
MLOF §	0.97	49	1.26	ns	-0.0926±0.024	-0.1284±0.033	-0.1014±0.007	ns	ns	ns
PDOF	1	49	1.4	ns	-0.2253±0.053	-0.245±0.072	-0.2488±0.014	ns	ns	ns
PDC §	1	49	1.78	ns	-0.1155±0.02	-0.1008±0.027	-0.1056±0.005	ns	ns	ns
MLC	0.754	49	0.09	ns	-0.22510±0.019	-0.21441±0.028	-0.22625±0.008	ns	ns	ns
PDT	1	46	1.23	ns	-0.223±0.053	-0.2426±0.078	-0.2453±0.014	ns	ns	ns
MLTR	1	49	2.86	<0.05	-0.1005 ±0.021	-0.0356±0.029	-0.1042±0.006	0.029	ns	0.022
MLCT	0.92	49	2.98	0.0404	0.139195±0.013	0.182101±0.018	0.138489±0.004	0.02	ns	0.019
BB	0.9	49	2.87	<0.05	0.3039±0.01	0.3337±0.014	0.3084±0.003	0.041	ns	0.084
GTH	1	49	5.2	<0.01	0.1533±0.017	0.1577±0.024	0.1684±0.005	ns	0.0022	ns
HHI	0.74	49	2.62	ns	0.0161±0.011	0.0123±0.017	0.0271±0.005	ns	0.029	ns
AME	0.992	49	7.82	<0.001	-0.2639±0.044	-0.3939±0.06	-0.2266±0.012	0.0336	0.0029	0.0074

Table 2.5d. Results for phylogenetic ANOVAs for humerus by locomotor group using guenon sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
HL	0.85	13	0.028	ns	1.044+0.008	1.0454+0.008	ns
MLHH	1	13	0.035	ns	0.0881+0.005	0.089+0.005	ns
SIHH §	0	13	17	<0.001	0.04914+0.003	0.03398+0.004	0.0012
MGT §	0	13	8.52	<0.01	0.04751+0.002	0.05782+0.004	0.012
MLT							
BGW	0.55	13	3.92	<0.05	-0.4107+0.015	-0.4428+0.016	0.069
MLOF							
PDOF	0.86	13	0.22	ns	-0.2018+0.022	-0.212+0.022	ns
PDC	1	13	0.013	ns	-0.1054+0.01	-0.1065+0.01	ns
MLC	0	13	0.1	ns	-0.25+0.01	-0.2456+0.014	ns
PDT	0	13	0.003	ns	-0.0313+0.005	-0.03086+0.007	ns
MLTR§	1	13	2.12	ns	-0.1065+0.007	-0.11678+0.0071	ns
MLCT	0	13	2.84	ns	0.1313+0.003	0.1235+0.005	ns
BB	0.72	13	4.03	<0.05	0.27658+0.005	0.28635+0.005	0.066
GTH							
HHI	0	13	22.7	<0.0001	0.03724+0.002	0.05311+0.003	0.00037
AME	1	13	1.8	ns	-0.1745+0.012	-0.159+0.012	ns

Table 2.5e. Results for phylogenetic ANOVAs for humerus by locomotor group using colobine sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
HL	1	11	4.44	<0.05	1.0553+0.012	1.0181+0.018	0.059
MLHH	0.75	11	0.036	ns	0.0822+0.006	0.084+0.01	ns
SIHH	0.55	11	2.35	ns	0.0417+0.004	0.0543+0.008	ns
MGT	1	11	0.34	ns	0.0484+0.008	0.0414+0.012	ns
MLT	0.54	11	0.52	ns	-0.1224+0.007	-0.1126+0.014	ns
BGW	0	11	1.06	ns	-0.4933+0.011	-0.4637+0.029	ns
MLOF	0.94	11	2.69	ns	-0.1019+0.01	-0.0755+0.016	ns
PDOF	0.6	11	0.076	ns	-0.2107+0.021	-0.2211+0.038	ns
PDC	0	11	0.53	ns	-0.0965+0.004	-0.09+0.009	ns
MLC	0	11	0.53	ns	-0.2004+0.006	-0.2121+0.016	ns
PDT	1	11	3.97	0.0504	-0.06359+0.009	-0.03595+0.014	0.072
MLTR	0	11	0.013	ns	-0.08202+0.005	-0.0805+0.013	ns
MLCT §	0	11	0.089	ns	0.1655+0.004	0.1655+0.011	ns
BB	0.29	11	9.04	<0.01	0.30671+0.002	0.29156+0.005	0.012
GTH	0.06	11	8.79	<0.01	0.15651+0.004	0.18566+0.01	0.013
HHI	0.09	11	0.94	ns	0.04+0.005	0.0296+0.011	ns
AME	0	11	5.6	<0.05	-0.2408+0.01	-0.1823+0.025	0.037

Table 2.5f. Results for phylogenetic ANOVAs for humerus by locomotor group using papionin sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
HL	0.47	14	1.13	ns	1.0393+0.013	1.0265+0.012	ns
MLHH	0	14	4.33	<0.05	0.0724+0.006	0.0871+0.007	0.056
SIHH	0.71	14	0.23	ns	0.0344+0.005	0.0365+0.004	ns
MGT	0	14	0.96	ns	0.0462+0.006	0.053+0.007	ns
MLT	0.73	14	3.12	0.0756	-0.1029+0.013	-0.0845+0.01	0.0756
BGW	0	14	0.007	ns	-0.39+0.014	-0.391+0.016	ns
MLOF	0	14	4.93	<0.05	-0.09399 +0.008	0.11535+0.01	0.043
PDOF	0	14	3.98	<0.05	-0.1948+0.015	-0.2284+0.017	0.0427
PDC	1	14	6.45	<0.05	-0.10584+0.011	-0.08664+0.008	0.024
MLC	0.06	14	0.008	ns	-0.2184+0.011	-0.217+0.012	ns
PDT	0	14	0.3	ns	-0.0374+0.009	-0.0316+0.011	ns
MLTR	0	14	0.15	ns	-0.1014+0.005	-0.1038+0.006	ns
MLCT §	0.78	14	2.48	ns	0.14+0.005	0.146+0.004	ns
BB	0.13	14	1.66	ns	0.285+0.006	0.2929+0.006	ns
GTH	1	14	3.88	<0.05	0.17422+0.011	0.18987+0.008	0.069
HHI	0.1	14	1.61	ns	0.0398+0.009	0.0522+0.01	ns
AME	0.54	14	5.56	<0.05	-0.1501+0.018	-0.1122+0.016	0.033

Table 2.6a. Results for standard ANOVAs for humerus by locomotor group using cercopithecoid-only dataset and Coding 1

Variable	**F**	**df**	**overall p**	**arboreal mean**	**semi-t mean**	**terrestrial mean**	**arb-semi**	**arb-ter**	**semi-ter**
HL	2.62	41	0.085	1.0472±0.004	1.03251±0.006	1.0301±0.017	0.045	ns	ns
MLHH	2.17	41	ns	0.0811±0.003	0.0848±0.002	0.0934±0.005	ns	0.051	ns
SIHH	4.3	41	<0.05	0.0434±0.002	0.0337±0.002	0.0402±0.006	0.0055	ns	ns
MGT	3.1	41	0.056	0.0451±0.003	0.0534±0.002	0.0572±0.006	0.043	0.076	0.058
MLT	7.33	41	<0.01	-0.1102±0.005	-0.0917±0.005	-0.066±0.013	0.0199	0.0013	0.059
BGW	3.79	41	<0.05	-0.4465±0.012	-0.4135±0.009	-0.388±0.021	0.042	0.031	ns
MLOF	2.35	41	ns	-0.1011±0.004	-0.1088±0.005	-0.1215±0.015	ns	0.051	ns
PDOF	2.21	41	ns	-0.2099±0.009	-0.2206±0.008	-0.2521±0.008	ns	0.045	ns
PDC	3.91	41	<0.05	-0.1016±0.002	-0.0944±0.005	-0.0776±0.012	ns	0.01	0.076
MLC	0.83	41	ns	-0.22±0.006	-0.2307±0.008	-0.2151±0.013	ns	ns	ns
PDT	5.32	41	<0.01	0.049±0.004	-0.0296±0.005	-0.0325±0.01	0.0031	ns	ns
MLTR	5.31	41	<0.01	-0.092±0.03	-0.1088±0.004	-0.10285±0.009	0.0025	ns	ns
MLCT	2.19	41	ns	0.1491±0.004	0.1377±0.004	0.1457±0.005	0.043	ns	ns
BB	0.11	41	ns	0.2923±0.003	0.2902±0.003	0.2918±0.008	ns	ns	ns
GTH	12.3	41	<0.0001	0.1633±0.003	0.1764±0.005	0.2045±0.013	0.0158	<0.0001	0.0033
HHI	6.19	41	<0.01	0.03818±0.03	0.05182±0.003	0.0539±0.011	0.0027	0.034	ns
AME	27.3	41	<0.0001	-0.2053±0.008	-0.1395±0.006	-0.0873±0.021	<0.0001	<0.0001	0.014

Table 2.6b. Results for standard ANOVAs for humerus by locomotor group using cercopithecoid-only dataset and Coding 2

Variable	F	df	overall p	arboreal mean	terrestrial mean
HL	4.7	41	<0.05	1.04714±0.004	1.03282±0.05
MLHH	2.33	41	ns	0.08106±0.003	0.08636±0.002
SIHH	3.37	41	0.073	0.04238±0.002	0.03647±0.002
MGT	3.2	41	0.081	0.04597±0.003	0.0528±0.002
MLT	6.91	41	<0.05	-0.10903±0.005	-0.08898±0.006
BGW	4.12	41	<0.05	-0.44374±0.012	-0.41317±0.009
MLOF	1.34	41	ns	-0.1025±0.003	-0.10925±0.005
PDOF	1.45	41	ns	-0.21088±0.009	-0.22496±0.007
PDC	3.59	41	0.065	-0.10145±0.002	-0.09168±0.005
MLC	0.38	41	ns	-0.22088±0.006	-0.22631±0.007
PDT	7.17	41	<0.05	-0.04801±0.004	-0.03214±0.004
MLTR	6.96	41	<0.05	-0.09282±0.004	-0.106±0.003
MLCT	1.71	41	ns	0.1479±0.004	0.1411±0.004
BB	0.25	41	ns	0.29249±0.003	0.29044±0.002
GTH	15.4	41	<0.0001	0.16206±0.002	0.18242±0.005
HHI	7.66	41	<0.01	0.03909±0.03	0.05055±0.003
AME	31.7	41	<0.0001	-0.20425±0.009	-0.13387±0.009

Table 2.6c. Results for standard ANOVAs for humerus by locomotor group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**F**	**df**	**overall p**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
HL	1.57	48	ns	1.0442±0.004	1.0335±0.013	1.0328±0.005	ns	0.089	ns
MLHH	26.3	49	<0.0001	0.0789±0.003	0.1329±0.007	0.0864±0.002	<0.0001	0.042	<0.0001
SIHH	38.1	48	<0.0001	0.047±0.003	0.1084±0.006	0.0365±0.002	<0.0001	0.0094	<0.0001
MGT	2.89	49	0.065	0.0462±0.002	0.0339±0.021	0.0528±0.002	ns	ns	0.036
MLT	69.7	49	<0.001	-0.1165±0.006	-0.2956±0.018	-0.089±0.006	<0.0001	0.0015	<0.0001
BGW	22.2	49	<0.001	-0.4361±0.011	-0.6261±0.024	-0.4132±0.009	<0.0001	ns	<0.0001
MLOF	2.97	49	0.06	-0.0989±0.005	-0.1305±0.02	-0.1093±0.005	0.034	ns	ns
PDOF	0.26	49	ns	-0.2166±0.012	-0.2331±0.008	-0.225±0.007	ns	ns	ns
PDC	3.31	49	<0.05	-0.1068±0.003	-0.0951±0.022	-0.0917±0.005	ns	0.014	ns
MLC	0.38	49	ns	-0.2234±0.005	-0.2108±0.019	-0.2263±0.007	ns	ns	ns
PDT	5.52	48	<0.01	-0.0547±0.005	-0.0425±0.01	-0.0321±0.004	ns	0.0017	ns
MLTR	17.1	49	<0.0001	-0.0953±0.005	-0.0309±0.004	-0.106±0.003	<0.0001	0.081	<0.0001
MLCT	9.14	49	<0.001	0.1444±0.004	0.188±0.005	0.1411±0.004	0.00021	ns	<0.0001
BB	8.52	49	<0.001	0.2964±0.003	0.3281±0.002	0.2904±0.002	0.00093	ns	<0.0001
GTH §	11.8	49	<0.0001	0.1589±0.002	0.1625±0.003	0.1824±0.005	ns	<0.0001	0.063
HHI	7.66	48	<0.001	0.0336±0.003	0.0248±0.006	0.0506±0.003	ns	0.00089	0.0144
AME	29.97	48	<0.0001	-0.2188±0.011	-0.3514±0.06	-0.1339±0.009	<0.0001	<0.0001	0.0001

Table 2.7a. Results for phylogenetic ANOVAs for humerus by phylogenetic group using cercopithecoid-only dataset

Variable	**Lambda**	**df**	**F**	**model p-value**	**Colobine mean**	**Guenon mean**	**Papionin mean**	**col-guen**	**col-pap**	**guen-pap**
HL	0.00	41	5.46	<0.01	1.0507±0.006	1.0457±0.008	1.02688	ns	0.0038	0.016
MLHH	0.00	41	0.72	ns	0.0809±0.003	0.0862±0.004	0.0834±0.004	ns	ns	ns
SIHH	0.95	41	0.23	ns	0.0438±0.009	0.0415±0.014	0.0363±0.013	ns	ns	ns
MGT	0.00	41	2.21	ns	0.0431±0.003	0.0523±0.005	0.0513±0.005	0.06	0.089	ns
MLT	0.83	41	1.17	ns	-0.1241±0.016	-0.0918±0.024	-0.0882±0.024	ns	ns	ns
BGW	0.00	41	34.00	<0.0001	-0.4888±0.009	-0.4186±0.012	-0.3907±0.012	<0.0001	<0.0001	0.021
MLOF	0.00	41	0.72	ns	-0.1013±0.005	-0.105±0.007	-0.11±0.007	ns	ns	ns
PDOF	0.54	41	0.08	ns	-0.2114±0.023	-0.2151±0.034	-0.2228±0.034	ns	ns	ns
PDC	1.00	41	0.47	ns	-0.094±0.015	-0.1061±0.024	0.0903±0.023	ns	ns	ns
MLC	0.00	41	15.30	<0.0001	-0.2022±0.006	-0.2479±0.009	-0.2178±0.008	<0.0001	0.07	0.00057
PDT	0.00	41	12.90	<0.0001	-0.0604±0.005	-0.0914±0.006	-0.033±0.006	<0.0001	<0.0001	ns
MLT	0.00	41	16.00	<0.0001	-0.0818±0.004	-0.1098±0.005	-0.1032±0.005	<0.0001	0.00013	ns
MLCT	0.00	41	40.90	<0.0001	0.1628±0.003	0.1277±0.004	0.14584±0.004	<0.0001	<0.0001	<0.0001
BB	0.00	41	20.90	<0.0001	0.3043±0.003	0.2805±0.004	0.2914±0.004	<0.0001	0.00095	0.0034
GTH	1.00	41	1.03	ns	0.1617±0.016	0.1656±0.024	0.1869±0.024	ns	ns	ns
HHI	0.00	41	2.36	0.0853	0.03812±0.004	0.0447±0.005	0.0497±0.005	ns	0.036	ns
AME	0.50	41	8.58	<0.001	-0.2321±0.018	-0.1651±0.028	-0.1208±0.027	0.02	0.0002	0.039

Table 2.7b. Results for phylogenetic ANOVAs for humerus by phylogenetic group using entire anthropoid dataset

Variable	Lambda	df	F	p-value (overall)	cerc mean	col mean	hom mean	plat mean	cerc-col	cerc-hom	cerc-plat	col-hom	col-plat	hom-plat
HL	1.00	46	0.96	ns	1.0364±0.051	1.0537±0.037	1.1168±0.052	1.0313±0.071	ns	ns	ns	ns	ns	ns
MLHH	0.00	48	19.10	<0.0001	0.0847±0.002	0.0807±0.004	0.1329±0.007	0.0691±0.006	ns	<0.0001	0.01	<0.0001	0.071	<0.0001
SIHH	0.94	48	7.03	<0.001	0.0388±0.016	0.0438±0.011	0.1091±0.016	0.0785±0.021	ns	<0.0001	0.069	0.00016	ns	ns
MGT	0.00	47	2.22	0.08121	0.0518±0.003	0.0428±0.005	0.0339±0.009	0.0474±0.007	0.07	0.043	ns	ns	0.56	ns
MLT	0.9	48	15.2	<0.0001	-0.0898±0.03	-0.1241±0.022	-0.2976±0.031	-0.15±0.042	ns	<0.0001	ns	<0.0001	ns	0.00099
BGW	0.00	48	42.50	<0.0001	-0.4042±0.007	-0.4888±0.013	-0.6261±0.023	-0.4008±0.018	<0.0001	<0.0001	ns	<0.0001	<0.0001	<0.0001
MLOF	0.00	48	0.85	<0.05	-0.1076±0.004	-0.1013±0.008	-0.1305±0.014	-0.0826±0.011	ns	ns	0.031	0.057	ns	0.0071
PDOF	1.00	48	0.03	ns	-0.2154±0.083	-0.2151±0.06	-0.2336±0.084	-0.246±0.113	ns	ns	ns	ns	ns	ns
PDC	1.00	48	0.30	ns	-0.0979± 0.031	-0.094±0.023	-0.0923±0.032	-0.131±0.043	ns	ns	ns	ns	ns	ns
MLT	0.63	47	1.23	ns	-0.2335±0.023	-0.2021±0.018	-0.2101±0.026	-0.234±0.032	0.08125	ns	ns	ns	ns	ns
PDT	0.00	48	23.80	<0.0001	-0.0321±0.003	-0.0604±0.006	-0.0425±0.012	-0.1057±0.009	<0.0001	ns	<0.0001	ns	<0.0001	<0.0001
MLTR	0.99	47	2.25	0.07801	-0.1086±0.032	-0.0812±0.024	-0.0313±0.033	-0.1083±0.044	ns	0.021815	ns	ns	ns	0.087
MLCT	0.69	48	6.89	<0.001	0.1365±0.013	0.16274±0.01	0.1879±0.014	0.1284±0.018	0.00864	0.00056	ns	0.079	0.0595	0.00228
BB	0.55	48	6.42	<0.001	0.2863±0.009	0.3043±0.007	0.3382±0.01	0.327±0.012	0.01204	0.00017	0.02787	0.026	ns	ns
GTH	1.00	48	0.31	ns	0.1767±0.029	0.1617±0.021	0.1629±0.029	0.144±0.04	ns	ns	0.41	ns	ns	ns
HHI	0.00	48	19.90	<0.0001	0.0473±0.003	0.0381±0.005	0.0024±0.009	-0.008±0.007	0.074	0.018	<0.0001	ns	<0.0001	0.0047
AME	0.97	48	4.03	<0.05	-0.1414±0.065	-0.2319±0.047	-0.3596±0.066	-0.3255±0.089	0.0615	0.0019	0.0446	0.06	ns	ns

Table 2.8a. Between group PCA on humerus using cercopithecoid-only sample and Coding 1

	PC 1	**PC 2**	**PC 3**
Standard Deviation	1.794	0.329	1.70E-16
Proportion of Variance	0.968	0.032	0
Cumulative Proportion	0.968	1	1
Loadings			
width of lesser tubercle (MLT)	-0.458	-0.162	0.725
height of greater tubercle (GTH)	-0.581	-0.573	-0.567
humeral head index (HHI)	-0.293	0.738	-0.353
angle of medial epicondyle (AME)	-0.605	0.317	0.166

Table 2.8b. Between group PCA on humerus using cercopithecoid-only sample and Coding 2

	PC 1	**PC 2**
Standard Deviation	1.496	0
Proportion of Variance	1	0
Cumulative Proportion	1	1
Loadings		
width of greater tubercle (MGT)	0.249	-0.352
width of lesser tubercle (MLT)	0.352	0.901
height of capitulum (PDC)	0.263	-0.074
height of greater tubercle (GTH)	0.484	-0.136
humeral head index (HHI)	0.367	-0.103
angle of medial epicondyle (AME)	0.613	-0.173

Table 2.8c. Between group PCA on humerus using entire anthropoid sample

	PC 1	**PC 2**	**PC 3**
Standard Deviation	3.803	0.804	4.53E-16
Proportion of Variance	0.957	0.043	0
Cumulative Proportion	0.957	1	0
Loadings			
width of humeral head (MLHH)	0.429	0.525	-0.561
height of humeral head (SIHH)	0.461	-0.073	0.718
width of lesser tubercle (MLT)	-0.541	-0.008	-0.035
width of biciptal groove (BGW)	-0.438	-0.058	0.007
height of greater tubercle (GTH)	-0.080	0.683	0.334
angle of medial epicondyle (AME)	-0.334	0.499	0.239

Table 2.9a. Results for phylogenetic PCA of the femur using cercopithecoid-only sample. Lambda = 0.43

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**
Proportion of Variance	26.7711	14.4022	12.8511	8.6479	7.4477	7.0248	4.9660	4.6830	3.8540	3.0521	2.2772	1.7905	1.5499	0.4861	0.1965
Loadings															
FL	0.3967	-0.2073	0.1680	-0.6110	0.0624	-0.3532	0.3341	-0.2026	0.1110	-0.1599	0.1403	0.1474	0.1890	0.0119	-0.0413
APFH	-0.8966	-0.0590	-0.0071	-0.0902	0.1567	-0.1054	0.1270	0.1552	0.0803	0.1964	-0.1485	-0.0671	0.0868	-0.1587	-0.0650
PDFH	-0.8633	-0.0564	0.0657	-0.2357	0.1220	-0.0559	0.2673	0.1999	0.0623	0.0870	0.0021	-0.1425	-0.0516	0.1664	0.0101
PDLT	-0.3234	-0.2410	-0.0292	-0.0128	0.2081	0.8100	-0.1625	0.0255	-0.1894	-0.1970	0.0668	0.0664	0.0932	0.0645	-0.1162
APMC	-0.3068	0.6191	-0.4235	0.2152	0.0041	0.0898	0.2307	-0.1496	-0.1524	0.3228	0.0706	0.2594	0.1105	0.0356	0.0098
PDMC	-0.3103	0.7669	0.2540	-0.1277	-0.2039	-0.1544	-0.2185	0.1899	-0.0397	-0.0678	0.2758	-0.0487	0.0002	-0.0184	-0.0247
MLMC	0.1009	-0.6038	-0.4697	-0.0493	-0.4504	-0.2744	-0.1733	0.1932	-0.1488	0.1615	0.0622	0.0439	-0.0112	0.0325	-0.0398
APLC	0.4785	0.3604	-0.5477	0.1331	-0.0598	-0.0911	0.2580	-0.3367	-0.1241	-0.0340	0.0120	-0.3263	-0.0628	0.0069	-0.0669
PDLC	0.6238	0.5434	0.0206	0.0101	-0.1063	-0.1223	0.0101	0.3503	-0.0280	-0.1055	-0.3655	0.0457	0.1182	0.0602	-0.0303
MLLC	0.3752	-0.0589	0.1187	0.5149	0.5142	-0.3172	-0.2488	-0.0044	0.3238	0.1623	0.0994	0.0050	0.0390	0.0653	-0.0523
BCB	-0.6780	0.0777	-0.3257	0.2636	-0.3032	-0.0758	0.0744	-0.0898	0.3589	-0.2771	-0.0508	0.1480	-0.1288	0.0072	-0.0261
PH	0.4167	0.2414	0.2782	-0.5164	-0.2287	0.2806	-0.1342	-0.1974	0.2736	0.3286	-0.1018	0.0474	-0.1960	0.0182	-0.0421
PW	0.0345	-0.1331	0.7875	0.3543	-0.0901	-0.1565	0.2852	-0.0063	-0.2797	0.0182	-0.0102	0.0974	-0.1774	-0.0017	-0.0430
FNA	-0.4237	-0.1205	0.5100	0.2527	-0.5124	0.0210	-0.1208	-0.3267	0.0615	0.0627	-0.0778	-0.1223	0.2588	0.0439	0.0057
ACON	0.6030	-0.1112	0.0526	0.2439	-0.2707	0.3596	0.3686	0.3302	0.2667	0.0705	0.1728	-0.0582	0.0633	-0.0307	0.0046

Table 2.9b. Results for phylogenetic PCA of the femur using the entire anthropoid sample. Lambda = 0.68

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**
Proportion of Variance	29.1693	16.4550	12.5702	10.2042	8.8520	4.9886	4.3284	3.2381	2.8771	2.6786	1.6384	1.2690	1.1619	0.3785	0.1908
Loadings															
FL	0.5660	-0.4920	-0.3411	0.1430	-0.2201	0.3597	-0.0153	-0.0028	-0.1690	0.1135	-0.1992	-0.1120	0.1665	-0.0030	0.0375
APFH	-0.8553	-0.0409	-0.1277	0.2771	0.0196	0.1623	-0.2914	-0.0234	0.1016	-0.1364	0.0692	0.0506	0.0564	0.1319	0.0680
PDFH	-0.8224	-0.1052	-0.2437	0.3225	-0.0482	0.1050	-0.3078	0.0265	0.0948	-0.0313	-0.0015	-0.0638	-0.0385	-0.1573	-0.0143
PDLT	0.0092	-0.2753	-0.0382	-0.0912	0.8765	-0.2475	0.0764	-0.0422	0.1947	0.1403	-0.0415	-0.0732	0.0709	-0.0386	0.0775
APMC	-0.1471	0.7787	-0.0025	0.1748	0.3339	0.1616	0.1786	0.2405	-0.0338	-0.2564	-0.1936	0.0455	0.0850	-0.0162	-0.0094
PDMC	-0.5435	0.5302	-0.3466	-0.0033	-0.3739	-0.1754	0.2470	-0.1564	0.1167	0.0877	-0.0947	-0.1245	-0.0230	0.0144	0.0263
MLMC	0.0691	-0.2812	0.7331	0.5200	-0.2307	-0.0909	0.1604	-0.0397	0.0942	-0.0841	-0.0466	-0.0031	0.0135	-0.0204	0.0269
APLC	0.6247	0.5552	0.1089	0.1676	0.0312	0.2482	0.0370	0.1938	-0.1211	-0.0031	0.2631	-0.2178	-0.1494	-0.0194	0.0778
PDLC	0.5934	0.4812	-0.1516	-0.0469	-0.3657	0.0052	-0.0072	0.0990	0.2821	0.1377	0.1944	0.2078	0.2493	-0.0687	0.0326
MLLC	0.0308	0.2557	0.4969	-0.7125	-0.1053	0.1842	-0.2018	-0.2388	0.0344	-0.1494	-0.0951	-0.0166	0.0027	-0.0415	0.0422
BCB	-0.7062	0.3343	0.3470	0.0936	0.0478	-0.0302	-0.0384	-0.0157	-0.3631	0.3235	-0.0241	0.1288	0.0124	-0.0225	0.0329
PH	0.5918	0.0310	-0.5270	0.2718	0.0257	-0.2338	-0.0018	-0.3072	-0.2240	-0.2570	0.0084	0.1493	-0.0664	-0.0454	0.0490
PW	-0.3549	-0.5367	-0.1654	-0.4346	-0.3150	-0.1669	0.1157	0.4376	-0.0307	-0.0934	-0.0695	0.0900	-0.1005	-0.0232	0.0677
FNA	-0.6831	-0.1962	0.0781	-0.2431	-0.0640	-0.2979	0.1219	-0.0018	-0.3006	-0.2547	0.2273	-0.1815	0.2853	-0.0230	-0.0158
ACON	0.5683	0.3510	0.1058	0.1100	-0.1221	-0.4761	-0.4807	0.1733	-0.0314	0.0181	-0.1261	-0.0934	0.0328	0.0287	-0.0007

Table 2.10a. Results for phylogenetic ANOVAs for femur by locomotor group using cercopithecoid-only sample and coding 1. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	Lambda	df	F	p-value (overall)	arboreal mean	semi-t mean	terrestrial mean	arb-semi	arb-ter	semi-ter
FL	0.63	41	2.58	0.067	1.0076±0.01	0.9961±0.007	0.9808±0.013	ns	0.04615	ns
APFH	0.31	41	1.00	ns	-0.0655±0.004	-0.0668±0.005	-0.0566±0.007	ns	ns	ns
PDFH	0.00	41	1.97	ns	-0.0807±0.002	-0.0846±0.004	-0.0712±0.007	ns	ns	0.057
PDLT	0.82	41	0.69	ns	-0.2911±0.015	-0.2817±0.01	-0.2889±0.15	ns	ns	ns
APMC	0.40	41	0.95	ns	0.0877±0.004	0.0923±0.003	0.0925±0.006	ns	ns	ns
PDMC	0.00	41	0.39	ns	-0.0389±0.002	-0.0406±0.003	-0.0363±0.005	ns	ns	ns
MLMC	0.00	41	0.18	ns	-0.259±0.026	-0.2837±0.041	-0.2748±0.069	ns	ns	ns
APLC	0.65	41	1.99	ns	0.0827±0.006	0.092±0.009	0.0855±0.008	0.059	ns	ns
PDLC	0.58	41	0.37	ns	-0.0242±0.004	0.0213±0.003	-0.0214±0.005	ns	ns	ns
MLLC §	0.69	41	1.87	ns	-0.356±0.01	-0.3548±0.007	-0.35604±0.011	0.084	ns	ns
BCB	0.54	41	1.23	ns	0.1714±0.004	0.1805±0.003	0.1802±0.006	ns	ns	ns
PH	0.44	41	3.08	ns	-0.0501±0.007	-0.063±0.006	0.072±0.01	0.052	0.042	ns
PW	0.70	40	0.04	ns	-0.1463±0.007	-0.1448±0.005	-0.1473±0.008	ns	ns	ns
API §	0.00	41	0.36	ns	0.0146±0.009	0.003±0.014	0.0142±0.024	ns	ns	ns
PDI	0.29	41	0.88	ns	-0.015±0.004	-0.0187±0.004	-0.0108±0.007	ns	ns	ns
MLI §	0.00	41	0.20	ns	0.1055±0.031	0.0695±0.048	0.0948±0.081	ns	ns	ns
FNA	0.48	41	2.70	0.0593	0.2518±0.003	0.2131±0.002	0.25±0.004	0.06	ns	0.092
ACON	0.12	41	1.67	ns	0.1874±0.002	0.1848±0.004	0.1806±0.004	ns	0.092	ns

Table 2.10b. Results for phylogenetic ANOVAs for femur by locomotor group using cercopithecoid-only sample and coding 2. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	Lambda	df	F	model p-value	Arboreal mean	Terrestrial Mean	arb-ter
FL	0.66	42	7.16	<0.01	1.009±0.01	0.9907±0.007	0.011
APFH	0.37	42	0.01	ns	-0.0654±0.005	-0.0649±0.004	ns
PDFH	0.27	42	0.38	ns	-0.0803±0.004	-0.0827±0.004	ns
PDLT	0.86	42	0.52	ns	-0.291±0.016	0.2975±0.009	ns
APMC	0.42	42	1.48	ns	0.0878±0.004	0.0917±0.003	ns
PDMC	0.00	42	0.11	ns	-0.0388±0.002	-0.0397±0.003	ns
MLMC	0.00	42	0.36	ns	-0.2586±0.026	-0.2814±0.038	ns
APLC	0.68	42	2.73	0.0769	0.0826±0.007	0.09±0.004	ns
PDLC	0.58	42	0.51	ns	-0.0241±0.004	-0.0219±0.003	ns
MLLC §	0.67	42	3.23	<0.05	-0.3573±0.009	-0.3458±0.006	0.079
BCB	0.36	42	0.93	ns	0.1717±0.004	0.1748±0.003	ns
PH	0.58	42	4.42	<0.05	-0.0503±0.008	-0.063±0.006	0.041
PW	0.74	42	0.10	ns	-0.1463±0.007	-0.1445±0.005	ns
API §	0.33	41	0.07	ns	-0.016±0.004	-0.017±0.004	ns
PDI	0.00	42	0.58	ns	0.0151±0.009	-0.0051±0.013	ns
MLI §	0.00	42	0.05	ns	0.1078±0.031	0.0777±0.045	ns
FNA	0.46	42	0.94	ns	0.2515±0.003	0.2493±0.002	ns
ACON	0.12	42	1.97	ns	0.1874±0.002	0.1842±0.002	ns

Table 2.10c. Results for phylogenetic ANOVAs for femur by locomotor group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation)

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
FL	1.00	49	4.04	<0.05	1.0107±0.031	0.9599±0.043	0.9883±0.008	ns	ns	ns
APFH	0.49	49	4.70	<0.01	-0.0667±0.007	-0.0298±0.012	-0.06584±0.005	0.0036	ns	0.0052
PDFH	0.00	49	8.04	<0.001	-0.082±0.003	0.0487±0.008	-0.0816±0.004	0.00026	ns	0.00036
PDLT	0.97	49	0.26	ns	-0.2784±0.032	-0.2708±0.045	-0.2849±0.01	ns	ns	ns
APMC	0.57	49	2.18	ns	0.09±0.006	0.0742±0.01	0.0939±0.003	ns	ns	0.054
PDMC	0.00	49	0.88	ns	-0.0393±0.002	0.0308±0.007	-0.0397±0.003	ns	ns	ns
MLMC	0.00	49	0.13	ns	-0.2681±0.022	-0.2499±0.072	-0.2814±0.034	ns	ns	ns
APLC	0.81	49	8.63	<0.001	0.0798±0.012	0.0191±0.017	0.0873±0.005	0.00064	ns	0.00018
PDLC	0.74	49	8.58	<0.001	-0.0342±0.007	-0.0747±0.01	-0.0315±0.003	0.00025	ns	0.000125
MLLC §	0.91	49	1.25	ns	-0.3544±0.022	-0.352±0.031	-0.343±0.007	ns	ns	ns
BCB	0.89	49	1.71	ns	0.1765±0.011	0.2015±0.016	0.1805±0.004	ns	ns	ns
PH	0.94	49	2.36	0.083	-0.0390±0.024	-0.0915±0.033	-0.0507±0.007	ns	ns	ns
PW	0.97	49	3.46	<0.05	-0.1529±0.019	-0.2203±0.026	-0.1516±0.005	0.011	ns	0.0136
API §	0.00	49	1.88	ns	0.0151±0.008	0.05311±0.025	0.0051±0.012	ns	ns	0.062
PDI	0.73	49	6.52	<0.001	-0.0059±0.01	0.0427±0.014	-0.0092±0.004	0.0012	ns	0.00071
MLI §	0.00	49	0.11	ns	0.0957±0.026	0.1006±0.084	0.0776±0.04	ns	ns	ns
FNA	0.84	49	11.90	<0.0001	0.2575±0.007	0.3039±0.01	0.2553±0.003	0.0001	ns	0.0001
ACON	0.33	49	7.84	<0.001	0.1839±0.003	0.1605±0006	0.1815±0.002	0.00026	ns	0.00115

Table 2.10d. Results for phylogenetic ANOVAs for femur by locomotor group using guenon sample. § indicates analyses that did not meet the assumption of normality (see text for explanation)

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
FL	0	13	1.35	ns	1.014+0.004	1.0078+0.005	ns
APFH	0	13	2.3	ns	-0.0716+0.004	-0.0801+0.006	ns
PDFH	0	13	7.38	<0.01	-0.0806+0.004	-0.0953+0.005	0.018
PDLT	0.92	13	0.25	ns	-0.2601+0.014	-0.267+0.014	ns
APMC	0	13	0.25	ns	0.0971+0.003	0.0991+0.004	ns
PDMC	0.86	13	0.92	ns	-0.0402+0.006	-0.0459+0.006	ns
MLMC	0	13	0.72	ns	-0.3024+0.005	-0.2969+0.007	ns
APLC §	0	13	3.89	<0.05	0.0937+0.005	0.1089+0.008	0.07
PDLC	1	13	0.35	ns	-0.0281+0.006	-0.0246+0.006	ns
MLLC	0	13	3.83	<0.05	-0.3784+0.006	-0.03615+0.009	0.072
BCB	0	13	0.2	ns	0.175+0.003	0.1735+0.003	ns
PH	0	13	0.003	ns	-0.0526+0.006	-0.05208+0.009	ns
PW	0.56	13	0.12	ns	-0.1572+0.007	-0.1544+0.008	ns
API	0	13	1.21	ns	0.0391+0.026	-0.0097+0.038	ns
PDI	0	13	2.76	ns	-0.0121+0.006	-0.02112+0.005	ns
MLI	0	13	1.71	ns	0.0771+0.006	0.0653+0.009	ns
FNA	1	13	1.69	ns	0.2449+0.003	0.2408+0.003	ns
ACON	1	13	0.003	ns	0.1839+0.003	0.184+0.003	ns

Table 2.10e. Results for phylogenetic ANOVAs for femur by locomotor group using colobine sample. § indicates analyses that did not meet the assumption of normality (see text for explanation)

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
FL	0.79	11	1.09	ns	1.0104+0.01	0.9961+0.016	ns
APFH §	0.37	11	0.45	ns	-0.0655+0.003	-0.06149+0.006	ns
PDFH	0.39	11	0.107	ns	-0.0824+0.003	-0.0802+0.007	ns
PDLT	0	11	0.27	ns	-0.3223+0.009	-0.22265+0.022	ns
APMC	0.32	11	0.006	ns	0.08356+0.004	0.0842+0.008	ns
PDMC	0	11	0.4	ns	-0.0401+0.003	-0.0366+0.007	ns
MLMC	0	11	0.11	ns	-0.218+0.072	-0.2789+0.18	ns
APLC	0	11	0.078	ns	0.0803+0.003	0.0826+0.008	ns
PDLC	0	11	0.58	ns	-0.0201+0.002	-0.0154+0.006	ns
MLLC	0.56	11	0.41	ns	-0.3391+0.009	-0.3293+0.015	ns
BCB	0.8	11	0.96	ns	0.1702+0.003	0.1759+0.006	ns
PH	0	11	0.5	ns	-0.0435+0.003	-0.0492+0.008	ns
PW	0.38	11	0.00004	ns	-0.143+0.004	-0.143+0.008	ns
API	0.2	11	0.21	ns	0.0035+0.003	0.0002+0.007	ns
PDI	0	11	0.001	ns	-0.0197+0.002	-0.0195+0.006	ns
MLI	0	11	0.13	ns	0.1367+0.086	0.0576+0.22	ns
FNA	0	11	0.085	ns	0.254+0.002	0.2555+0.005	ns
ACON	0	11	1.84	ns	0.191+0.002	0.1842+0.005	ns

Table 2.10f. Results for phylogenetic ANOVAs for femur by locomotor group using papionin sample

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
FL	0.41	14	3.02	ns	1.002+0.015	0.9769+0.015	ns
APFH	0	14	0.42	ns	-0.0609+0.007	-0.0554+0.008	ns
PDFH	0	14	0.41	ns	-0.0789+0.006	-0.0742+0.007	ns
PDLT	0	14	2.17	ns	-0.2472+0.01	-0.2644+0.012	ns
APMC	0	14	0.98	ns	0.0877+0.005	0.0937+0.006	ns
PDMC	0	14	0.14	ns	-0.0403+0.004	-0.0384+0.005	ns
MLMC	0.08	14	1.06	ns	-0.289+0.009	-0.2733+0.01	ns
APLC	0	14	0.8	ns	0.0741+0.005	0.0794+0.006	ns
PDLC	0	14	0.43	ns	-0.0337+0.005	-0.0302+0.006	ns
MLLC	0	14	1.19	ns	-0.3715+0.009	-0.36+0.01	ns
BCB	0.74	14	2.48	ns	0.1633+0.009	0.1743+0.007	ns
PH	0.42	14	5.24	<0.05	-0.0582+0.011	-0.0825+0.01	0.03817
PW	1	14	0.33	ns	-0.1426+0.011	-0.1419+0.008	ns
API	0.13	14	0.05	ns	0.0122+0.007	0.0138+0.007	ns
PDI	0	14	0.03	ns	-0.0064+0.008	-0.0078+0.009	ns
MLI	0.22	14	0.006	ns	0.0867+0.011	0.0876+0.012	ns
FNA	0	14	0.4	ns	0.2535+0.003	0.251+0.004	ns
ACON	0	14	0.12	ns	0.1839+0.004	0.1821+0.005	ns

Table 2.11a. Results for standard ANOVAs for femur by locomotor group using cercopithecoid-only sample and coding 1

Variable	**F**	**df**	**overall p**	**arboreal mean**	**semi-t mean**	**terrestrial mean**	**arb-semi**	**arb-ter**	**semi-ter**
FL	5.66	39	<0.01	1.0072±0.004	0.9935±0.006	0.9672±0.018	0.0753	0.0028	0.0501
APFH	1.78	39	ns	-0.0663±0.002	-0.0671±0.004	-0.0531±0.007	ns	0.082	0.076
PDFH	1.97	39	ns	-0.0807±0.002	-0.0845±0.004	-0.0712±0.006	ns	ns	0.057
PDLT	2.17	39	ns	-0.2914±0.009	-0.2787±0.008	-0.2538±0.015	ns	0.055	ns
APMC	2.12	39	ns	0.0886±0.002	0.0955±0.002	0.09372±0.004	0.05	ns	ns
PDMC	0.18	40	ns	-0.0389±0.002	-0.0385±0.002	-0.0363±0.005	ns	ns	ns
MLMC	0.144	39	ns	-0.2935±0.004	-0.2837±0.005	-0.2748±0.004	ns	0.079	ns
APLC	2.05	39	ns	0.0836±0.003	0.0928±0.005	0.0799±0.004	0.077	ns	ns
PDLC	0.61	39	ns	-0.0237±0.002	-0.0247±0.003	-0.0298±0.003	ns	ns	ns
MLLC	0.38	39	ns	-0.3584±0.005	-0.3577±0.004	-0.3684±0.009	ns	ns	ns
BCB	0.67	39	ns	0.1727±0.002	0.1757±0.003	0.17791±0.009	ns	ns	ns
PH	8.66	41	<0.001	-0.049±0.003	-0.0668±0.006	-0.08615±0.005	0.0063	0.00084	0.07618
PW	0.59	39	ns	-0.1478±0.003	-0.1483±0.004	-0.1397±0.01	ns	ns	ns
API	1.336	40	ns	0.0032±0.002	0.0029±0.004	0.0142±0.008	ns	ns	ns
PDI	0.96	39	ns	-0.0149±0.002	-0.0152±0.004	-0.0061±0.007	ns	ns	ns
MLI	2.252	40	ns	0.0654±0.006	0.07486±0.005	0.0948±0.011	ns	0.049	ns
FNA	2.95	39	0.063	0.2517±0.001	0.2465±0.002	0.2528±0.004	0.028	ns	ns
ACON	2.61	39	0.086	0.1872±0.001	0.1836±0.002	0.1797±0.005	ns	0.055	ns

Table 2.11b. Results for standard ANOVAs for femur by locomotor group using cercopithecoid-only sample and coding 2

Variable	F	df	overall p	arboreal mean	terrestrial mean
FL	8.96	42	<0.05	1.0088±0.004	0.9875±0.006
APFH	0.35	42	ns	-0.0666±0.002	-0.0641±0.004
PDFH	0.04	42	ns	-0.0809±0.002	-0.0817±0.003
PDLT	1.77	42	ns	-0.2902±0.008	-0.2758±0.007
APMC	2.91	42	0.095	0.0889±0.002	0.0944±0.002
PDMC	0.08	41	ns	-0.0388±0.002	-0.0381±0.002
MLMC	0.011	40	ns	-0.2945±0.004	-0.281±0.004
APLC	1.35	42	ns	0.08391±0.003	0.0895±0.004
PDLC	0.38	42	ns	-0.0237±0.002	-0.0256±0.003
MLLC	0.07	42	ns	-0.3599±0.005	-0.3581±0.004
BCB	1.26	42	ns	0.1726±0.002	0.1761±0.002
PH	11.5	42	<0.01	-0.0491±0.003	-0.06952±0.005
PW	0.24	42	ns	-0.1482±0.003	-0.1461±0.003
API	0.231	41	ns	0.0032±0.002	0.0051±0.003
PDI	0.11	42	ns	-0.0148±0.002	-0.0136±0.003
MLI	2.001	41	ns	0.0659±0.042	0.0776±0.005
FNA	1.47	42	ns	0.2512±0.001	0.2485±0.002
ACON	3.7	42	0.061	0.1872±0.001	0.1831±0.002

Table 2.11c. Results for standard ANOVAs for femur by locomotor group using entire anthropoid sample

Variable	**F**	**df**	**overall p**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
FL	26.11	48	<0.0001	1.0092±0.004	0.8933±0.012	0.9875±0.006	0.0001	0.0019	0.0001
APFH	8.82	49	<0.001	-0.0669±0.002	-0.0289±0.011	-0.0641±0.004	0.00011	ns	0.00038
PDFH	8.04	49	<0.001	-0.082±0.003	-0.0487±0.009	-0.0816±0.003	0.00026	ns	0.00036
PDLT	0.4	49	ns	-0.2857±0.008	-0.2786±0.012	-0.2758±0.007	ns	ns	ns
APMC	4.6	49	<0.05	0.0896±0.002	0.0737±0.013	0.09444±0.021	0.026	ns	0.0049
PDMC	0.967	48	ns	-0.0393±0.002	-0.0308±0.012	-0.0381±0.002	ns	ns	ns
MLMC	0.65	46	ns	-0.2955±0.004	-0.25±0.02	-0.281±0.004	0.00046	0.01768	0.01471
APLC	22.8	49	<0.0001	0.0828±0.003	0.0209±0.003	0.0895±0.004	0.0001	ns	0.0001
PDLC	19.2	49	<0.0001	-0.0275±0.002	-0.0693±0.003	-0.0256±0.003	0.0001	ns	0.0001
MLLC	0.17	49	ns	-0.3583±0.005	-0.3491±0.037	-0.3581±0.004	ns	ns	ns
BCB	5.58	49	<0.01	0.1744±0.002	0.2006±0.022	0.1761±0.002	0.0016	ns	0.0035
PH	9.6	49	<0.0001	-0.045±0.005	-0.1016±0.03	-0.0695±0.005	0.00086	0.00217	0.05345
PW	16.4	49	<0.0001	-0.1507±0.004	-0.0837±0.015	-0.1461±0.003	0.0001	ns	0.0001
API	19.85	47	<0.0001	0.0036±0.002	0.0531±0.011	0.00509±0.003	0.0001	ns	0.0001
PDI	22.53	48	<0.0001	-0.0134±0.002	0.0387±0.013	-0.0136±0.003	0.0001	ns	0.0001
MLI	3.06	47	0.0563	0.0646±0.006	0.1006±0.02	0.0776±0.005	0.035	ns	ns
FNA	41.5	49	<0.0001	0.2534±0.002	0.3012±0.014	0.2485±0.002	0.0001	0.074	0.0001
ACON	11.2	49	<0.0001	0.1857±0.002	0.1623±0.003	0.1831±0.002	0.0001	ns	0.00014

Table 2.12a. Results for phylogenetic ANOVAs for femur by phylogenetic group using cercopithecoid-only sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**col mean**	**guen mean**	**pap mean**	**col-guen**	**col-pap**	**guen-pap**
FL	0.00	41	10.60	<0.0001	1.0083±0.006	1.0111±0.008	0.979±0.008	ns	0.0007	0.00015
APFH	0.00	41	10.10	<0.0001	-0.0642±0.003	-0.0756±0.004	-0.0568±0.004	0.014	0.097	0.0001
PDFH	0.00	41	4.24	<0.05	-0.0812±0.003	-0.0875±0.004	-0.0754±0.004	ns	ns	0.0058
PDLT	0.00	41	26.60	<0.001	-0.3241±0.007	-0.2729±0.009	-0.2601±0.009	0.0001	0.0001	ns
APMC	0.00	41	8.44	<0.001	0.08334±0.003	0.098±0.004	0.0922±0.004	0.00019	0.01651	0.09277
PDMC	0.00	41	0.02	ns	-0.0394±0.003	-0.0395±0.004	0.0389±0.004	ns	ns	ns
MLMC	0.00	41	1.21	ns	-0.2274±0.035	0.2999±0.047	-0.2754±0.046	ns	ns	ns
APLC	0.00	41	14.70	<0.0001	0.0807±0.004	0.0605±0.005	0.0781±0.005	0.00013	ns	0.0001
PDLC	0.00	41	6.93	<0.0001	-0.0194±0.002	-0.0164±0.003	-0.0311±0.003	ns	0.0011	0.0091
MLLC §	0.00	41	8.67	<0.001	-0.3411±0.005	-0.3705±0.007	-0.3629±0.007	0.00023	0.00412	ns
BCB	0.00	41	0.74	ns	0.1717±0.003	0.169±0.004	0.1763±0.004	ns	ns	ns
PH	0.00	41	13.60	<0.0001	-0.0443±0.005	-0.0524±0.007	-0.0767±0.007	ns	0.0001	0.00042
PW	0.63	41	1.79	ns	-0.1425±0.009	-0.1582±0.013	-0.1447±0.013	ns	ns	0.076
API §	0.00	41	0.27	ns	0.0029±0.012	0.0125±0.017	0.0143±0.016	ns	ns	ns
PDI	0.00	41	4.71	<0.01	-0.0196±0.003	-0.0168±0.004	-0.0074±0.004	ns	0.0063	0.027
MLI §	0.00	41	0.46	ns	0.1245±0.041	0.0716±0.056	0.0885±0.056	ns	ns	ns
FNA	0.00	41	10.20	<0.0001	0.2543±0.002	0.2442±0.002	0.2517±0.002	0.00011	ns	0.00174
ACON	0.00	41	4.61	<0.01	0.19±0.002	0.184±0.003	0.1826±0.003	0.0255	0.0059	ns

Table 2.12b. Results for phylogenetic ANOVAs for femur by phylogenetic group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	Lambda	df	F	model p-value	cerc mean	col mean	hom mean	plat mean	cerc-col	cerc-hom	cerc-plat	col-hom	col-plat	hom-plat
FL	0.95	48	0.43	0.79	0.9956±0.045	1.0073±0.033	0.9594±0.046	1.0102±0.24	ns	ns	ns	ns	ns	ns
APFH	0.49	48	3.06	<0.05	-0.0656±0.011	-0.0647±0.009	-0.0291±0.013	-0.0682±0.016	ns	0.0079	ns	0.011	ns	0.0271
PDFH	0.00	48	5.62	<0.001	-0.0812±0.003	-0.0812±0.005	-0.0487±0.008	-0.0873±0.007	ns	0.00034	ns	0.00065	ns	0.00042
PDLT	0.00	48	12.20	<0.0001	-0.2663±0.005	-0.3241±0.01	0.2786±0.018	-0.265±0.93	0.0001	ns	ns	0.0204	0.00041	0.53
APMC	0.00	48	6.42	<0.001	0.095±0.002	0.0834±0.004	0.0737±0.006	0.0928±0.005	0.0017	0.0017	ns	ns	0.0977	0.0174
PDMC	0.00	48	0.64	ns	-0.0392±0.002	-0.0394±0.004	-0.0308±0.007	-0.0417±0.005	ns	ns	ns	ns	ns	ns
MLMC	0.00	48	1.05	ns	-0.2872±0.021	-0.2274±0.038	-0.2499±0.07	-0.3117±0.056	ns	ns	ns	ns	ns	ns
APLC	0.79	48	5.04	<0.01	0.0904±0.017	0.0809±0.013	0.0207±0.018	0.0768±0.024	ns	0.00044	ns	0.0021	ns	0.02744
PDLC	0.00	48	27.80	<0.0001	-0.0268±0.002	-0.0193±0.003	-0.0693±0.006	-0.0448±0.005	0.02092	0.0001	0.00026	0.0001	0.0001	0.00091
MLLC §	0.89	48	0.48	ns	-0.3662±0.032	-0.3377±0.024	-0.3531±0.34	-0.3517±0.045	ns	nss	ns	ns	ns	ns
BCB	0.84	48	0.96	ns	0.1738±0.016	0.1713±0.012	0.1985±0.016	0.1825±0.022	ns	ns	ns	ns	ns	
PH	0.94	48	1.00	ns	-0.0657±0.037	-0.0458±0.027	-0.098±0.038	-0.0271±0.05	ns	ns	ns	ns	ns	ns
PW	0.97	48	2.35	0.0676	-0.1495±0.028	-0.142±0.021	-0.0818±0.029	-0.1597±0.039	ns	0.023	ns	0.042	ns	0.0515
API §	0.00	48	1.21	ns	0.0134±0.007	0.0028±0.014	0.0531±0.025	0.0153±0.2	ns	ns	ns	0.063	ns	ns
PDI	0.00	48	17.00	<0.0001	-0.012±0.002	-0.0196±0.004	0.0387±0.008	0.0033±0.007	0.093	0.0001	0.023	0.0001	0.0023	0.0001
MLI §	0.00	48	0.54	ns	0.0803±0.025	0.1245±0.046	0.1006±0.084	0.0403±0.067	ns	ns	ns	ns	ns	ns
FNA	0.00	46	38.33	<0.0001	0.2484±0.002	0.255±0.003	0.3012±0.005	0.2638±0.004	0.03129	0.0001	0.0004352	0.0001	0.04978	0.0001
ACON	0.00	48	11.60	<0.0001	0.1932±0.001	0.19±0.003	0.1623±0.005	0.179±0.004	0.0098	0.0001	ns	0.0001	0.0001	0.004

Table 2.13a. Between group PCA on femur using cercopithecoid-only sample and Coding 1

	PC 1	**PC 2**
Standard Deviation	1.148	0.088
Proportion of Variance	0.994	0.006
Cumulative Proportion	0.994	1
Loadings		
length of femur (FL)	-0.687	-0.727
height of patellar groove (PH)	-0.727	0.687

Table 2.13b. Between group PCA on femur using cercopithecoid-only sample and Coding 2

	PC 1	**PC 2**
Standard Deviation	0.876	0.000
Proportion of Variance	1.000	0.000
Cumulative Proportion	1.000	0.000
Loadings		
length of femur (FL)	-0.670	0.742
height of patellar groove (PH)	-0.742	-0.670

Table 2.13c. Between group PCA on femur using entire anthropoid sample

	PC 1	**PC 2**	**PC3**
Standard Deviation	4.009	0.291	0
Proportion of Variance	0.995	0.005	0
Cumulative Proportion	0.995	1	1
Loadings			
width of femoral head (APFH)	0.309	0.339	-0.067
height of femoral head (PDFH)	0.304	0.095	0.414
anteroposterior depth of lateral condyle (APLC)	-0.419	0.441	0.378
patellar groove width (PW)	0.381	0.391	-0.641
proximodistal height condylar index (PDI)	0.392	-0.115	0.430
femoral neck angle (FNA)	0.479	-0.478	0.073
condylar asymmetry (ACON)	-0.330	-0.535	-0.283

Table 2.14a. Results for phylogenetic PCA of the astragalus using cercopithecoid-only sample. Lambda = 0.33

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**
Proportion of Variance	18.4260	15.6570	13.5600	10.2140	9.1020	7.7790	5.7590	5.0400	4.3910	3.3720	2.0400	1.7220	1.4080	1.0080	0.5210
Loadings															
AL	0.4360	-0.2685	0.5396	-0.2690	-0.1659	0.2734	-0.3837	-0.0176	0.0582	0.2330	-0.0581	-0.0303	0.2318	0.0903	0.0233
BPD	0.6255	-0.2763	-0.5119	-0.0182	0.1047	0.0002	-0.0036	-0.0678	-0.2891	0.2780	0.0564	0.0185	-0.1995	0.2227	0.0275
HNPD	0.1829	0.1089	0.8314	-0.1814	0.2768	-0.1365	0.2086	-0.0630	0.0599	0.1462	-0.0878	-0.1298	-0.1849	-0.0453	0.0453
DHTF	0.3687	0.7457	-0.0365	-0.2548	0.0885	-0.1811	-0.2653	-0.0771	0.0725	-0.3053	0.0940	-0.0357	-0.0049	0.0840	0.0962
TW	-0.4125	-0.4108	0.4143	0.3305	-0.4606	-0.2904	0.1235	0.0008	-0.1312	-0.0641	0.1462	0.0406	0.0204	0.0737	0.1354
HMR	-0.7212	0.3980	0.0626	-0.0634	-0.0126	-0.1259	-0.3175	0.1123	-0.1654	0.1100	-0.3044	0.2089	-0.0749	0.0415	0.0307
HLR	-0.3407	-0.0484	-0.3095	-0.2165	0.5053	-0.5018	0.0096	0.3340	-0.1105	0.2116	0.0742	-0.1554	0.1750	-0.0249	0.0481
DHFF	-0.0550	-0.6528	-0.0868	-0.3834	0.1326	0.1910	0.1777	0.0483	-0.2512	-0.4061	-0.2764	-0.1327	0.0307	0.0637	0.0359
PDFF	0.4075	-0.4840	-0.4674	-0.0725	0.0203	-0.1389	-0.2105	-0.4387	-0.0010	0.0779	-0.0929	0.0955	-0.0027	-0.2703	0.1506
EW	-0.2200	0.2324	-0.1761	-0.4405	-0.2178	0.6485	0.1447	0.3627	-0.0047	0.1008	0.1292	0.0163	-0.0746	-0.0788	0.1148
EL	0.0030	-0.3715	0.0118	0.6107	0.4223	0.2224	-0.3100	0.2767	0.2645	-0.0818	-0.0169	-0.0340	-0.0829	0.0171	0.0569
WTH	-0.5323	0.3343	-0.4098	0.2512	-0.2144	0.1560	0.1082	-0.3244	0.2343	0.1565	-0.1449	-0.2746	0.0318	0.0823	0.0551
WED	-0.4387	-0.4706	-0.0712	-0.4511	-0.3131	-0.1979	-0.3940	0.0060	0.1534	-0.0265	0.0965	-0.1386	-0.1679	-0.0128	-0.0631
ATH	0.4797	0.3196	0.0157	0.4006	-0.4252	-0.0410	-0.2130	0.2427	-0.3876	-0.0059	-0.0771	-0.2232	-0.0309	-0.1141	-0.0191
TAS	0.5623	-0.0710	-0.2308	-0.0868	-0.3963	-0.3471	0.2160	0.3367	0.3787	0.0195	-0.1789	0.0595	-0.0043	0.0282	0.0154

Table 2.14b. Results for phylogenetic PCA of the astragalus using the entire anthropoid sample. Lambda = 0.74

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**	**PC16**
Proportion of Variance	22.8557	15.3299	13.8912	10.2692	7.7618	6.5156	5.5943	3.6484	3.1504	2.8465	2.5928	2.0948	1.5598	1.0339	0.8422	0.0134
Loadings																
AL	0.1504	-0.4991	-0.2063	-0.5704	0.1555	-0.1959	0.0671	0.3699	-0.1265	-0.0223	-0.0103	-0.0528	0.0199	0.3689	0.0209	0.0109
BPD	-0.5354	-0.3187	-0.5460	0.2020	-0.3217	-0.0553	-0.0111	0.0048	-0.1293	0.2343	-0.1857	0.1915	-0.0725	-0.0012	-0.1346	0.0075
HNPD	0.2418	-0.4277	0.1866	-0.6272	0.3248	0.0177	-0.1666	0.0317	0.0003	0.3087	-0.0352	-0.0681	-0.2244	-0.1924	0.0826	0.0188
DHTF	-0.5529	-0.4515	0.5442	-0.0014	0.1272	-0.0565	0.2875	-0.1457	-0.0156	-0.1430	0.1657	0.1399	0.0214	-0.0101	-0.0512	0.0136
TW	0.8246	0.2140	0.0425	-0.2148	-0.2675	0.0902	-0.1137	0.0431	0.0262	0.1300	0.2351	0.1006	0.1850	-0.0236	-0.1181	0.0121
HMR	-0.4204	0.4199	0.5713	-0.2256	-0.0738	0.3265	-0.1090	0.0763	0.1499	-0.0478	-0.3107	-0.0759	0.0308	0.0398	-0.1009	0.0094
HLR	-0.1415	0.5310	0.1329	-0.0363	-0.2706	0.1824	0.0254	-0.5834	-0.3030	0.2407	-0.0353	0.0011	0.0663	0.1652	0.2206	0.0151
DHFF	-0.2546	0.5012	-0.5258	-0.2668	0.0166	-0.2783	-0.1510	-0.1935	0.3695	-0.1491	0.0949	0.0922	-0.1393	0.0498	-0.0048	0.0106
PDFF	-0.4981	-0.2317	-0.4958	-0.0160	-0.3941	0.1525	0.3249	0.1745	0.2085	-0.0229	0.0258	-0.1934	0.1725	-0.0977	0.1265	0.0139
EW	-0.0859	0.5386	0.1744	0.2442	0.1523	-0.7088	-0.0179	0.1621	-0.1529	0.0102	-0.1182	-0.0372	0.1229	-0.0766	0.0198	0.0141
EL	-0.0391	-0.0278	-0.5711	0.1378	0.2751	0.3605	-0.3885	-0.0430	-0.3608	-0.3772	0.0435	-0.1171	0.0112	-0.0586	-0.0472	0.0179
MLH	-0.0847	0.4866	0.1338	0.6558	0.1078	0.2714	0.1183	0.2949	0.0346	0.1464	0.2232	-0.0103	-0.2092	0.0708	0.0180	0.0118
PT	0.5109	-0.5349	0.0559	0.5374	0.1412	-0.0514	-0.1729	-0.1542	0.2390	0.0417	-0.1150	-0.0727	0.0576	0.0624	0.0008	0.0097
DT	0.8555	0.0569	0.0039	0.0140	-0.2286	0.0201	0.3273	0.0140	-0.0419	-0.2049	-0.1809	0.1052	-0.1246	-0.0263	0.0300	0.0071
ATH	-0.2016	-0.2970	0.4281	0.0917	-0.5504	-0.0842	-0.5236	0.1795	-0.0059	-0.1426	0.0562	0.1421	-0.0509	-0.0017	0.1292	0.0003
TAS	0.0732	-0.1375	0.2622	-0.0076	-0.6301	-0.3451	0.0435	-0.1860	-0.1129	-0.0274	0.1547	-0.4976	-0.2104	0.0248	-0.1563	0.0001

Table 2.15a. Results for phylogenetic ANOVAs for astragalus by locomotor group using cercopithecoid-only sample and coding 1

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**semi-t mean**	**terrestrial mean**	**arb-semi**	**arb-ter**	**semi-ter**
AL	0.5	38	6.34	<0.01	0.324±0.003	0.3171±0.003	0.3105±0.00	0.013721	0.002947	ns
BPD	0.69	40	0.36	ns	0.0744±0.0063	0.0761±0.0045	0.0706±0.0071	ns	ns	ns
HNPD	0	40	0.492	ns	0.0627±0.0032	0.0606±0.005	0.0547±0.0083	ns	ns	ns
DHTF	0	39	0.899	ns	-0.1143±0.005	-0.1154±0.008	-0.1317±0.013	ns	ns	ns
TW	0.37	40	0.348	ns	-0.035±0.0057	-0.0312±0.0055	-0.0288±0.009	ns	ns	ns
HMR	0.47	40	0.964	ns	0.00095±0.0039	0.005±0.0034	0.0071±0.0055	ns	ns	ns
HLR	0.53	40	1.68	ns	0.0225±0.0031	0.0272±0.0026	0.0556±0.0042	ns	ns	ns
DHFF	0.79	40	1.58	ns	-0.0437±0.0081	-0.0521±0.0052	-0.0438±0.008	ns	ns	ns
PDFF	0.86	40	0.327	ns	0.0598±0.0078	0.0581±0.0047	0.0541±0.0071	ns	ns	ns
EW	0.4	39	0.002	ns	-0.189±0.008	-0.189±0.007	-0.1896±0.012	ns	ns	ns
EL	0	40	3.63	<0.05	-0.0128±0.003	-0.025±0.0074	-0.0237±0.0079	0.01367	ns	ns
WTH	0.6	40	3.18	<0.05	-0.0456±0.0061	-0.0376±0.0047	-0.0279±0.0075	0.091	0.023	ns
PT	0.31	40	0.197	ns	-0.0804±0.0056	-0.083±0.0058	-0.0779±0.0095	ns	ns	ns
DT	0	40	1.06	ns	-0.0123±0.0024	-0.0094±0.0037	-0.0038±0.0061	ns	ns	ns
ASM	0.84	40	0.265	ns	0.0218±0.006	0.0208±0.0037	0.0178±0.0056	ns	ns	ns
WED	0	40	1.49	ns	0.0679±0.0041	0.0775±0.0064	0.0806±0.011	ns	ns	ns
ATH	0.49	40	2.51	ns	0.3117±0.016	0.3135±0.014	0.2659±0.023	ns	0.05	0.034
TAS	0.14	40	0.67	ns	0.2148±0.003	0.2194±0.004	0.2136±0.007	ns	ns	ns

Table 2.15b. Results for phylogenetic ANOVAs for astragalus by locomotor group using cercopithecoid-only sample and coding 2

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
AL	0.65	41	10.1	<0.001	0.324±0.0036	0.3161±0.0025	0.0029
BPD	0.69	40	0.27	ns	0.0753±0.006	0.0731±0.004	ns
HNPD	0	41	1.08	ns	0.0635±0.0032	0.0587±0.0046	ns
DHTF	0	41	1.55	ns	-0.1117 ±0.0051	-0.1207±0.0072	ns
TW	0.39	41	1.86	ns	-0.0362±0.0056	-0.0293±0.005	ns
HMR	0.46	41	2.15	ns	0.0007±0.0038	0.0053±0.0032	ns
MLR	0.42	41	2.91	ns	0.0225±0.0031	0.0266±0.0024	ns
DHFF	0.73	41	1.27	ns	-0.0439±0.0077	-0.0494±0.0049	ns
PDFF	0.86	41	0.472	ns	0.0601±0.0078	0.0571±0.0044	ns
EW	0.41	41	0.162	ns	-0.1901±0.0076	-0.1874±0.0065	ns
EL	0	41	8.46	<0.001	-0.0122±0.003	-0.0248±0.0043	0.00583
WTH	0.67	41	6.34	<0.01	-0.0462±0.0065	-0.0353±0.0044	0.016
PT	0.18	41	0.256	ns	-0.0798±0.00483	-0.0825±0.0053	ns
DT	0	41	3.51	ns	-0.0135±0.0023	-0.0072±0.0034	ns
ASM	0.83	41	0.296	ns	0.022±0.00592	0.0201±0.0034	ns
WED	0	41	4.37	<0.05	0.0667±0.0041	0.0789±0.0059	0.043
ATH	0.43	41	0.415	ns	0.3119±0.016	0.3032±0.014	ns
TAS	0.13	41	0.91	ns	0.2145±0.003	0.2184±0.004	ns

Table 2.15c. Results for phylogenetic ANOVAs for astragalus by locomotor group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
AL	0.93	48	5.46	<0.01	0.343±0.01	0.3191±0.013	0.3341±0.003	0.079	0.0055	ns
BPD	0.89	48	0.246	ns	0.0835±0.013	0.0946±0.018	0.0824±0.004	ns	ns	ns
HNPD	0.72	48	7.25	0.000416	0.0874±0.012	0.0242±0.017	0.08176±0.005	0.00049	ns	0.00154
DHTF	0	48	1.6	ns	-0.117±0.005	-0.1453±0.016	-0.1207±0.008	ns	ns	ns
TW	0.89	48	1.79	ns	-0.0439±0.017	-0.0744±0.024	-0.0361±0.006	ns	ns	ns
HML	0.99	48	1.12	ns	-0.008±0.017	-0.0251±0.024	-0.0022±0.005	ns	ns	ns
HLR	0.94	48	0.895	ns	0.000087±0.011	0.00864±0.015	0.0042±0.003	ns	ns	ns
DHFF	0.72	48	3.38	<0.05	-0.043±0.01	-0.0081±0.015	-0.0478±0.005	0.02731	ns	0.014
PDFF	0.93	48	0.291	ns	0.066±0.014	0.071±0.019	0.0629±0.004	ns	ns	ns
EW	0.9	48	2.6	0.064	-0.212±0.015	-0.1729±0.02	-0.2053±0.005	0.0599	ns	ns
EL	0.67	48	6.05	<0.01	0.0071±0.012	0.0484±0.016	-0.0036±0.005	0.014	0.045	0.0027
WTH	0.77	48	6.2	<0.01	-0.0564±0.01	-0.0176±0.015	-0.0451±0.004	0.013	0.012	0.076
PT	0	48	0.427	ns	-0.0804±0.004	-0.0775±0.011	-0.0849±0.005	ns	ns	ns
DT	0	48	3.2	0.0314	-0.0129±0.003	-0.0264±0.008	0.0073±0.004	0.097	ns	0.022
ASM	1	48	0.803	ns	0.0085±0.017	0.0344±0.017	0.0062±0.005	ns	ns	ns
WED	0	47	3.37	<0.05	0.0683±0.004	0.0522±0.012	0.079±0.006	ns	0.0676	0.0298
ATH	0.64	48	2.4	0.079	0.2734±0.028	0.181±0.042	0.2669±0.014	0.034	ns	0.052
TAS §	0.83	48	1.13	ns	0.1865±0.012	0.1604±0.017	0.189±0.005	ns	ns	ns

Table 2.15d. Results for phylogenetic ANOVAs for astragalus by locomotor group using guenon sample. § indicates analyses that did not meet the assumption of normality (see text for explanation)

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
AL	0.61	13	1.28	ns	0.3311+0.004	0.3264+0.004	ns
BPD	0.93	13	1.57	ns	0.08+0.005	0.0855+0.004	ns
HNPD §	0	13	0.12	ns	0.0633+0.006	0.0605+0.008	ns
DHTF	0	13	2.36	ns	-0.108+0.006	-0.1204+0.008	ns
TW							
HMR	0	13	0.52	ns	-0.0043+0.003	-0.0013+0.004	ns
HLR	0	13	4.09	<0.05	0.01537+0.002	0.02144+0.003	0.064
DHFF			0.29	ns	-0.039+0.005	-0.0429+0.007	ns
PDFF	0	13	0.39	ns	0.0705+0.004	0.0739+0.005	ns
EW	0	13	0.54	ns	-0.2086+0.004	0.2048+0.005	ns
EL	0	13	3.39	0.0655	-0.01385+0.005	'-0.0262+0.007	0.0887
WTH	0	13	1.55	ns	-0.0591+0.004	-0.052+0.006	ns
PT	0.64	13	0.11	ns	-0.0871+0.011	-0.0909+0.0012	ns
DT §	0.88	13	0.29	ns	-0.0113+0.005	-0.0083+0.005	ns
ASM							
WED	0	13	0.57	ns	0.0718+0.008	0.0805+0.012	ns
ATH	0	13	1.25	ns	0.3075+0.009	0.3229+0.014	ns
TAS	0	13	0.03	ns	0.2216+0.005	0.2204+0.008	ns

Table 2.15e. Results for phylogenetic ANOVAs for astragalus by locomotor group using colobine sample. § indicates analyses that did not meet the assumption of normality (see text for explanation)

Variable	**Lambda**	**df**	**F**	**model p-value**	**arboreal mean**	**terrestrial mean**	**arb-ter**
AL	0.72	10	1.62	ns	0.3212+0.002	0.3163+0.004	ns
BPD	0	10	1.02	ns	0.0662+0.003	0.0585+0.008	ns
HNPD	0	10	1.81	ns	0.0654+0.005	0.048+0.0013	ns
DHTF	0.67	10	1.67	ns	-0.1140+0.012	-0.1401+0.02	ns
TW	0.16	10	3.49	0.0707	-0.03831+0.005	-0.01691+0.011	0.091
HMR	0	10	1.15	ns	0.0065+0.004	0.0158+0.009	ns
HLR	0	10	0.09	ns	0.0231+0.004	0.02487+0.006	ns
DHFF	0	10	1.32	ns	-0.0553+0.005	-0.0693+0.012	ns
PDFF	0	10	0.93	ns	0.0442+0.004	0.0339+0.011	ns
EW §	0	10	0.15	ns	-0.176+0.01	-0.1661+0.024	ns
EL	0	10	0.61	ns	-0.0094+0.005	-0.0191+0.0013	ns
WTH	0	10	1.6	ns	-0.03831+0.004	-0.026+0.01	ns
PT	1	10	0.61	ns	-0.0752+0.006	-0.0675+0.01	ns
DT	0.34	10	8.55	<0.01	-0.0141+0.004	0.0088+0.008	0.0152
ASM	0	10	0.54	ns	0.0189+0.004	0.01185+0.01	ns
WED	1	10	1.88	ns	0.0626+0.009	0.0807+0.013	ns
ATH	0.1	10	0.044	ns	0.3244+0.013	0.3308+0.031	ns
TAS §	0.06	10	0.88	ns	0.2073+0.004	0.2171+0.011	ns

Table 2.15f. Results for phylogenetic ANOVAs for astragalus by locomotor group using papionin sample

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
AL	0.088	14	8.22	<0.01	0.32447+0.004	0.31225+0.004	0.012
BPD	0	14	0.81	ns	0.0911+0.008	0.083+0.009	ns
HNPD	0.52	14	0.062	ns	0.0562+0.008	0.058+0.007	ns
DHTF	0	14	0.016	ns	-0.121+0.014	-0.1189+0.016	ns
TW	0	14	0.011	ns	-0.041+0.008	-0.0401+0.009	ns
HMR	0.23	14	2.04	ns	-0.0072+0.005	-0.0002+0.005	ns
HLR	0.15	14	0.11	ns	0.0287+0.004	0.03+0.004	ns
DHFF	0.79	14	1.86	ns	-0.0246+0.009	-0.0342+0.007	ns
PDFF	1	14	1.62	ns	0.0809+0.009	0.0732+0.006	ns
EW	0	14	1.47	ns	-0.2047+0.005	0.1977+0.006	ns
EL	1	14	0.08	ns	-0.0245+0.011	-0.0267+0.008	ns
MLS	0.67	14	4.2	<0.05	-0.05247+0.008	-0.03803+0.007	0.06
PT	0	14	0.003	ns	-0.0871+0.007	-0.0813+0.008	ns
DT	0	14	0.85	ns	-0.0159+0.006	-0.0091+0.007	ns
ASM	0.62	14	0.99	ns	0.0358+0.007	0.0301+0.006	ns
WED	0	14	0.5	ns	0.072+0.008	0.0786+0.009	ns
ATH	0.05	14	0.55	ns	0.2866+0.025	0.2656+0.028	ns
TAS	0	14	0.009	ns	0.221+0.005	0.2215+0.005	ns

Table 2.16a. Results for standard ANOVAs for astragalus by locomotor group using cercopithecoid-only sample and coding 1. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**F**	**df**	**p-value**	**arboreal mean**	**semi-t mean**	**terrestrial mean**	**arb-semi**	**arb-ter**	**semi-ter**
AL	6.41	40	<0.01	0.324±0.001	0.3191±0.002	0.3092±0.004	0.0667	0.0015	0.0328
BPD	1.84	40	ns	0.0756±0.003	0.0845±0.004	0.0784±0.006	0.062	ns	ns
HNPD	0.49	40	ns	0.0627±0.003	0.0606±0.004	0.0547±0.004	ns	ns	ns
DHTF	0.95	40	ns	-0.1139±0.005	-0.1154±0.004	-0.1317±0.022	ns	ns	ns
TW	0.1	40	ns	-0.0344±0.003	-0.032±0.004	-0.0328±0.004	ns	ns	ns
HMR	0.13	40	ns	0.00038±0.002	-0.00058±0.003	0.0025±0.004	ns	ns	ns
HLR	1.9	40	ns	0.0222±0.002	0.0271±0.002	0.0274±0.004	0.078	ns	ns
DHFF	0.69	40	ns	-0.0441±0.003	-0.041±0.005	-0.0332±0.006	ns	ns	ns
PDFF	2.34	40	ns	0.059±0.004	0.0707±0.004	0.06902±0.007	0.043	ns	ns
EW	0.24	39	ns	-0.1956±0.004	-0.1994±0.003	-0.1981±0.003	ns	ns	ns
EL	3.63	40	<0.05	-0.0128±0.003	-0.025±0.003	-0.0237±0.011	0.014	ns	ns
WTH	2.49	40	0.096	-0.0481±0.003	-0.0471±0.004	-0.0299±0.009	ns	0.033	0.051
PT	0.7	40	ns	-0.0793±0.003	-0.0857±0.005	-0.0836±0.009	ns	ns	ns
DT	1.06	40	ns	-0.0123±0.002	-0.0094±0.002	-0.00385±0.009	ns	ns	ns
ASM	1.09	40	ns	0.0222±0.003	0.0279±0.003	0.0252±0.004	ns	ns	ns
WED §	1.49	40	ns	0.0679±0.004	0.0775±0.006	0.0806±0.005	ns	ns	ns
ATH	3.02	40	0.06	0.3106±0.007	0.2997±0.013	0.2532±0.023	ns	0.0075	0.0123
TAS	3.144	39	0.0542	0.2152±0.003	0.2246±0.002	0.2167±0.008	0.018	ns	ns

Table 2.16b. Results for standard ANOVAs for astragalus by locomotor group using cercopithecoid-only sample and coding 2. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	F	df	p-value	arboreal mean	terrestrial mean
AL	7	40	<0.05	0.3241±0.001	0.3174±0.002
BPD	1.41	40	ns	0.0766±0.003	0.0819±0.003
HNPD	1.08	40	ns	0.0635±0.003	0.0587±0.003
DHTF	0.683	39	ns	-0.1117±0.005	-0.117±0.004
TW	0.79	40	ns	-0.0355±0.003	-0.0311±0.003
HMR	0.07	40	ns	-0.00019±0.002	0.00064±0.002
HLR	3.85	40	0.056	0.0221±0.002	0.027±0.002
DHFF	0.54	40	ns	-0.0439±0.004	-0.0399±0.004
PDFF §	2.89	40	0.097	0.0599±0.004	0.0689±0.004
EW §	0.004	39	ns	-0.1974±0.004	-0.1971±0.003
EL	8.46	40	<0.01	-0.0122±0.003	-0.0248±0.003
WTH	2.02	40	ns	-0.0494±0.003	-0.0426±0.004
PT	1.14	40	ns	-0.0794±0.003	-0.0849±0.004
DT	3.51	40	0.068	-0.0135±0.002	-0.0072±0.003
ASM	1.16	40	ns	0.0227±0.003	0.0266±0.002
WED §	4.37	40	<0.05	0.0667±0.004	0.0789±0.004
ATH	2.27	40	ns	0.3112±0.008	0.2907±0.011
TAS	4.514	39	<0.05	0.2151±0.003	0.2227±0.002

Table 2.16c. Results for standard ANOVAs for astragalus by locomotor group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	**F**	**df**	**p-value**	**arboreal mean**	**sus mean**	**terrestrial mean**	**arb-sus**	**arb-ter**	**sus-ter**
AL §	6.65	47	<0.001	0.3294±0.003	0.3084±0.015	0.3173±0.002	0.0131	0.0035	ns
BPD	0.51	48	ns	0.0794±0.003	0.0885±0.014	0.0819±0.003	ns	ns	ns
HNPD	12.7	48	<0.0001	0.0729±0.005	0.0114±0.009	0.0587±0.003	<0.0001	0.02386	0.00059
DHTF	1.6	48	ns	-0.1167±0.005	-0.1453±0.025	-0.1207±0.005	0.081	ns	ns
TW	4.45	48	<0.05	-0.0386±0.004	-0.0679±0.029	-0.0311±0.003	0.021	ns	0.005
HMR	0.21	46	ns	-0.0027±0.002	0.0045±0.002	0.00064±0.002	ns	ns	ns
HLR	2.67	44	0.0807	0.0216±0.002	0.0208±0.003	0.027±0.002	ns	0.033	ns
DHFF	5.67	48	<0.01	-0.0435±0.003	-0.009±0.01	-0.0399±0.004	0.0015	ns	0.0045
PDFF	0.84	48	ns	0.0622±0.004	0.0659±0.016	0.0689±0.004	ns	ns	ns
EW	5.59	47	<0.01	-0.2033±0.005	-0.1622±0.018	-0.197±0.003	0.017	ns	0.0076
EL	20.16	48	<0.0001	-0.0071±0.004	0.0381±0.006	-0.0248±0.003	<0.0001	0.00085	<0.0001
WTH	9.39	48	<0.001	-0.0527±0.003	-0.0121±0.01	-0.0426±0.004	0.00015	0.0361	0.0037
PT	0.43	48	ns	-0.0804±0.003	-0.0775±0.021	-0.0849±0.004	ns	ns	ns
DT	3.2	48	0.05	-0.0129±0.002	-0.0264±0.021	-0.0072±0.003	0.097	ns	0.022
ASM	3.28	47	<0.05	0.0198±0.003	0.04381±0.024	0.0266±0.002	0.021	ns	0.098
WED §	3.48	48	<0.05	0.0683±0.004	0.0522±0.003	0.0789±0.004	ns	0.063	0.028
ATH	4.72	48	<0.05	0.2963±0.009	0.2019±0.042	0.2907±0.011	0.0036	ns	0.0066
TAS §	9.009	47	<0.001	0.2076±0.004	0.176±0.008	0.2207±0.003	0.00656	0.01741	0.00024

Table 2.17a. Results for phylogenetic ANOVAs for astragalus by phylogenetic group using cercopithecoid-only sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	Lambda	df	F	p-value (overall)	col mean	guen mean	pap mean	col-guen	col-pap	guen-pap
AL	0.00	40	9.15	<0.0001	0.3198±0.002	0.3272±0.003	0.31561±0.003	0.016	ns	0.00013
BPD	0.00	39	12.69	<0.0001	0.0649±0.003	0.08445±0.005	0.08575±0.005	0.0001128	<0.0001	ns
HNPD	0.00	40	0.19	ns	0.0625±0.004	0.061951±0.006	0.059323±0.006	ns	ns	ns
DHTF	0.00	39	0.21	ns	-0.1147±0.007	-0.11426±0.01	-0.119448±0.009	ns	ns	ns
TW §	0.00	40	4.69	<0.01	-0.0354±0.004	-0.02432±0.006	-0.04031±0.006	0.059	ns	0.0045
HMR	0.00	40	5.65	<0.01	0.008±0.003	-0.00292±0.004	-0.00269±0.004	0.0049	0.0051	ns
HLR	0.00	40	11.00	<0.0001	0.0252±0.002	0.01821±0.003	0.02988±0.003	0.013	0.088	<0.0001
DPFF	0.00	40	11.90	<0.0001	-0.0577±0.004	-0.04079±0.006	-0.03122±0.005	0.0039	<0.0001	0.0685
PDFF	0.00	40	28.60	<0.0001	0.0425±0.003	0.07209±0.005	0.07331±0.004	<0.0001	<0.0001	ns
EW	0.00	38	11.19	<0.0001	-0.1736±0.006	-0.20682±0.007	-0.0268±0.007	<0.0001	0.000729	ns
EL	0.00	40	2.13	ns	-0.011±0.004	-0.01961±0.006	-0.02261±0.006	ns	0.05	ns
WTH	0.42	40	2.27	0.0952	-0.0353±0.007	-0.05549±0.011	-0.04183±0.011	0.068	ns	ns
PT	0.00	40	2.69	0.0588	-0.0731±0.005	-0.08423±0.006	-0.0868±0.006	0.081	0.031	ns
DT	0.00	40	0.08	ns	-0.0112±0.003	-0.00951±0.004	-0.01077±0.004	ns	ns	ns
ASM	0.44	40	2.40	0.0825	0.0169±0.005	0.02095±0.008	0.03159±0.008	ns	0.0702	0.0878
WED	0.00	40	2.06	ns	0.063±0.006	0.07581±0.008	0.07692±0.007	0.097	0.068	ns
ATH	0.00	40	8.43	<0.001	0.3258±0.011	0.3146±0.015	0.2701±0.015	ns	0.00055	0.0028
TAS §	0.00	40	4.19	<0.05	0.2091±0.004	0.221±0.005	0.2214±0.005	0.016	0.013	ns

Table 2.17b. Results for phylogenetic ANOVAs for astragalus by phylogenetic group using entire anthropoid sample. § indicates analyses that did not meet the assumption of normality (see text for explanation).

Variable	Lambda	df	F	p-value (overall)	cerc mean	col mean	hom mean	plat mean	cerc-col	cerc-hom	cerc-plat	col-hom	col-plat	hom-plat
AL	0.74	47	3.93	0.00778	0.3209±0.011	0.3203±0.008	0.3087±0.012	0.362057±0.015	ns	ns	0.0093	ns	0.0086	0.0014
BPD	0.00	47	8.50	<0.0001	0.0847±0.002	0.0649±0.004	0.0885±0.008	0.0916±0.006	<0.0001	ns	ns	0.00692	0.00033	ns
HNPD	0.00	47	31.50	<0.0001	0.0606±0.003	0.0625±0.005	0.0114±0.009	0.1142±0.007	ns	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
DHTF	0.00	47	2.38	0.0652	-0.1167±0.005	-0.1147±0.009	-0.1453±0.015	-0.14±0.012	ns	0.069	0.063	0.068	0.067	ns
TW	0.00	47	3.89	<0.001	-0.0326±0.004	-0.0354±0.007	-0.0679±0.012	-0.0521±0.01	ns	0.0052	0.0475	0.015	ns	ns
HMR	1.00	46	0.41	ns	-0.0019±0.026	0.0079±0.019	-0.0202±0.027	-0.0169±0.036	ns	ns	ns	ns	ns	ns
HLR	0.90	47	2.14	0.0908	0.0242±0.014	0.02367±0.01	0.0209±0.015	-0.0227±0.02	ns	ns	0.02	ns	0.022	0.032
DPFF	0.00	47	11.70	<0.0001	-0.0359±0.003	-0.0577±0.005	-0.009±0.009	-0.0417±0.007	<0.0001	0.0032	ns	<0.0001	0.042	0.003
PDFF §	0.00	47	16.30	<0.0001	0.0727±0.002	0.0425±0.004	0.0659±0.008	0.072334±0.006	<0.0001	ns	ns	0.0075	<0.0001	ns
EW	0.00	46	13.76	<0.0001	-0.203±0.004	-0.1742±0.007	-0.1622±0.012	-0.228±0.009	<0.0001	0.001205	0.011074	ns	<0.0001	<0.0001
EL	0.00	47	24.40	<0.0001	-0.0212±0.003	-0.011±0.005	0.0381±0.01	0.0288±0.008	0.065	<0.0001	<0.00001	<0.0001	<0.0001	ns
MLT	0.55	47	4.05	<0.01	-0.0484±0.012	-0.0355±0.009	-0.0121±0.014	-0.0673±0.017	ns	0.01123	ns	ns	0.0675	0.0037
PT	0.00	47	1.44	ns	-0.08556±0.003	-0.0731±0.006	-0.0775±0.011	-0.08482±0.009	0.05	ns	ns	ns	ns	ns
DT	0.00	47	1.33	ns	-0.0102±0.002	-0.0112±0.005	-0.0264±0.008	-0.0102±0.007	ns	0.053	ns	0.0881	ns	ns
ASM	1.00	47	0.74	ns	0.026±0.026	0.0159±0.019	0.0419±0.026	-0.0051±0.035	ns	ns	ns	ns	ns	ns
WED	0.00	46	2.46	0.05822	0.0764±0.004	0.063±0.007	0.05216±0.012	0.0756±0.009	0.04946	0.04515	ns	ns	ns	ns
ATH	0.00	47	9.65	<0.0001	0.2917±0.008	0.3258±0.015	0.2019±0.027	0.2307±0.021	0.0272	0.0015	0.0061	<0.0001	0.00019	ns
TAS	0.00	47	41.00	<0.0001	0.2212±0.002	0.2091±0.004	0.1761±0.008	0.1584±0.006	0.0085	0.0001	0.0001	0.00027	0.0001	0.0673

Table 2.18a. Between group PCA on astragalus using cercopithecoid-only sample and Coding 1

	PC 1	**PC 2**	**PC 3**
Standard Deviation	1.277	0.370	6.60E-17
Proportion of Variance	0.923	0.077	0
Cumulative Proportion	0.923	1	1
Loadings			
Overall length (AL)	-0.657	-0.129	0.453
Ectal facet length (EL)	-0.221	-0.896	-0.339
Width of astragalar head (WTH)	0.495	-0.387	0.768
Angle of astragalar head (ATH)	-0.525	0.173	0.299

Table 2.18b. Between group PCA on astragalus using cercopithecoid-only sample and Coding 2

	PC 1	**PC 2**
Standard Deviation	0.948	0
Proportion of Variance	1.000	0
Cumulative Proportion	1.000	1
Loadings		
Overall length (AL)	-0.563	0.801
Ectal facet length (EL)	-0.610	-0.430
Width of astragalar head (WTH)	0.319	0.393
Trochlear wedging (WED)	0.457	0.137

Table 2.18c. Between group PCA on astragalus using entire anthropoid sample

	PC 1	**PC 2**	**PC 3**
Standard Deviation	2.153	0.681	0
Proportion of Variance	0.909	0.091	0
Cumulative Proportion	0.909	1	1
Loadings			
Overall length (AL)	-0.274	0.540	-0.786
Length of head and neck (HNPD)	-0.587	0.248	0.473
Ectal facet length (EL)	0.557	0.764	0.326
Width of astragalar head (WTH)	0.519	-0.254	-0.229

Table 2.19a. Results for phylogenetic PCA of the calcaneus using cercopithecoid-only sample. Lambda = 0.66

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Proportion of Variance	25.1132	22.3997	18.7116	14.0237	8.9926	7.4103	3.2594	0.0895
Loadings								
PC	-0.2471	-0.7418	0.2217	-0.3612	-0.0734	0.4354	-0.1185	0.0077
PDA	-0.6261	-0.3856	-0.3237	-0.4164	0.0343	-0.3171	0.2792	0.0379
CTL	0.5336	-0.0783	0.8066	0.0591	-0.1327	-0.1871	-0.0086	0.0493
PDF	0.0402	-0.6468	-0.4579	0.5430	0.0600	-0.1728	-0.2042	0.0187
MLF	-0.0427	0.1358	0.0048	0.6060	0.4996	0.5283	0.2873	0.0364
MLS	-0.7591	0.6099	0.0355	0.0129	-0.0165	0.0331	-0.2193	0.0303
HCF	0.4153	0.2423	-0.5888	-0.0077	-0.6013	0.2368	0.0611	0.0267
CTW	0.6299	0.1916	-0.3584	-0.4929	0.4210	0.0176	-0.1311	0.0202

Table 2.19b. Results for phylogenetic PCA of the calcaneus using the entire anthropoid sample. Lambda = 0.9

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Proportion of Variance	26.7845	19.9282	18.1732	14.6039	11.8036	5.9864	2.6478	0.0724
Loadings								
PC	-0.1982	-0.7641	-0.3781	0.1006	0.1920	0.3866	0.1932	0.0089
PDA	-0.5729	-0.3896	-0.3632	0.5085	0.0054	-0.2129	-0.2878	0.0361
CTL	0.5269	-0.4106	0.4134	-0.5234	0.2942	-0.1416	-0.0131	0.0463
PDF	-0.0603	0.0170	-0.4134	-0.1641	-0.8122	-0.2634	0.2612	0.0318
MLF	-0.0150	0.2897	0.3414	-0.1536	-0.5814	0.6245	-0.2160	0.0331
MLS	-0.7740	0.4559	0.3199	0.0782	0.2537	0.0108	0.1401	0.0231
HCF	0.2964	0.5405	-0.7137	-0.1689	0.2747	0.0751	-0.0281	0.0160
CTW	0.6936	0.1472	0.1810	0.6755	0.0159	0.0236	0.0847	0.0157

Table 2.20a. Results for phylogenetic ANOVAs for calcaneus by locomotor group using cercopithecoid-only sample and coding 1

Variable	Lambda	df	F	model p-value	arboreal mean	semi-t mean	terrestrial mean	arb-semi	arb-ter	semi-ter
CL	0.58	40	1.1	ns	0.4616±0.0047	0.4561±0.0038	0.4557±0.0061	ns	ns	ns
PDA	0.89	40	3.98	<0.05	0.2715±0.012	0.2549±0.0067	0.2479±0.01	0.018	0.023	ns
CTL	0.33	40	4.17	<0.05	-0.1480±0.013	-0.1175±0.013	-0.0987±0.021	0.021	0.024	ns
PDF	0.54	40	0.152	ns	-0.0676±0.0078	-0.0663±0.0064	-0.0619±0.01	ns	ns	ns
MLF	0.84	40	0.056	ns	-0.1104 ±0.011	-0.1122±0.0066	-0.1135±0.01	ns	ns	ns
MLS	0	40	4.62	<0.01	-0.2586±0.0062	-0.2822±0.0096	-0.2962±0.016	0.019	0.024	ns
HCF	0.49	40	2.91	<0.05	-0.0672±0.0078	-0.0568±0.0067	-0.0425±0.011	ns	0.027	ns
CTW	0.16	40	2.15	ns	-0.0757 ±0.0049	-0.0636±0.006	-0.0651±0.01	0.05	ns	ns

Table 2.20b. Results for phylogenetic ANOVAs for calcaneus by locomotor group using cercopithecoid-only sample and coding 2

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
CL	0.56	41	5.22	0.00952	0.4628±0.0046	0.455±0.0034	0.028
PDA	0.91	41	7.86	0.00129	0.272±0.012	0.2544±0.0063	0.0077
CTL	0.63	41	3.58	<0.05	-0.1446±0.018	-0.1211±0.012	0.066
PDF	0.4	41	0.268	ns	-0.0654±0.0068	-0.0685±0.0059	ns
MLF	0.84	41	0.213	ns	-0.11±0.011	-0.1128±0.006	ns
MLS	0.1	41	2.26	ns	-0.2621±0.0081	-0.2768±0.0098	ns
HCF	0.47	41	6.77	<0.01	-0.0688±0.0076	-0.0529±0.0061	0.013
CTW	0.22	41	3.05	ns	-0.0755±0.0054	-0.0657±0.0056	0.088

Table 2.20c. Results for phylogenetic ANOVAs for calcaneus by locomotor group using entire anthropoid sample

Variable	Lambda	df	F	model p-value	arboreal mean	sus mean	terrestrial mean	arb-sus	arb-ter	sus-ter
CL	0.67	48	11.5	<0.0001	0.4646±0.0075	0.4139±0.011	0.4567±0.0036	<0.0001	0.035	0.00051
PDA	0.98	48	4.65	<0.01	0.2986±0.023	0.2504±0.032	0.118±0.0066	ns	0.0085	ns
CTL	0.76	48	3.49	<0.05	-0.1803±0.03	-0.1266±0.043	-0.155±0.013	ns	0.048	0.046
PDF	0.89	48	3.25	<0.05	-0.0354±0.019	0.0339±0.027	-0.0347±0.0067	0.014	ns	0.016
MLF	0.92	48	2.46	0.0741	-0.1437±0.018	-0.0886±0.026	-0.1457±0.006	0.036	ns	0.0314
MLS	0	48	9.13	<0.0001	-0.2572±0.006	-0.2034±0.019	-0.2797±0.009	0.0062	0.0157	0.00022
HCF	0.53	48	3.44	<0.05	-0.0657±0.011	-0.0606±0.017	-0.0493±0.006	ns	0.012	ns
CTW	0	48	4.6	0.00658	-0.0769±0.004	-0.0918±0.013	-0.0613±0.006	ns	0.016	0.025

Table 2.20d. Results for phylogenetic ANOVAs for calcaneus by locomotor group using guenon sample

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
CL	0	13	1.65	ns	0.4684+0.002	0.4643+0.003	ns
PDA	0.57	13	0.82	ns	0.2932+0.007	0.28618+0.008	ns
CTL	0	13	2.76	ns	-0.1467+0.014	-0.1118+0.021	ns
PDF	0	13	1.26	ns	-0.0714+0.005	-0.0633+0.007	ns
MLF	0.34	13	0.74	ns	-0.137+0.009	-0.1458+0.01	ns
MLS	0	13	1.48	ns	-0.2651+0.008	-0.28+0.012	ns
HCF	0.67	13	0.69	ns	-0.0542+0.008	-0.04736+0.008	ns
CTW	1	13	1.69	ns	-0.6113+0.008	-0.0508+0.008	ns

Table 2.20e. Results for phylogenetic ANOVAs for calcaneus by locomotor group using colobine sample

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
CL	0.74	10	9.2	<0.01	0.4608+0.0046	0.3846+0.0078	0.013
PDA	0	10	3.63	0.0651	0.2721+0.048	0.2497+0.012	0.086
CTL	0.22	10	0.04	ns	-0.1578+0.017	-0.1511+0.036	ns
PDF	1	10	1.86	ns	-0.0563+0.007	-0.07171+0.011	ns
MLF	0	10	0.22	ns	-0.0905+0.006	-0.0841+0.014	ns
MLS	1	10	1.15	ns	-0.2629+0.016	-0.2366+0.025	ns
HCF	0	10	1.35	ns	-0.079+0.007	-0.0583+0.018	ns
CTW	0	10	0.2	ns	-0.0843+0.005	-0.0793+0.011	ns

Table 2.20f. Results for phylogenetic ANOVAs for calcaneus by locomotor group using papionin sample

Variable	Lambda	df	F	model p-value	arboreal mean	terrestrial mean	arb-ter
CL	0	14	0.15	ns	0.4581+0.006	0.4555+0.007	ns
PDA	0.68	14	4.45	<0.05	0.2571+0.013	0.235+0.011	0.053
CTL	0.58	14	0.66	ns	-0.1056+0.015	-0.095+0.012	ns
PDF	0.63	14	1.63	ns	-0.0855+0.013	-0.0744+0.011	ns
MLF	1	14	0.064	ns	-0.1232+0.011	-0.1251+0.008	ns
MLS	0.03	14	1.38	ns	-0.2646+0.017	-0.2877+0.02	ns
HCF	0	14	16.2	<0.001	-0.0619+0.0059	-0.0345+0.0068	0.0012
CTW	0	14	0.06	ns	-0.0653+0.01	-0.0623+0.012	ns

Table 2.21a. Results for standard ANOVAs for calcaneus by locomotor group using cercopithecoid-only sample and coding 1

Variable	F	df	overall p-value	arboreal mean	semi-t mean	terrestrial mean	arb-semi	arb-ter	semi-ter
CL	1.12	40	ns	0.4627±0.002	0.4589±0.003	0.4547±0.002	ns	ns	ns
PDA	7.98	40	<0.01	0.2755±0.003	0.2608±0.007	0.2305±0.011	0.04476	0.00045	0.01672
CTL	8.19	40	<0.001	-0.1494±0.009	-0.1101±0.007	-0.0848±0.017	0.0026	0.0029	ns
PDF	0.56	40	ns	-0.066±0.004	-0.072±0.004	-0.0727±0.014	ns	ns	ns
MLF	3.21	40	0.051	-0.1126±0.005	-0.133±0.007	-0.1266±0.006	0.017	ns	ns
MLS	4.62	40	<0.05	-0.2586±0.006	-0.2822±0.007	-0.2962±0.017	0.019	0.024	ns
HCF	7.09	40	<0.01	-0.069±0.004	-0.0517±0.006	-0.0334±0.003	0.012	0.0023	ns
CTW	3.85	40	<0.05	-0.0752±0.004	-0.0598±0.004	-0.0612±0.009	0.012	ns	ns

Table 2.21b. Results for standard ANOVAs for calcaneus by locomotor group using cercopithecoid-only sample and coding 2

Variable	F	df	overall p-value	arboreal mean	terrestrial mean
CL	4.68	41	<0.05	0.4641±0.02	0.4569±0.003
PDA	9.67	41	<0.01	0.2764±0.003	0.2548±0.006
CTL	9.85	41	<0.01	-0.1472±0.009	-0.1094±0.008
PDF	2.2	41	ns	-0.0647±0.004	-0.0731±0.04
MLF	4.75	41	<0.05	-0.1133±0.006	-0.1303±0.005
MLS	3.25	41	0.079	-0.2625±0.005	-0.2797±0.008
HCF	14.1	41	<0.001	-0.0704±0.004	-0.0475±0.005
CTW	5.98	41	<0.05	-0.0747±0.004	-0.0613±0.004

Table 2.21c. Results for standard ANOVAs for calcaneus by locomotor group using entire anthropoid sample

Variable	F	df	overall p-value	arboreal mean	sus mean	terrestrial mean	arb-sus	arb-ter	sus-ter
CL	26	48	<0.0001	0.4646±0.002	0.4127±0.011	0.4569±0.003	3.50E-09	0.029	2.10E-07
PDA	9.7	48	<0.001	0.2858±00.005	0.2339±0.016	0.2548±0.006	0.00412	0.00045	ns
CTL	12.8	48	<0.0001	-0.1605±0.01	-0.2232±0.016	-0.1094±0.008	0.02594	0.00028	0.00015
PDF	18.87	47	<0.0001	-0.0572±0.006	0.0167±0.004	-0.0731±0.004	<0.0001	0.027	<0.0001
MLF	4.92	48	<0.05	-0.1254±0.007	-0.0711±0.011	-0.1303±0.005	0.0055	ns	0.003
MLS	9.13	48	<0.001	-0.2572±0.005	-0.2034±0.004	-0.2797 ±0.008	0.0055	ns	0.003
HCF	6.28	48	<0.01	-0.0688±0.004	-0.0619±0.019	-0.0475±0.005	ns	0.00091	ns
CTW	4.6	48	<0.05	-0.0769±0.004	-0.0918±0.024	-0.0613±0.004	ns	0.016	0.025

Table 2.22a. Results for phylogenetic ANOVAs for calcaneus by phylogenetic group using the cercopithecoid-only dataset

Variable	Lambda	df	F	model p-value	col mean	guen mean	pap mean	col-guen	col-pap	guen-pap
CL	0.00	40	4.01	<0.05	0.4587±0.003	0.4667±0.004	0.4848±0.004	0.062	ns	0.009
PDA	0.61	40	6.86	<0.001	0.2661±0.012	0.2887±0.018	0.2405±0.017	ns	ns	0.00065
CTL	0.00	40	7.54	<0.001	-0.16±0.011	-0.1304±0.015	-0.1038±0.015	0.05079	0.00038	0.058
PDF	0.00	40	3.79	<0.05	-0.057±0.005	-0.0752±0.007	-0.0717±0.007	0.012	0.037	ns
MLF	0.58	40	5.6	<0.01	-0.0890±0.011	-0.1419±0.016	-0.126±0.016	0.0018	0.0223	ns
MLS	0.00	40	2.83	0.0504	-0.2545±0.009	-0.2418±0.012	-0.2824±0.012	ns	0.022	ns
DHC	0.00	40	13.4	<0.0001	-0.0755±0.005	-0.0652±0.007	-0.0415±0.007	ns	<0.0001	0.00074
CTW	0.00	40	6.97	<0.001	-0.0835±0.005	-0.0614±0.006	-0.063±0.006	0.0015	0.0027	ns

Table 2.22b. Results for phylogenetic ANOVAs for calcaneus by phylogenetic group using the entire dataset

Variable	Lambda	df	F	model p-value	cerc mean	col mean	hom mean	plat mean	cerc-col	cerc-hom	cerc-plat	col-hom	col-plat	hom-plat
CL	0.51	47	7.44	<0.0001	0.4613±0.009	0.4578±0.0075	0.4129±0.011	0.4663±0.013	ns	<0.0001	ns	0.00028	ns	0.00062
PDA	0.96	47	1.10	ns	0.2637±0.036	0.2645±0.026	0.2357±0.037	0.3257±0.049	ns	ns	ns	ns	ns	0.076
CTL	0.00	47	15.40	<0.0001	-0.1167±0.007	-0.16±0.014	-0.2232±0.024	-0.2191±0.019	0.0024	<0.0001	<0.0001	0.0176	0.0076	ns
PDF	0.00	47	30.20	<0.0001	-0.0734±0.004	-0.057±0.007	0.0162±0.012	-0.0041±0.01	0.024	<0.0001	<0.0001	<0.0001	<0.0001	ns
MLF	0.00	47	46.70	<0.0001	-0.134±0.003	-0.0894±0.006	-0.071±0.01	-0.1787±0.008	<0.0001	<0.0001	<0.0001	ns	<0.0001	<0.0001
MLS	0.00	47	8.44	<0.0001	-0.2773 ±0.005	-0.2545±0.01	0.2034±0.018	-0.2337±0.014	0.02805	0.00015	0.00369	0.01	ns	ns
DHC	0.45	47	1.26	ns	-0.0515±0.015	-0.0386±0.012	-0.0622±0.018	-0.0252±0.021	0.0582	ns	ns	ns	ns	ns
CTW	0.00	46	5.02	<0.01	-0.0623±0.004	-0.0823±0.007	-0.0918±0.012	-0.08661±0.01	0.007488	0.021007	0.017206	ns	ns	ns

Table 2.23a. Between group PCA on calcaneus using cercopithecoid-only sample and Coding 1

	PC 1	**PC 2**	**PC 3**
Standard Deviation	1.518	0.218	1.03E-16
Proportion of Variance	0.980	0.020	0
Cumulative Proportion	0.980	1	1
Loadings			
length of calcaneal body (PDA)	-0.593	-0.732	-0.332
length of tuber (CTL)	0.487	-0.503	0.128
width of sustentaculum (MLS)	-0.385	0.459	-0.430
height of cuboid facet (HCF)	0.512	-0.023	-0.830

Table 2.23b. Between group PCA on calcaneus using cercopithecoid-only sample and Coding 2

PCA 2		
	PC 1	**PC 2**
Standard Deviation	1.036	3.93E-17
Proportion of Variance	1	0
Cumulative Proportion	1	1
Loadings		
total length (CL)	-0.432	0.589
length of calcaneal body (PDA)	-0.589	-0.757
height of cuboid facet (HCF)	0.683	-0.281

Table 2.23c. Between group PCA on calcaneus using entire anthropoid sample

	PC 1	**PC 2**	**PC 3**
Standard Deviation	0.069	0.023	0
Proportion of Variance	0.899	0.101	0
Cumulative Proportion	0.899	1	1
Loadings			
total length (CL)	-0.391	-0.296	-0.676
length of calcaneal body (PDA)	-0.276	-0.763	0.575
length of astragalar facet (PDF)	0.678	-0.202	-0.038
width of sustentaculum (MLS)	0.556	-0.303	-0.105
height of cuboid facet (HCF)	-0.048	0.445	0.447

Table 2.24a. Between group PCA on a combination of humerus, femur, astragalus, and calcaneus using cercopithecoid-only sample and Coding 1

	PC 1	**PC 2**	**PC3**
Standard Deviation	2.901	0.606	4.25E-16
Proportion of Variance	0.958	0.042	0
Cumulative Proportion	0.958	1.000	0
Loadings			
MLT	0.281	0.032	0.903
GTH	0.363	0.226	-0.128
HHI	0.187	-0.476	-0.170
AME	0.372	-0.257	-0.023
FL	-0.275	-0.122	0.101
PH	-0.281	0.047	-0.051
AL	-0.2088	-0.158	0.267
EL	-0.115	0.460	-0.042
WTH	0.206	0.411	-0.019
ATH	-0.224	-0.293	0.068
PDA	-0.313	-0.183	0.125
CTL	0.253	-0.247	-0.054
MLS	-0.199	0.217	0.155
HCF	0.267	-0.078	0.078

Table 2.24b. Between group PCA on a combination of humerus, femur, astragalus, and calcaneus using cercopithecoid-only sample and Coding 2

	PC 1	**PC 2**
Standard Deviation	2.234	1.963E-16
Proportion of Variance	1.00	0.00
Cumulative Proportion	1.00	1.00
Loadings		
MGT	0.168	0.900
MLT	0.229	-0.024
PDC	0.173	-0.067
GTH	0.326	0.251
HHI	0.266	0.005
AME	0.410	-0.084
FL	-0.270	-0.008
PH	-0.276	-0.013
AL	-0.239	0.016
EL	-0.259	0.200
WTH	0.136	-0.095
WED	0.194	-0.050
CL	-0.200	0.046
PDA	-0.273	0.189
HCF	0.317	-0.156

Table 2.24c. Between group PCA on a combination of humerus, femur, astragalus, and calcaneus using entire anthropoid sample

	PC 1	**PC 2**	**PC3**
Standard Deviation	6.407	1.444	5.84E-16
Proportion of Variance	0.952	0.048	0.000
Cumulative Proportion	0.952	1.000	1.000
Loadings			
MLHH	0.261	0.214	0.739
SIHH	0.272	-0.146	-0.395
MLT	-0.320	0.113	-0.117
BGW	-0.260	0.063	0.106
GTH	-0.040	0.400	-0.092
AME	-0.192	0.353	-0.015
APFH	0.193	0.098	0.043
PDHF	0.189	0.041	0.125
APLC	-0.262	0.062	-0.050
PW	0.238	0.113	-0.240
PDI	0.245	0.006	-0.110
FNA	0.300	-0.063	-0.093
ACON	-0.204	-0.125	-0.207
AL	-0.084	-0.306	0.029
HNPD	-0.192	-0.231	0.114
EL	0.196	-0.248	0.076
WTH	0.169	0.220	-0.089
CL	-0.256	-0.208	0.223
PDA	-0.096	-0.346	0.157
PDF	0.212	-0.159	0.133
MLS	0.167	-0.188	-0.054
HCF	-0.018	0.321	0.024

Figure 2.1. Plots of phylogenetic PCA on humerus; a) cercopithecoid-only sample with species labeled according to locomotor group, b) cercopithecoid-only sample with species labeled according to phylogenetic group, c) anthropoid sample with species labeled according to locomotor group, d) anthropoid sample with species labeled according to phylogenetic group. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

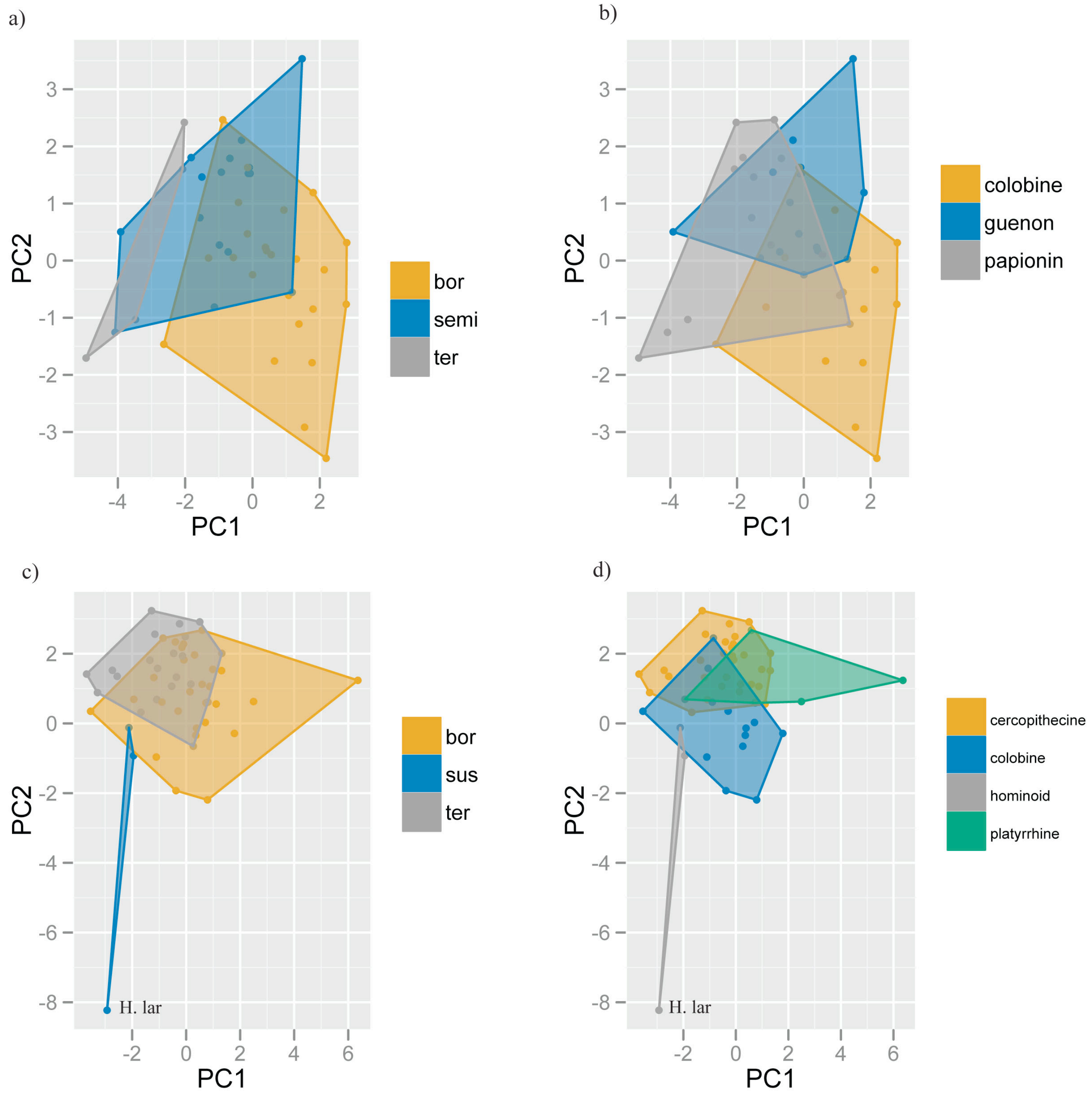


Figure 2.2a. Results for humerus by locomotor group (Coding 1) for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; HHI = humeral head index; GTH = height of the greater tubercle; MGT = width of the greater tubercle; MLT = width of the lesser tubercle; PDOF = height of the olecranon fossa; PDC = height of the capitulum; AME = angle of the medial epicondyle

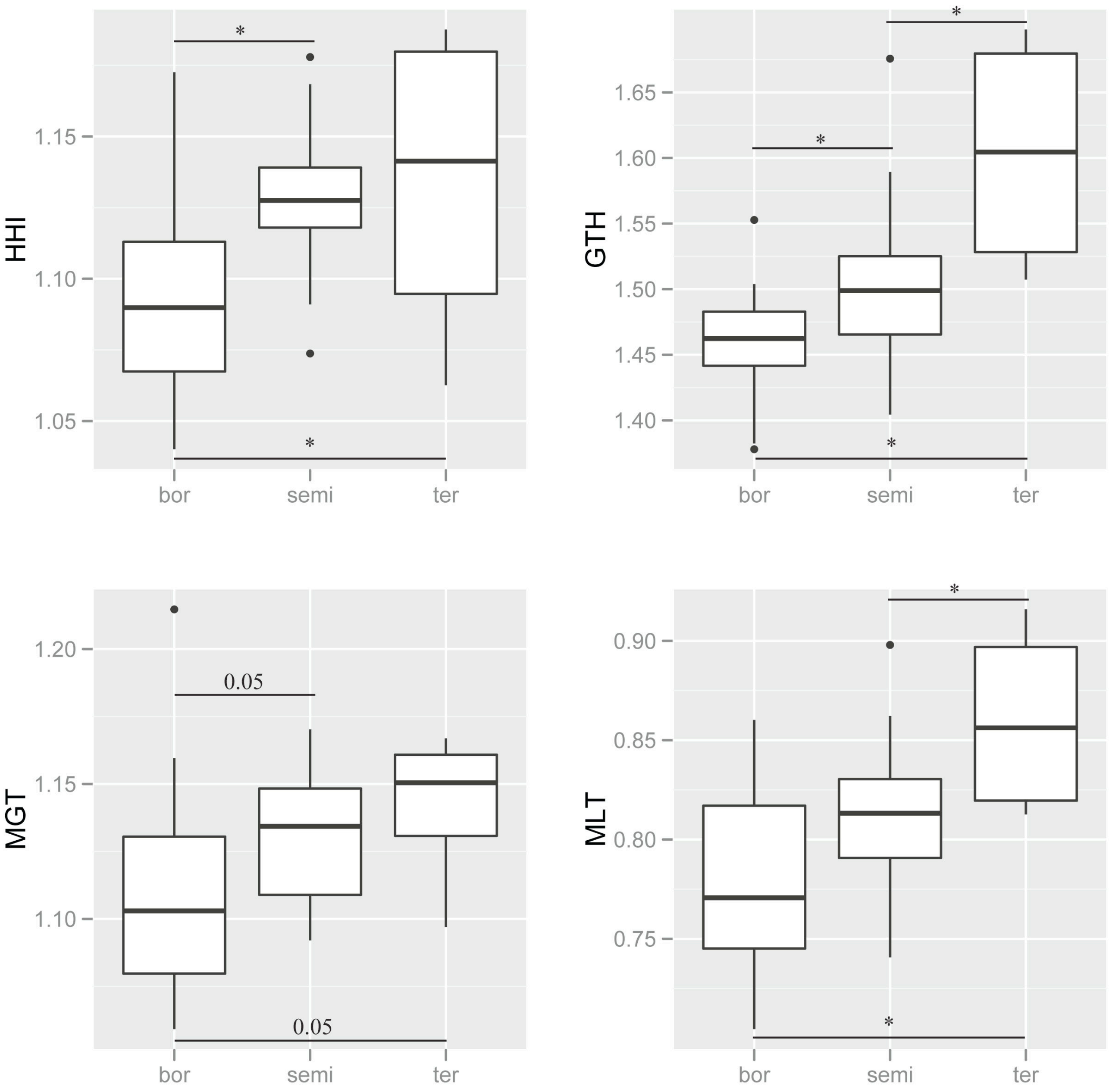


Figure 2.2a continued

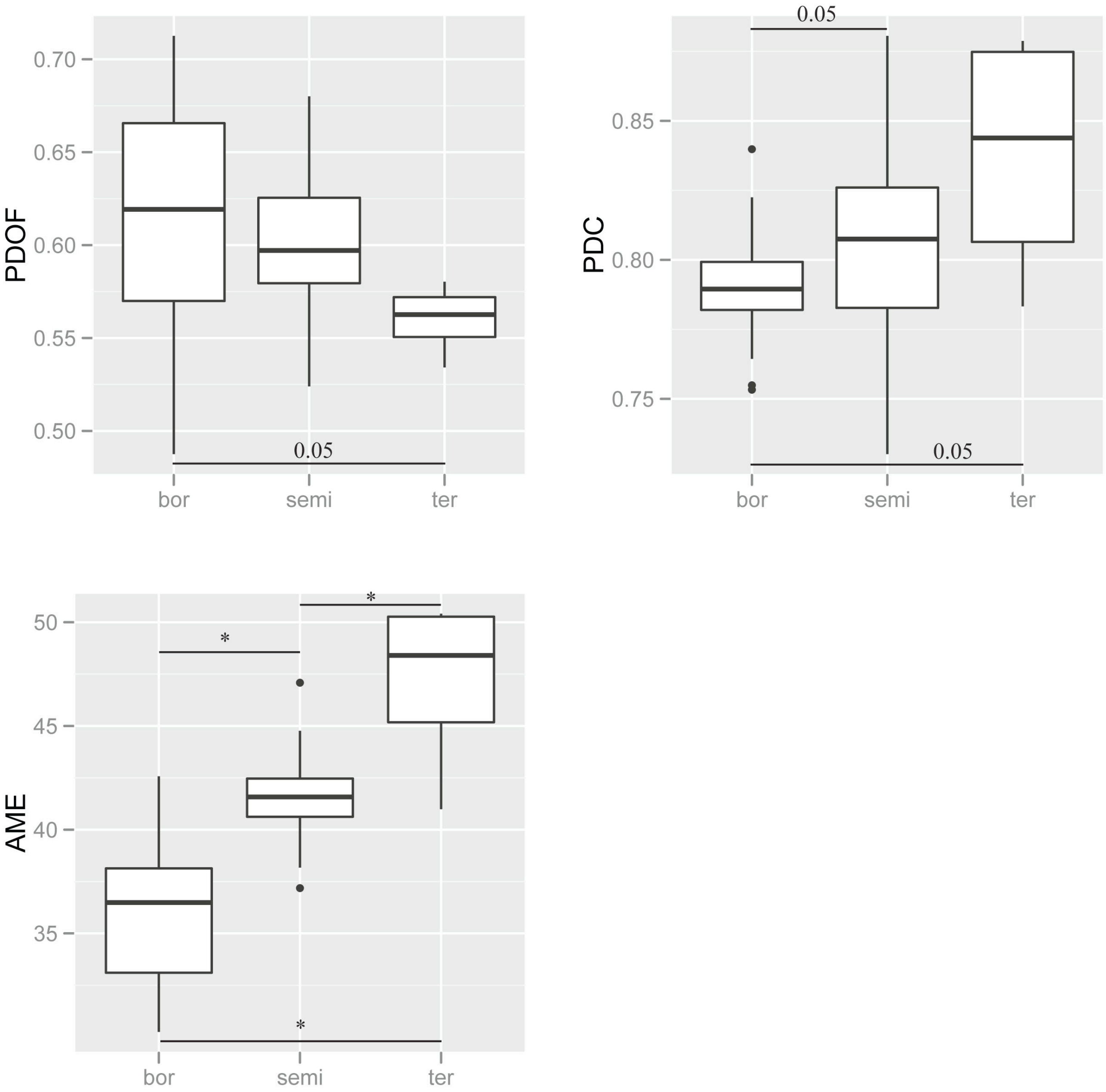


Figure 2.2b. Results for humerus by locomotor group (Coding 2) for cercopithecoid-only sample. All results significant. bor = arboreal; ter = terrestrial; HL = length of the humerus; HHI = humeral head index; GTH = height of the greater tubercle; MLT = width of the greater tubercle; MLT = width of the lesser tubercle; PDC = height of the capitulum; AME = angle of the medial epicondyle

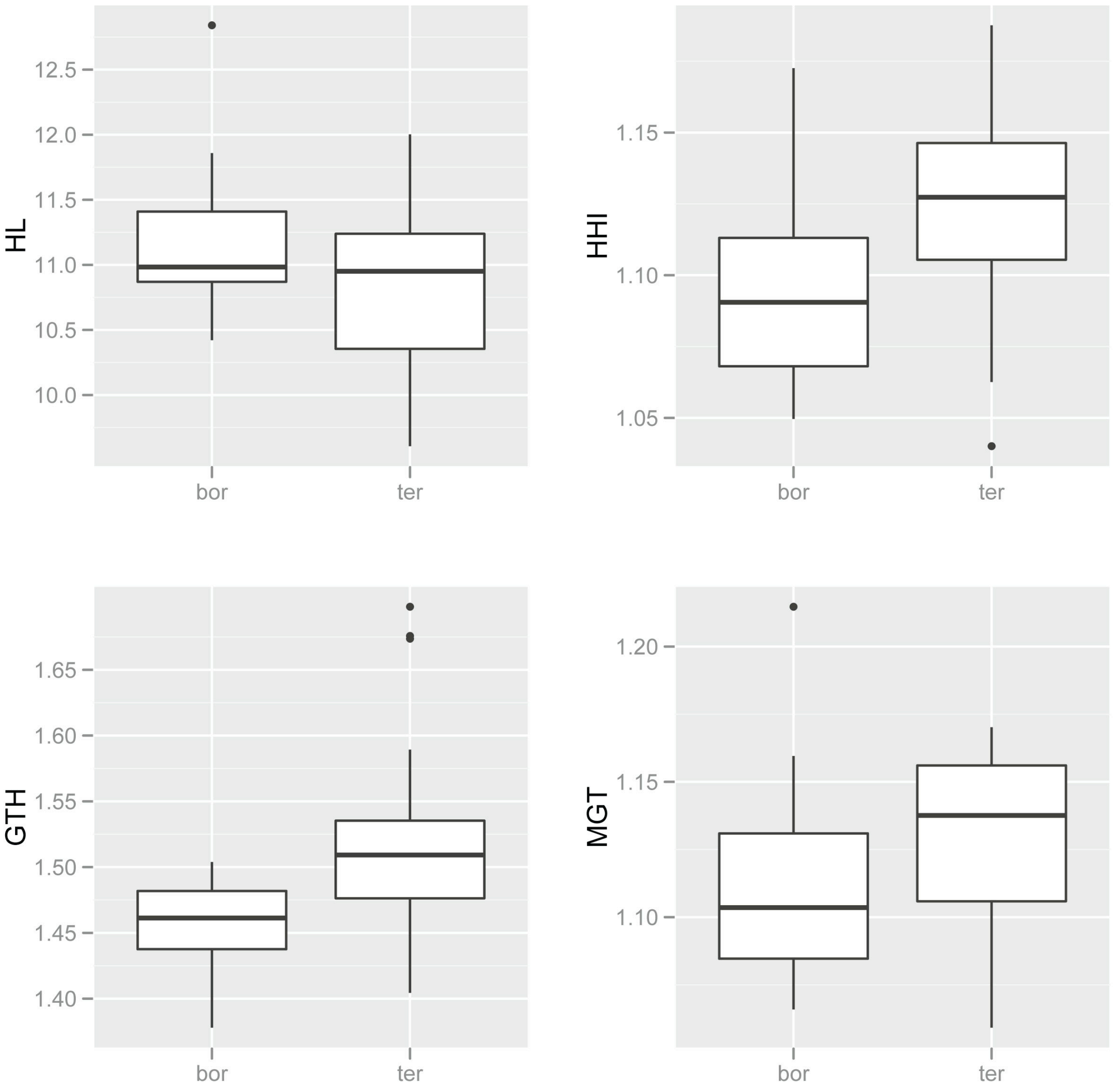


Figure 2.2b continued.

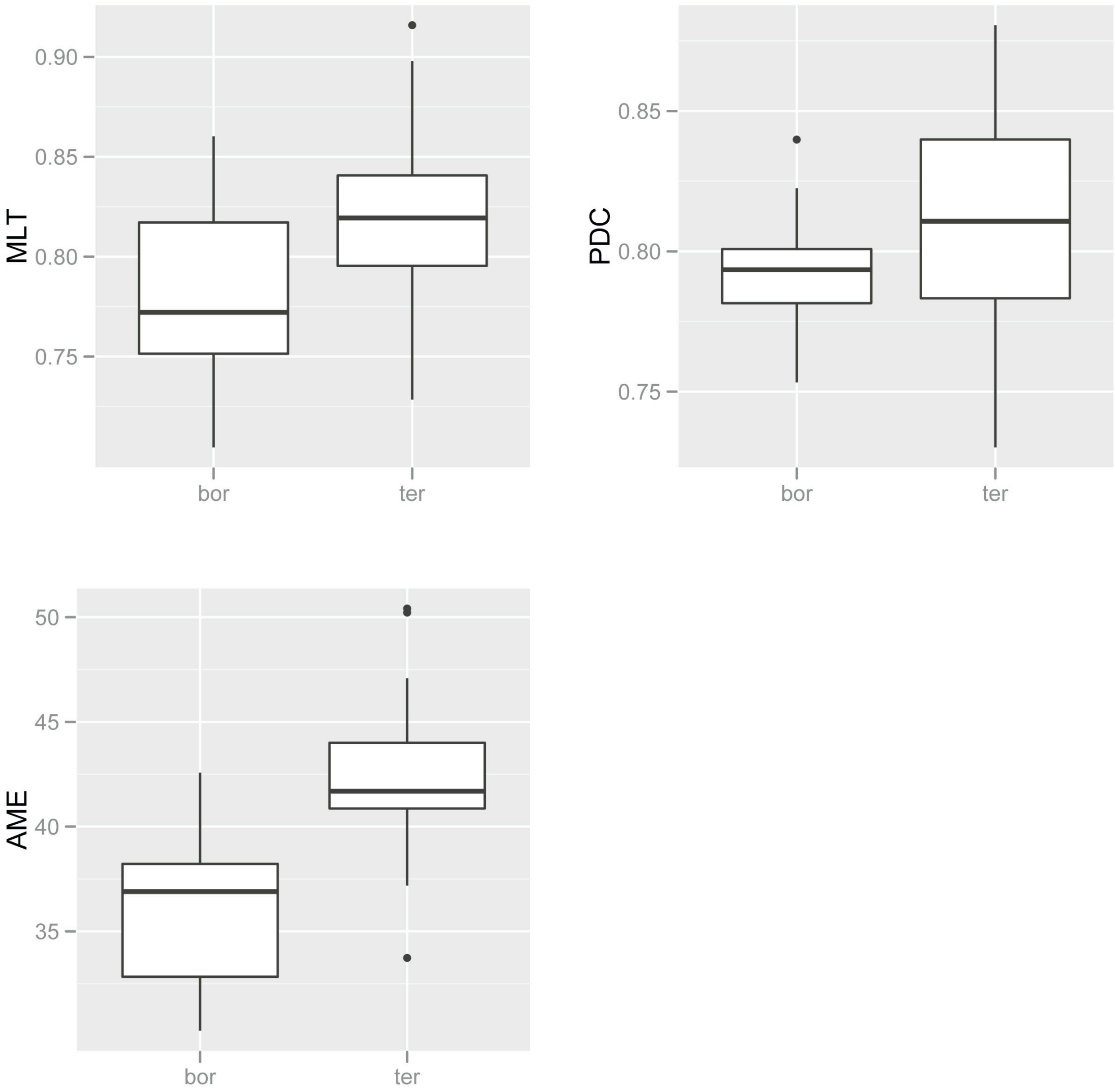
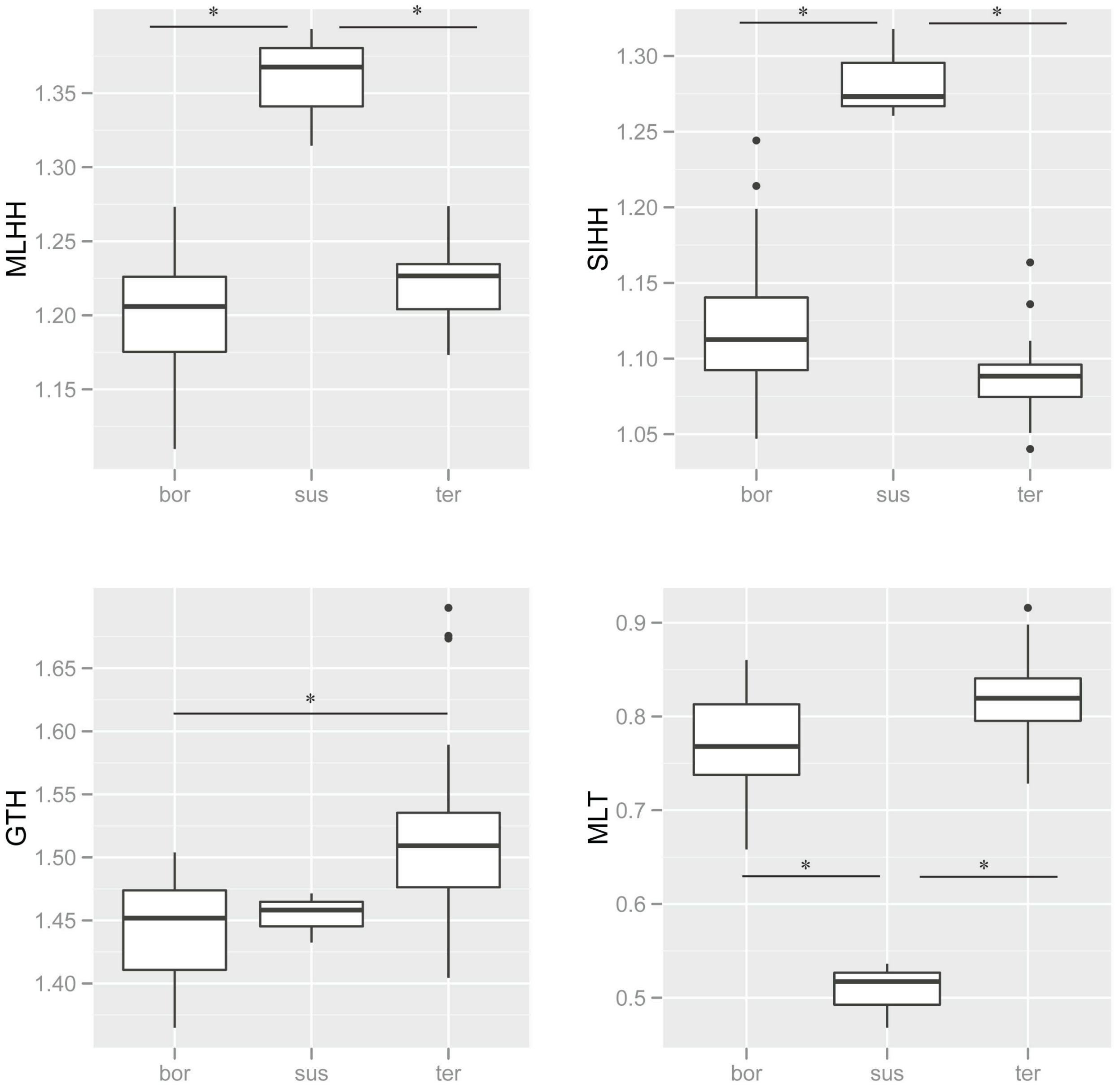


Figure 2.2c. Results for humerus by locomotor group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; ter = terrestrial; sus = suspensory; MLHH = width of the humeral head; SIHH = height of the humeral head; GTH = height of the greatertubercle; MLT = width of the lesser tubercle; BGW = width of biciptal groove; MLTR = width of the trochlea; MLCT = width of the distal articular surface; BB = biepicondylar breadth; AME = angle of the medial epicondyle



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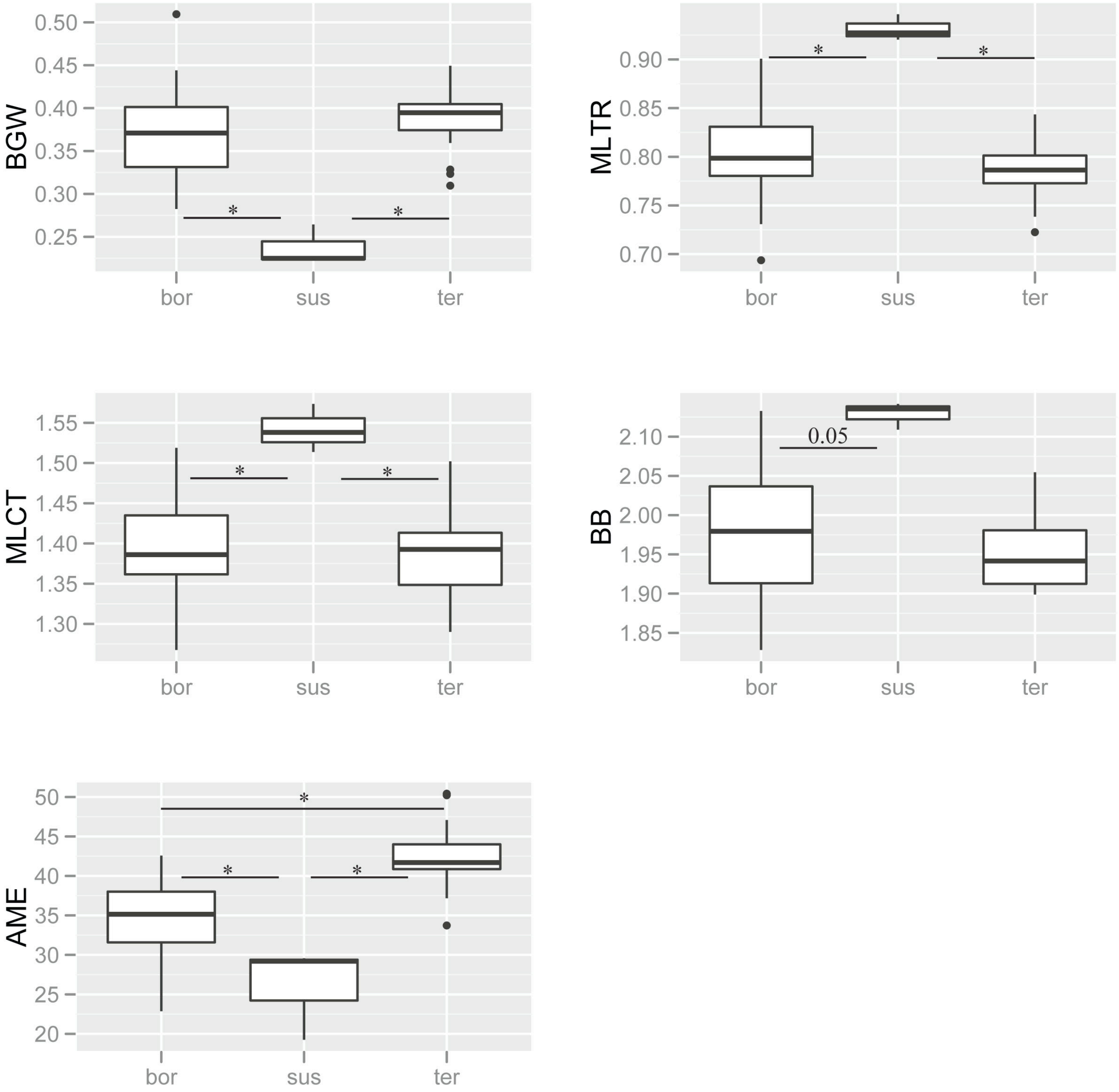
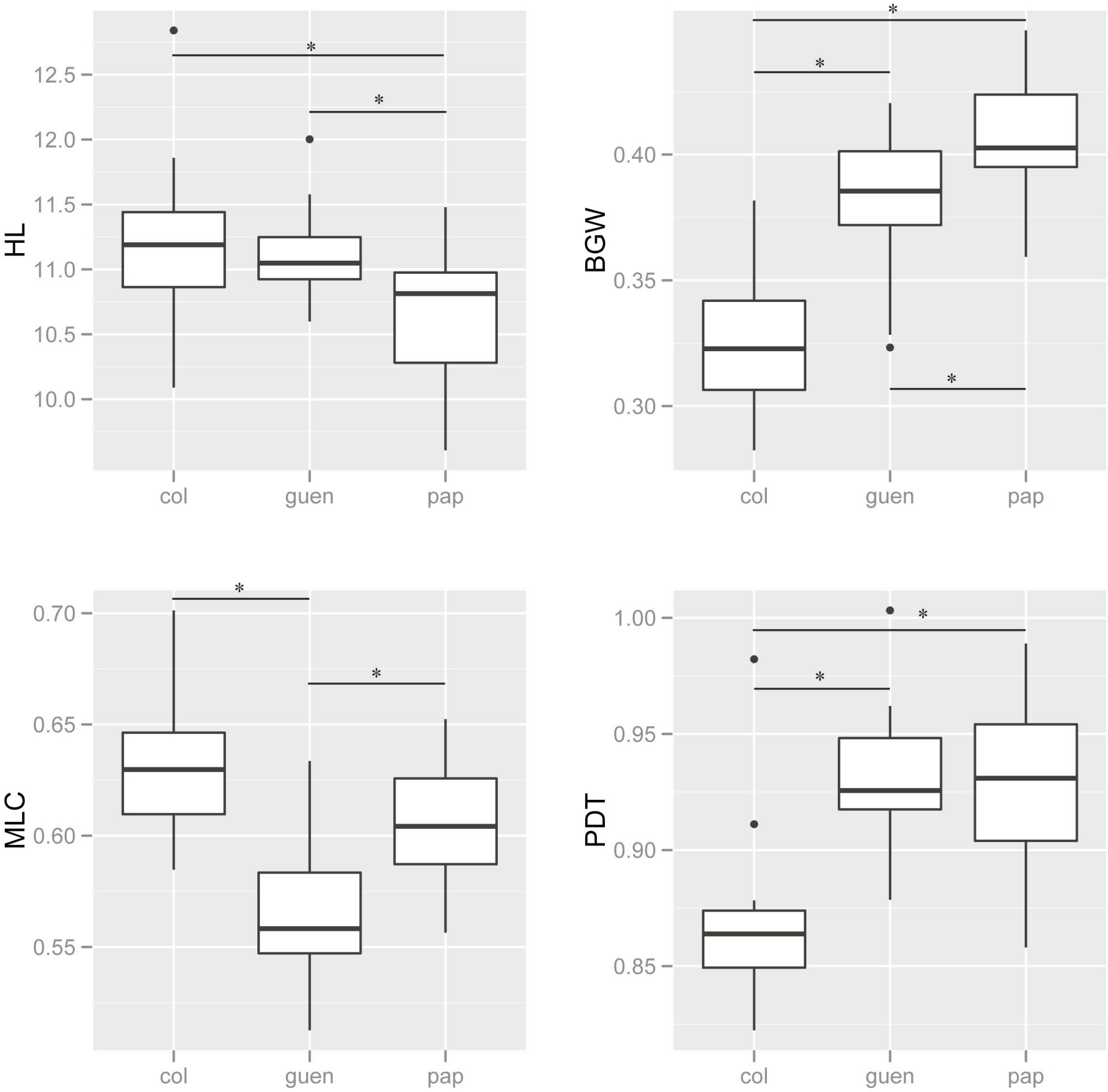


Figure 2.3a. Results for humerus by phylogenetic group for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. col = colobine; guen = guenon; pap = papionin; HL = length of humerus; BGW = width of bicipital groove; MLC = width of capitulum; PDT = depth of trochlea; MLCT = width of the distal articular surface; BB = biepicondylar breadth; AME = angle of the medial epicondyle



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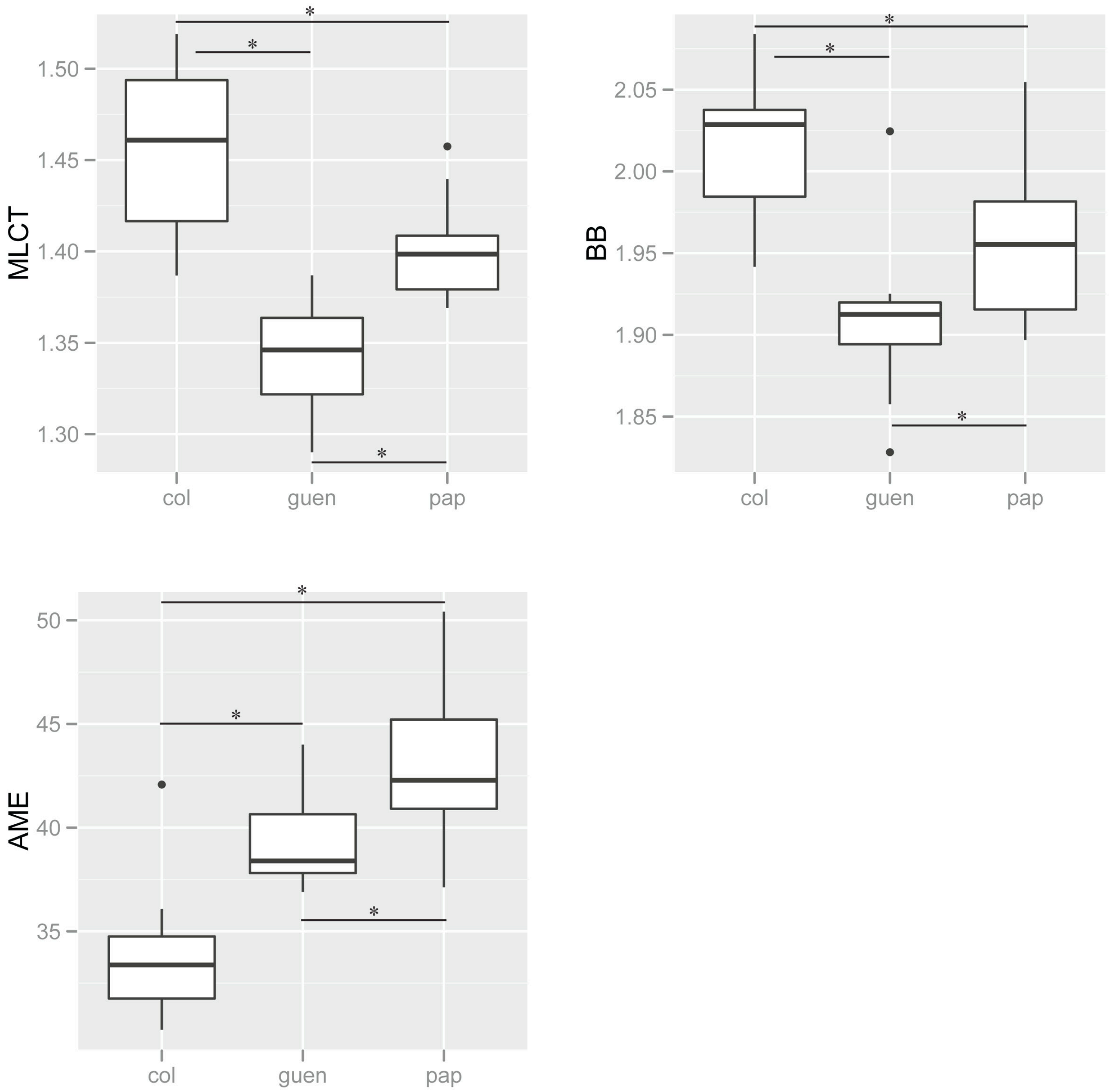
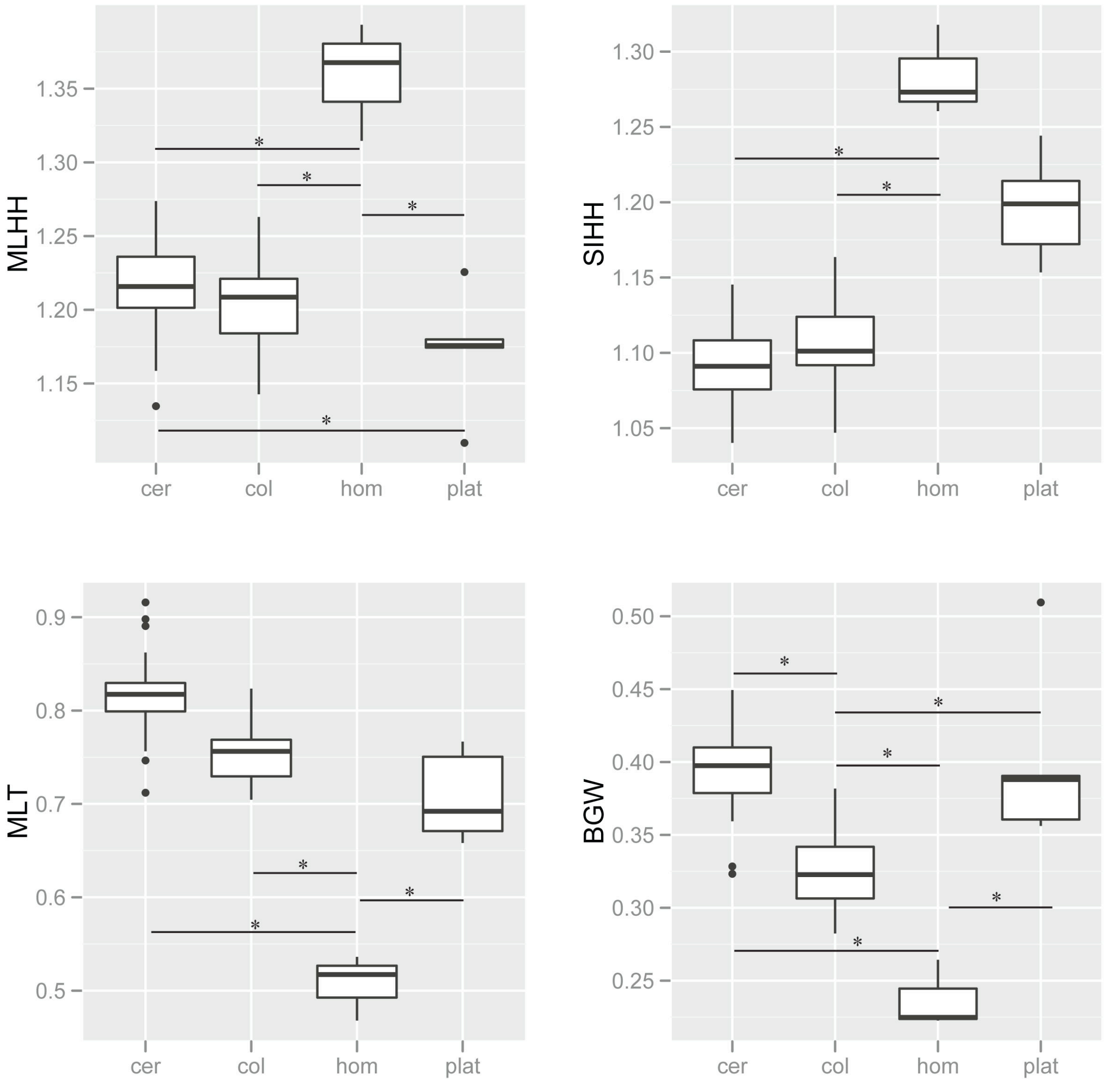


Figure 2.3b. Results for humerus by phylogenetic group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. cer = cercopithecine; col = colobine; hom = hominoid; plat = platyrrhine; MLHH = width of humeral head; SIHH = height of humeral head; MLT = width of lesser tubercle; BGW = width of bicipital groove; MLCT = width of the distal articular surface; BB = biepicondylar breadth; AME = angle of the medial epicondyle



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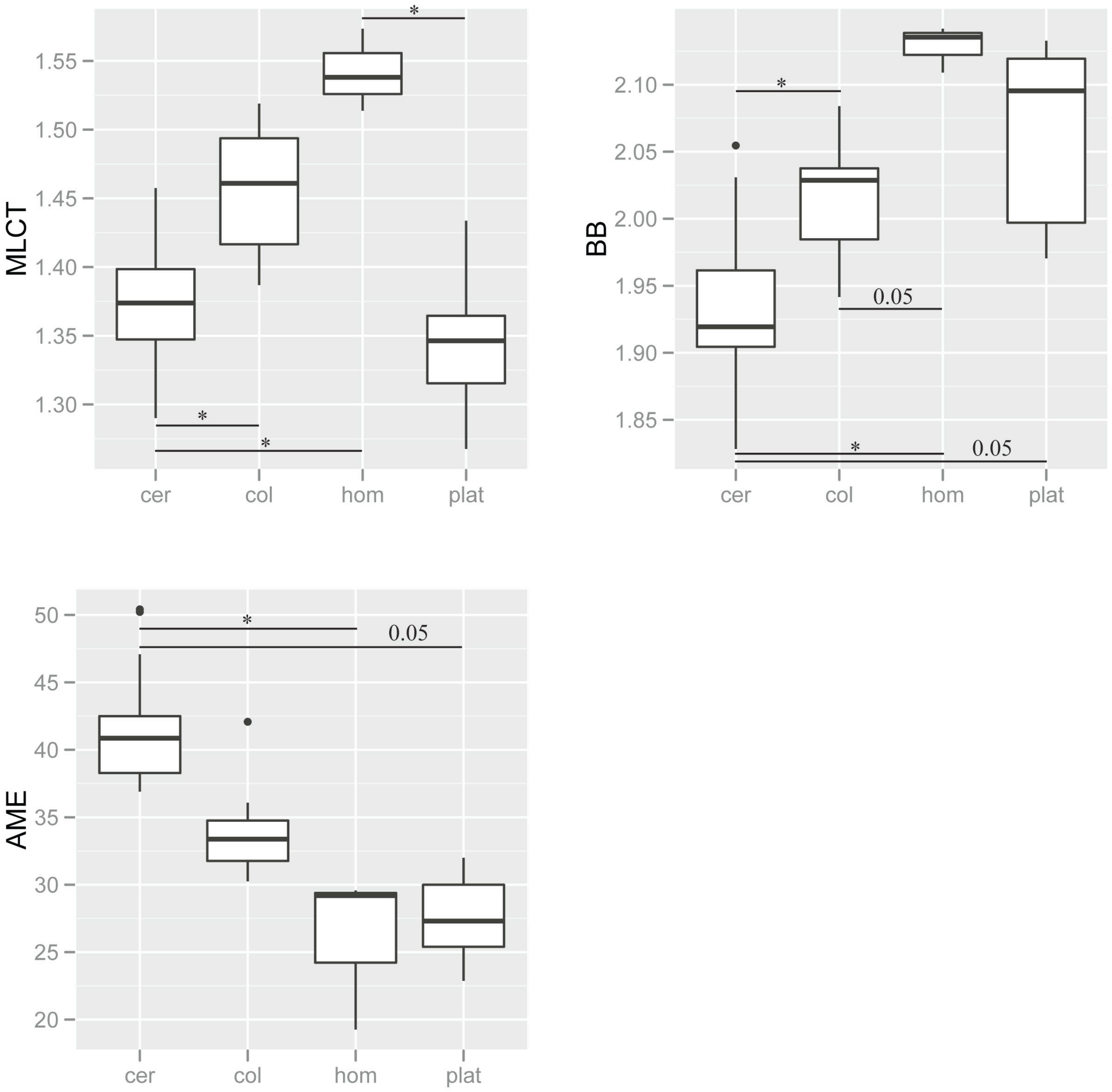


Figure 2.4. Plots of between-group PCAs on humerus; a) cercopithecoid-only sample with species assigned using Coding 1, b) cercopithecoid-only sample with species assigned using Coding 2, c) entire anthropoid sample. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

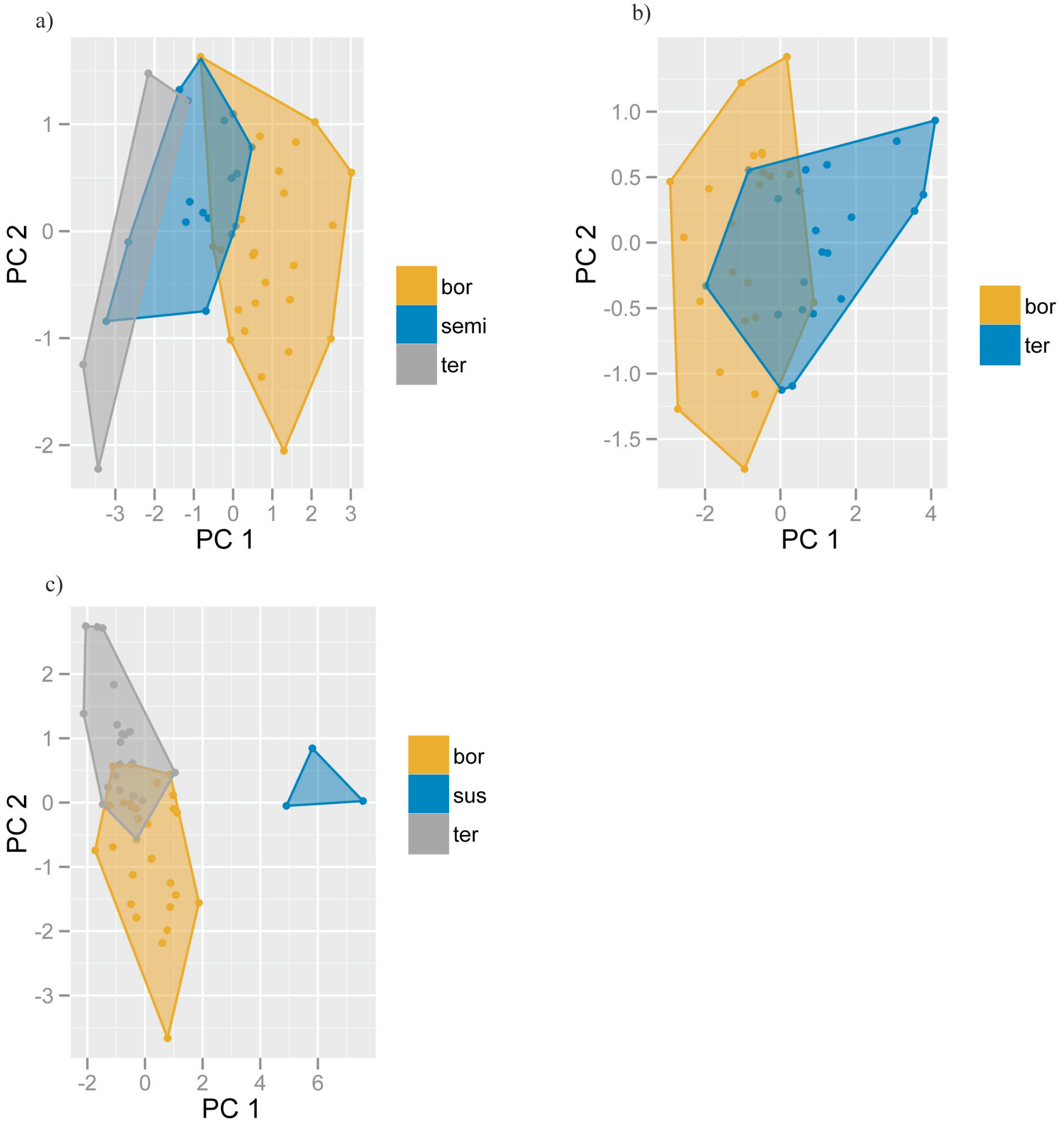


Figure 2.5. Plots of phylogenetic PCA on femur; a) cercopithecoid-only sample with species labeled according to locomotor group, b) cercopithecoid-only sample with species labeled according to phylogenetic group, c) anthropoid sample with species labeled according to locomotor group, d) anthropoid sample with species labeled according to phylogenetic group. bor = arboreal, semi = semi-terrestrial; ter = terrestrial, sus = suspensory

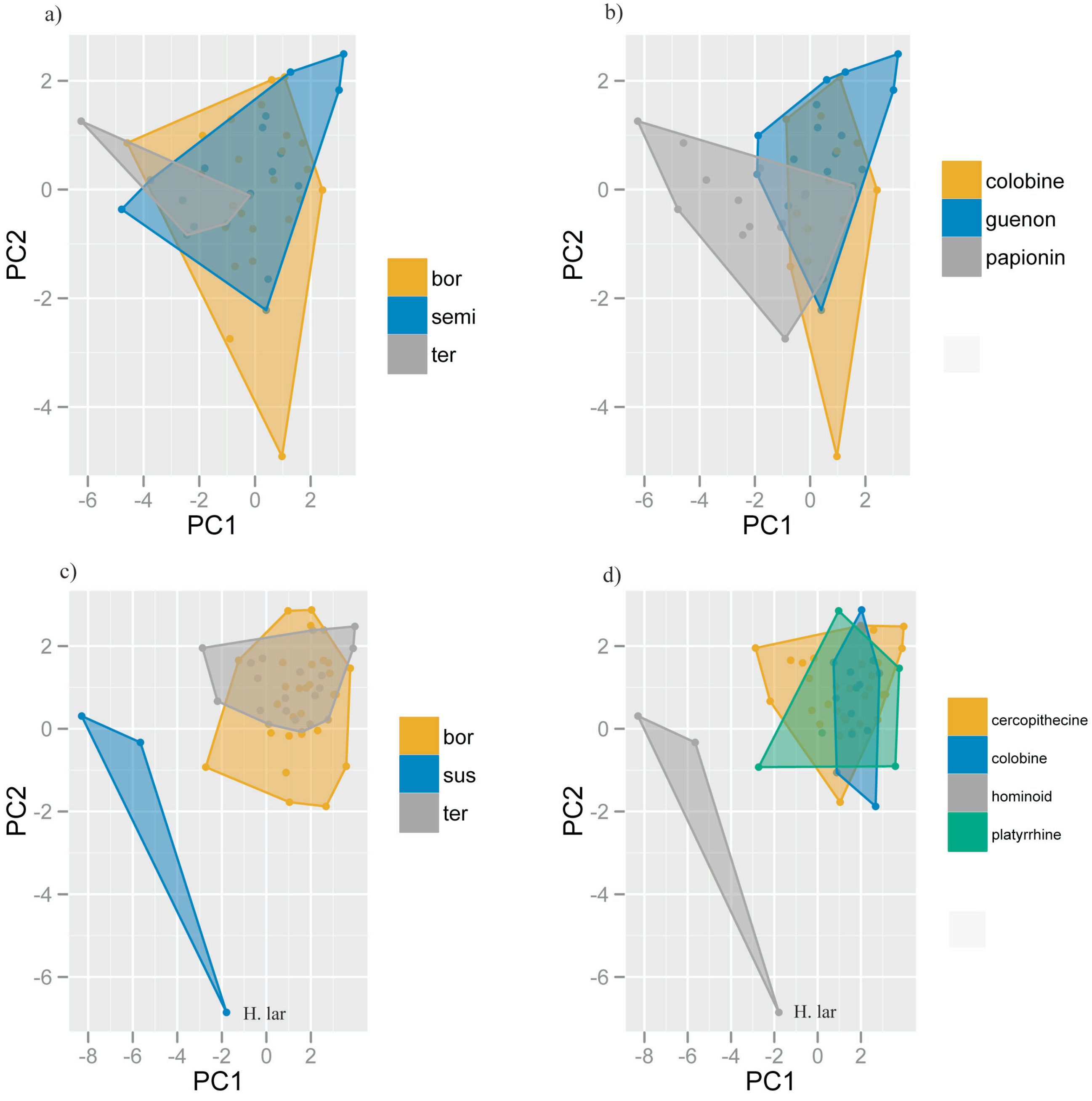


Figure 2.6a. Results for femur by locomotor group (Coding 1) for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; FL = length of femur; PH = height of patellar groove

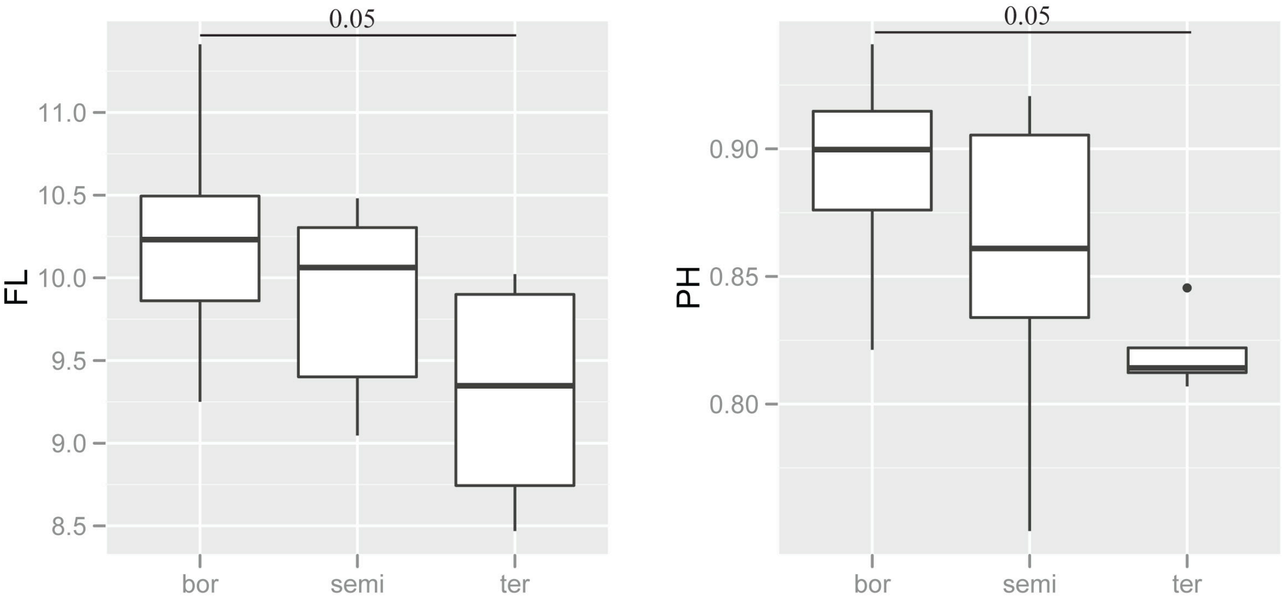


Figure 2.6b. Results for femur by locomotor group (Coding 2) for cercopithecoid-only sample. All results significant. bor = arboreal; ter = terrestrial; FL = length of femur; PH = height of patellar groove

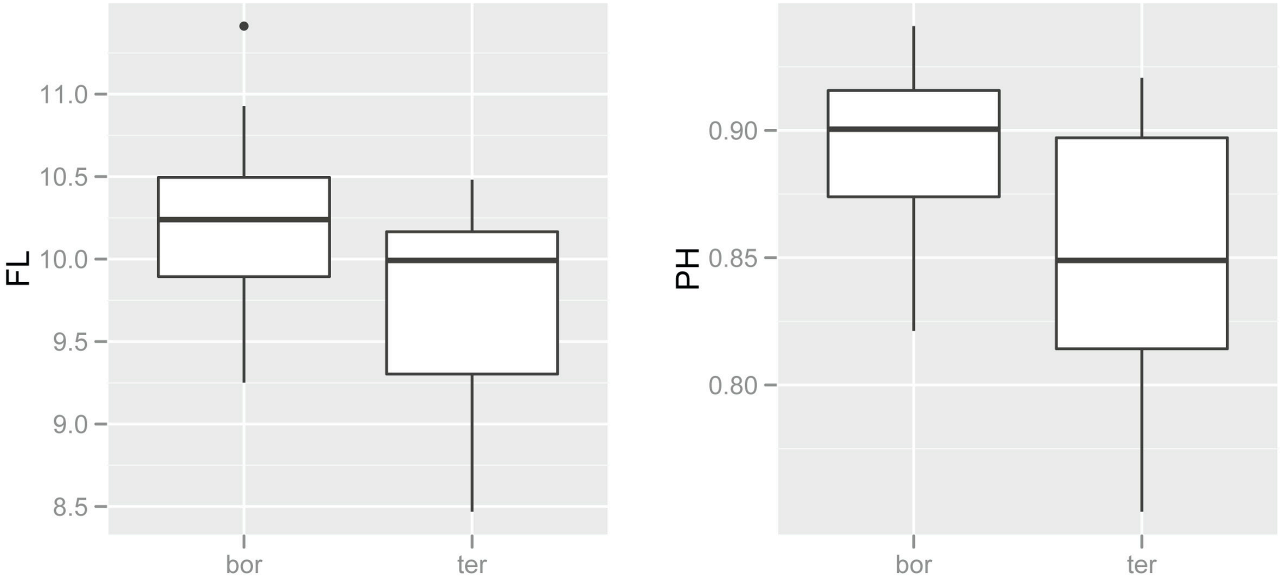
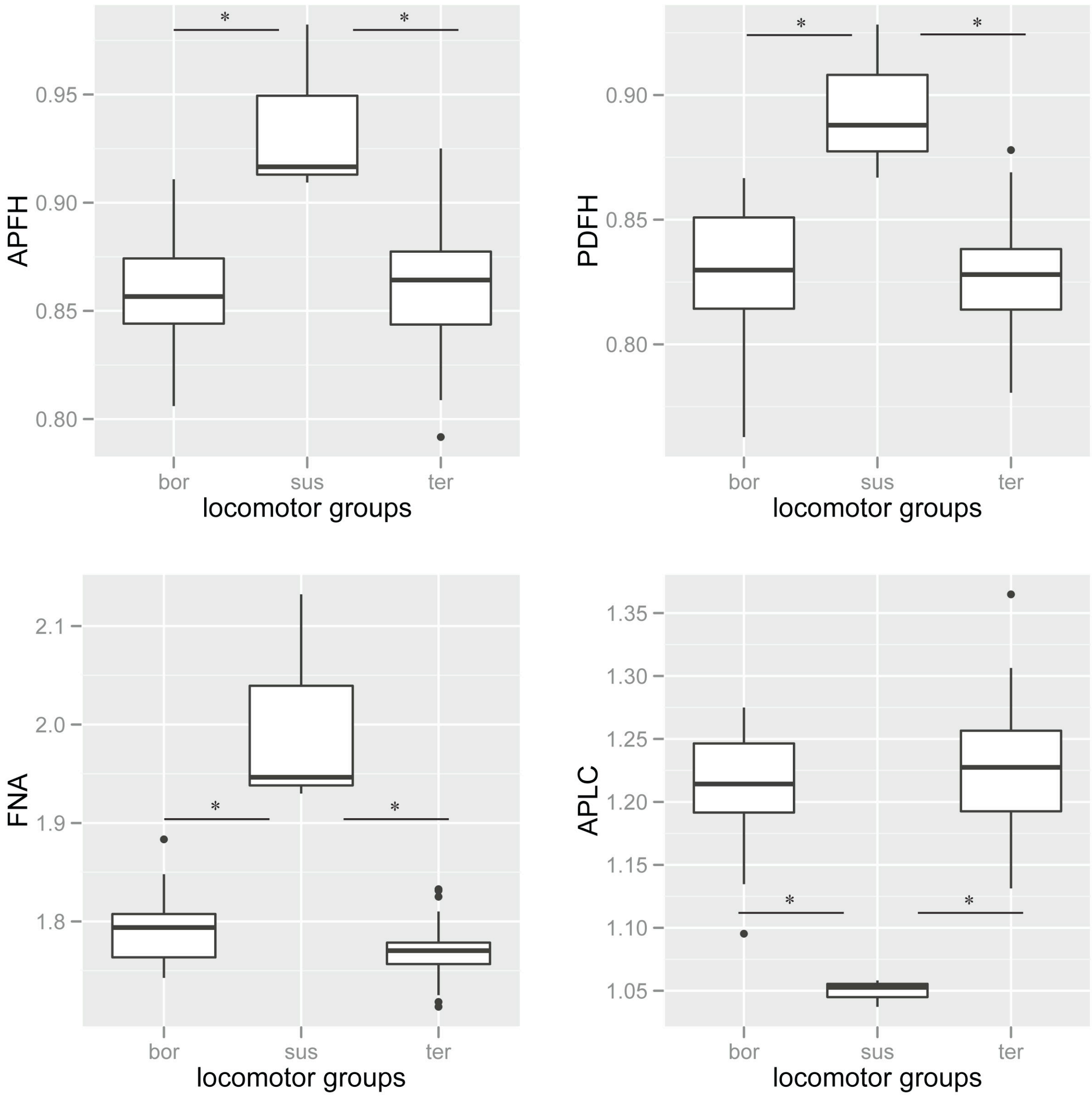


Figure 2.6c. Results for femur by locomotor group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; ter = terrestrial; sus = suspensory; APFH = width of femoral head; PDFH = height of femoral head; FNA = femoral neck angle; APLC = depth of lateral condyle; PDLC = height of lateral condyle; PDI = proximodistal height index; ACON = conylar asymmetry; PW = width of patellar groove



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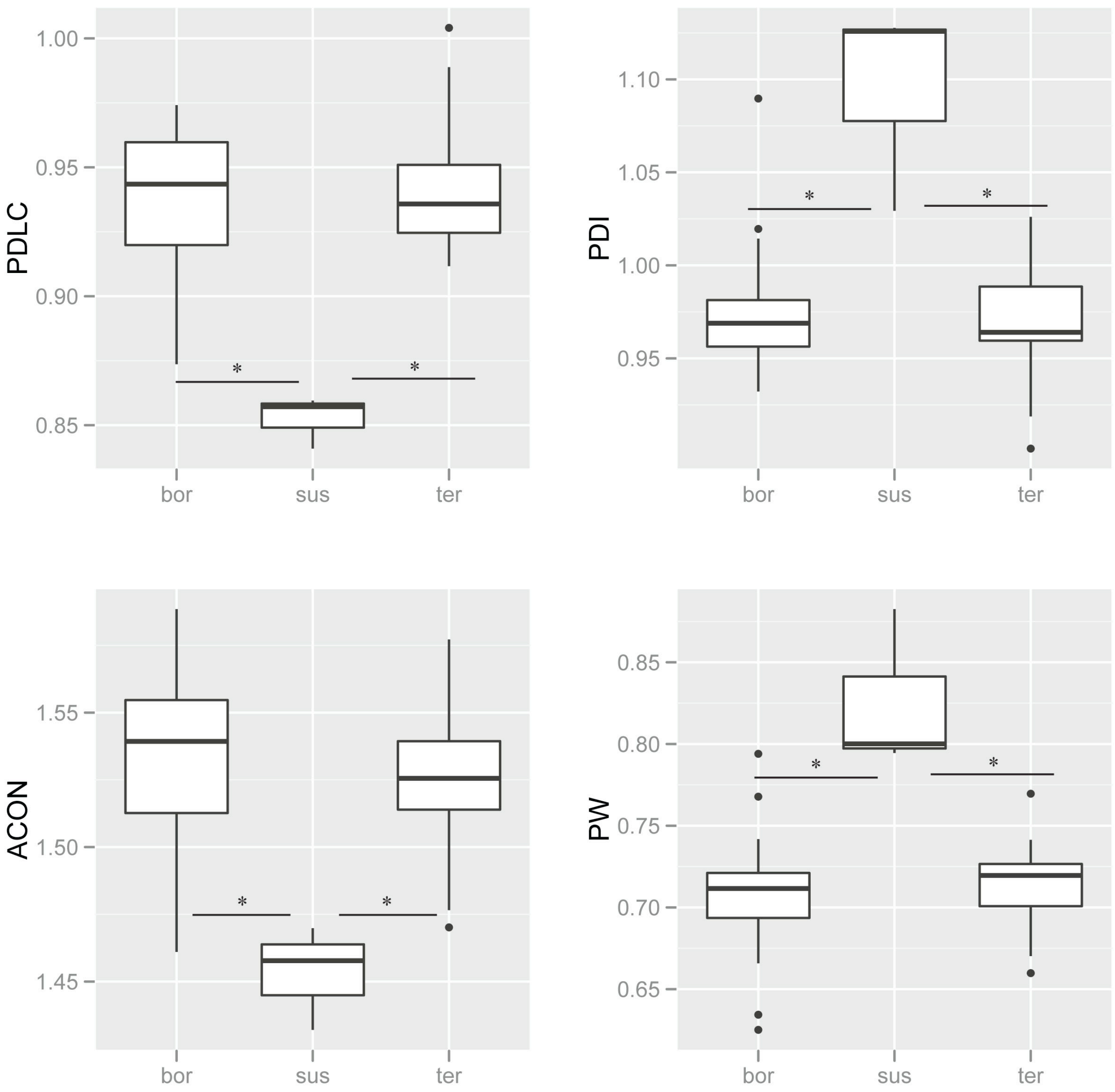
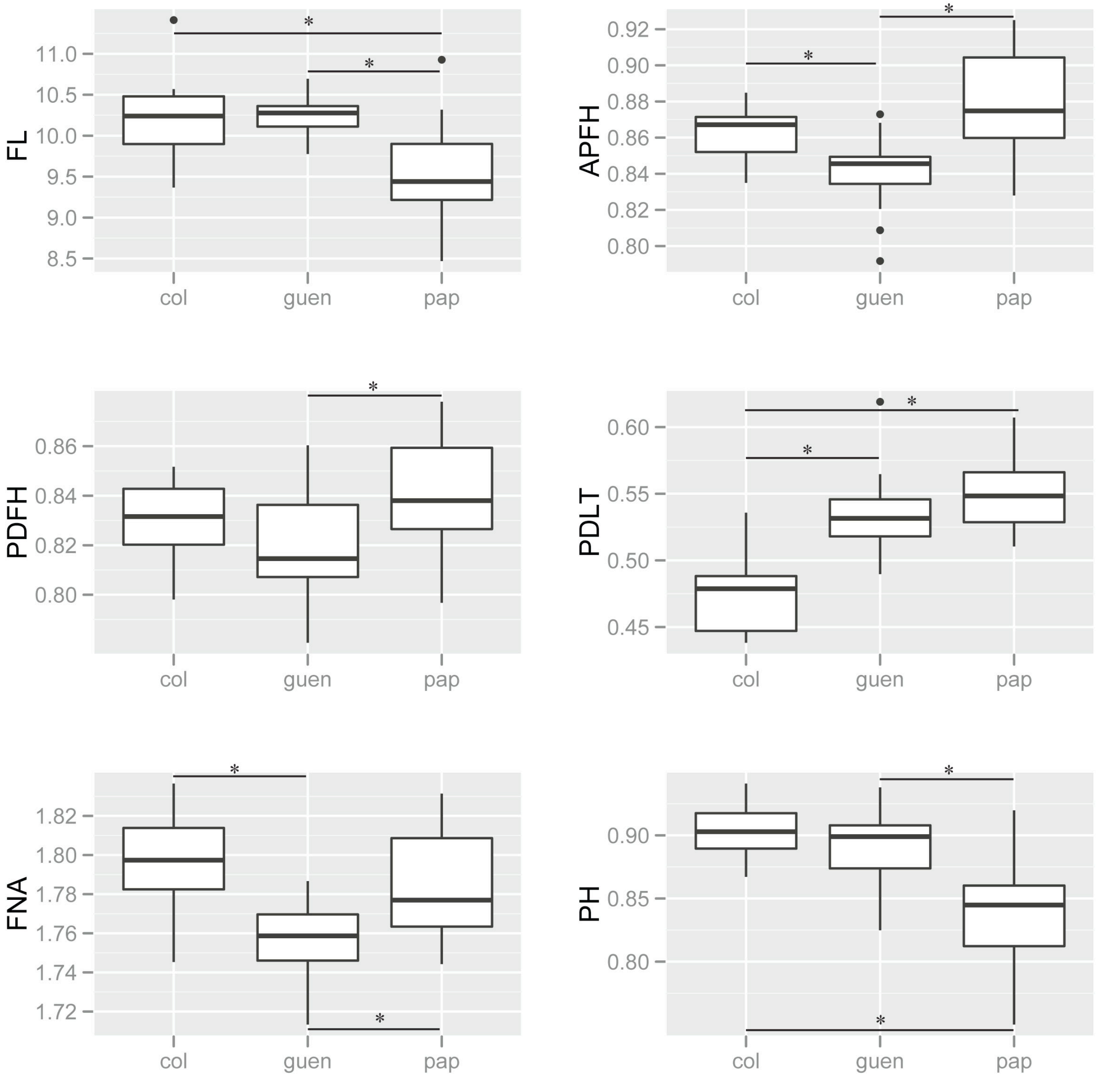


Figure 2.7a. Results for femur by phylogenetic group for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. col = colobine; guen = guenon; pap = papionin; FL = length of femur; APFH = width of femoral head; PDFH = height of femoral head; PDLT = height of lesser trochanter; FNA = femoral neck angle; PH = height of patellar groove; APMC = depth of medial condyle; APLC = depth of lateral condyle; PDLC = height of lateral condyle; MLLC = width of lateral condyle; PDI = proximodistal height condylar index; ACON = condylar asymmetry



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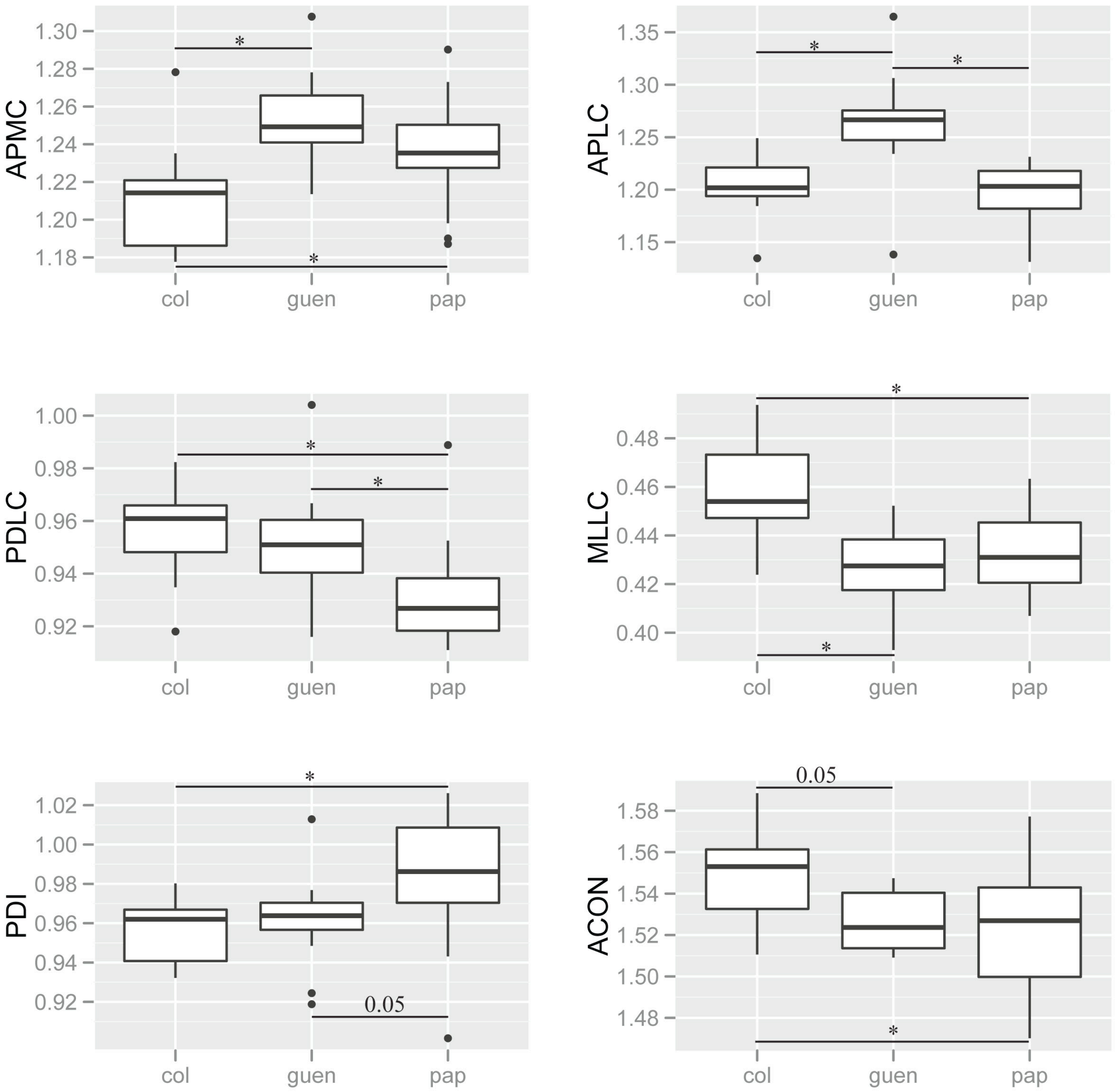
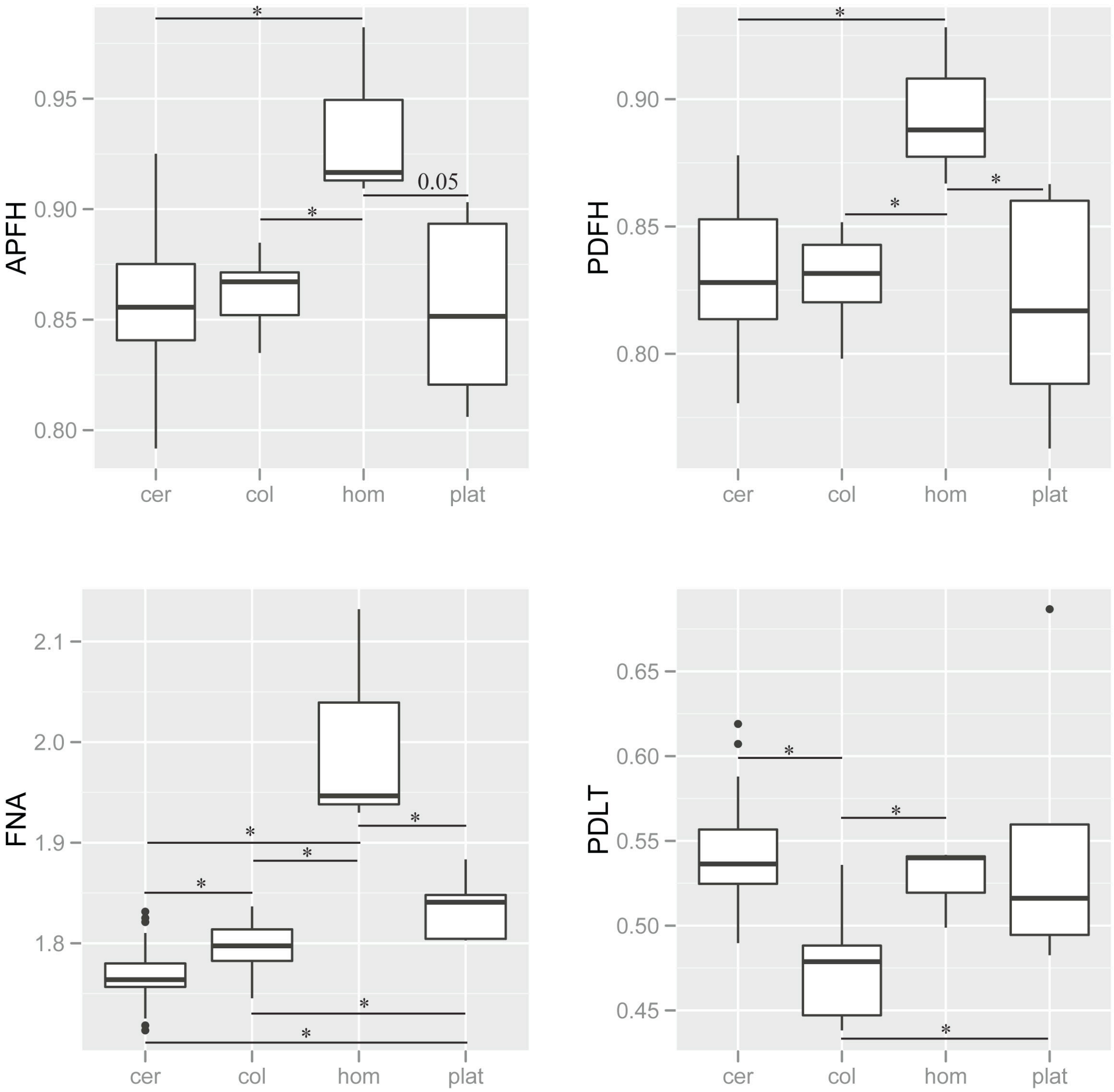


Figure 2.7b. Results for femur by phylogenetic group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. cer = cercopithecine; col = colobine; hom = hominoid; plat = platyrrhine; APFH = width of femoral head; PDFH = height of femoral head; FNA = femoral neck angle; PDLT = height of lesser trochanter; APMC = depth of medial condyle; APLC = depth of lateral condyle; PDLC = height of lateral condyle; PDI = proximodistal height condylar index; ACON = condylar asymmetry; PW = width of patellar groove



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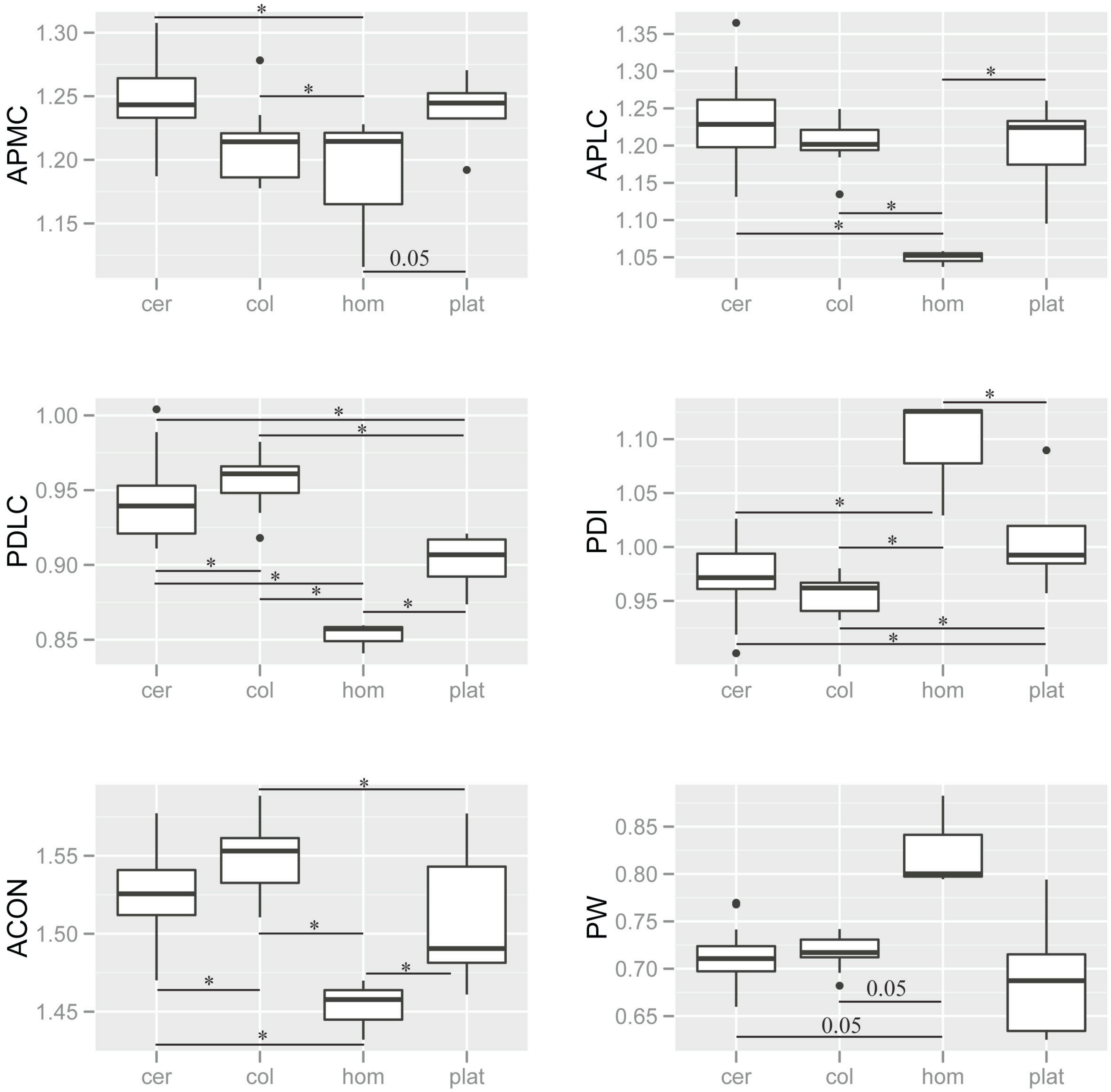


Figure 2.8. Plots of between-group PCAs on femur; a) cercopithecoid-only sample with species assigned using Coding 1, b) cercopithecoid-only sample with species assigned using Coding 2, c) entire anthropoid sample. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

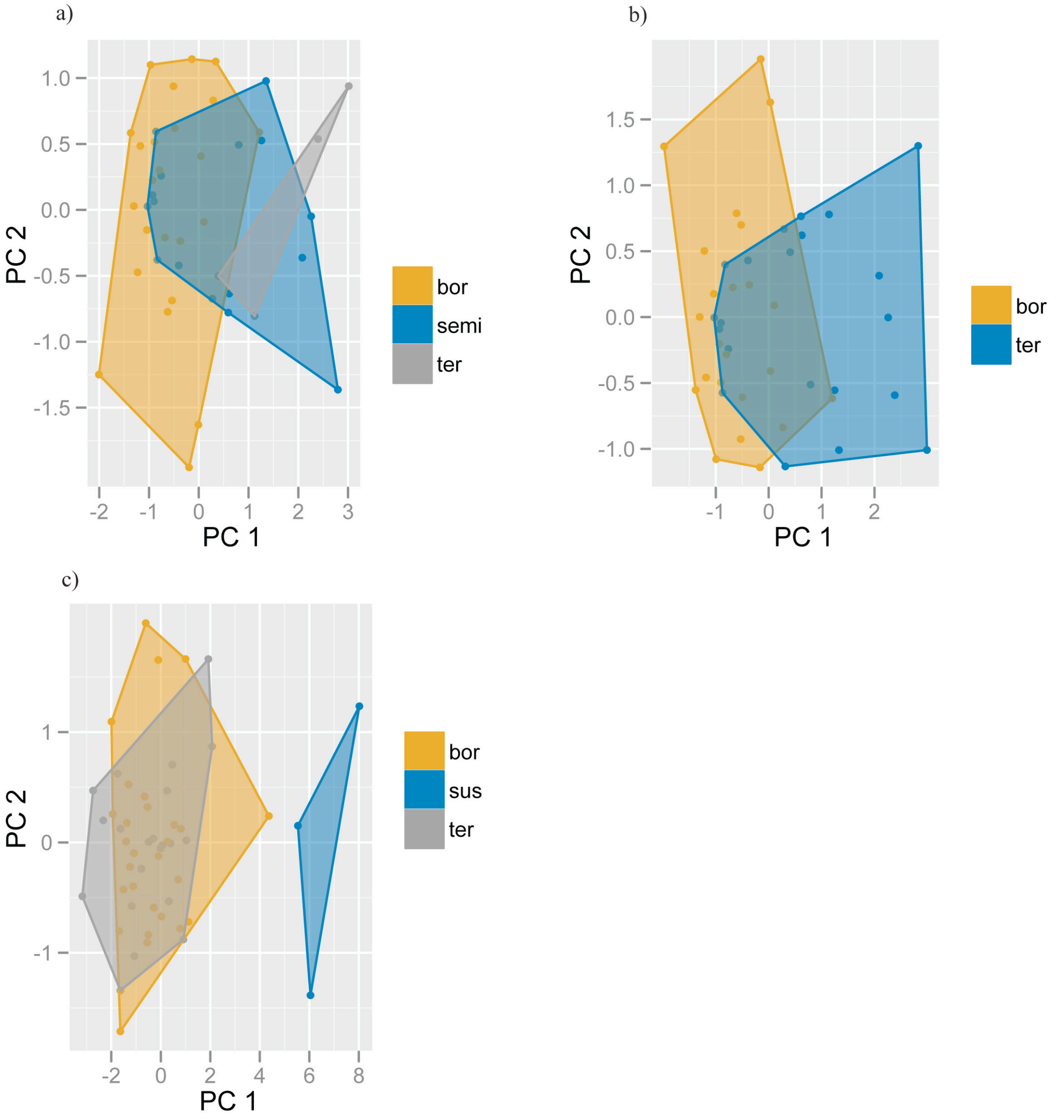


Figure 2.9. Plots of phylogenetic PCA on astragalus; a) cercopithecoid-only sample with species labeled according to locomotor group, b) cercopithecoid-only sample with species labeled according to phylogenetic group, c) anthropoid sample with species labeled according to locomotor group, d) anthropoid sample with species labeled according to phylogenetic group. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

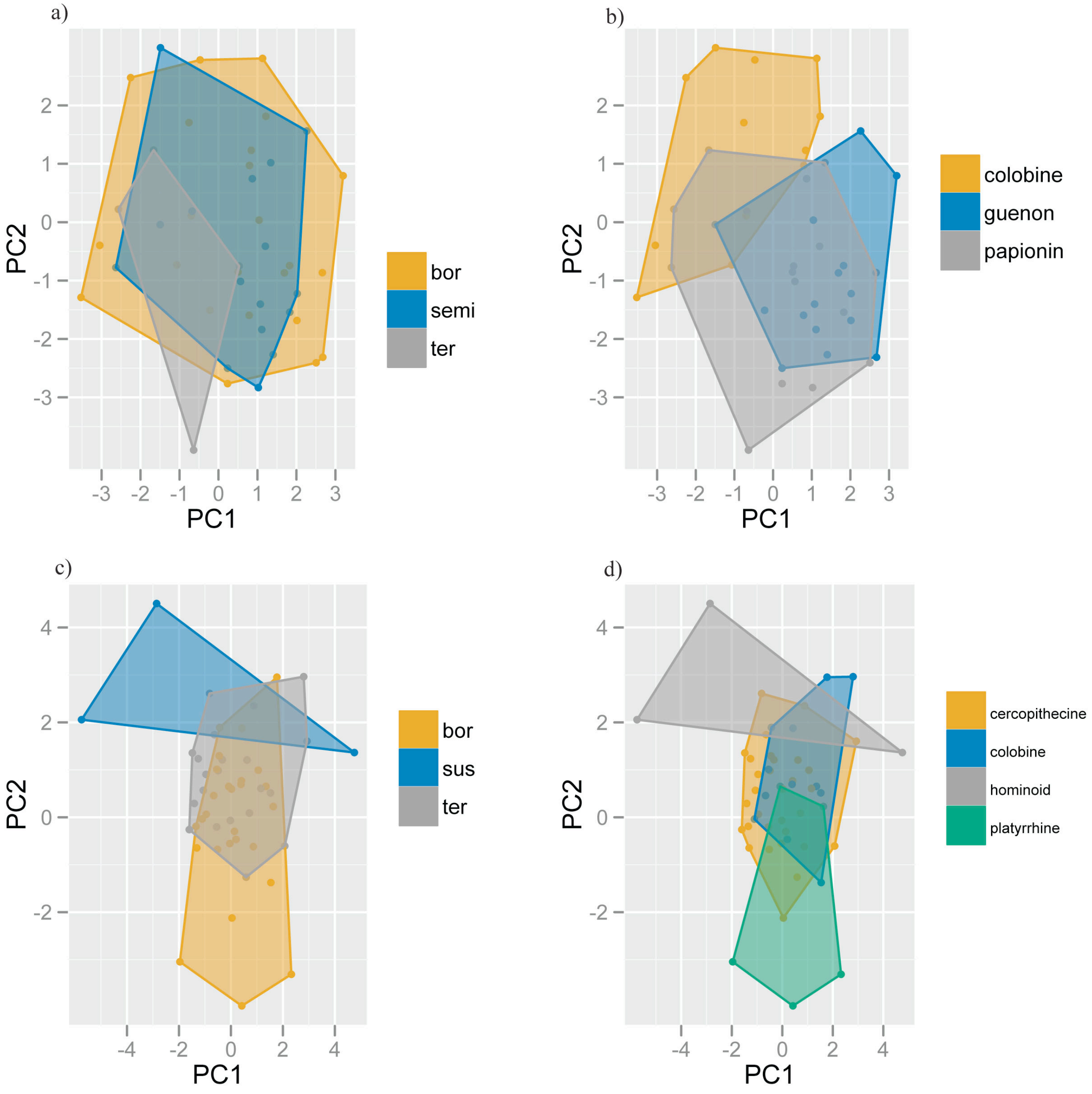


Figure 2.10a. Results for astragalus by locomotor group (Coding 1) for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; AL = length of astragalus; EL = ectal facet length; WTH = width of astragalar head; ATH = angle of astragalar head

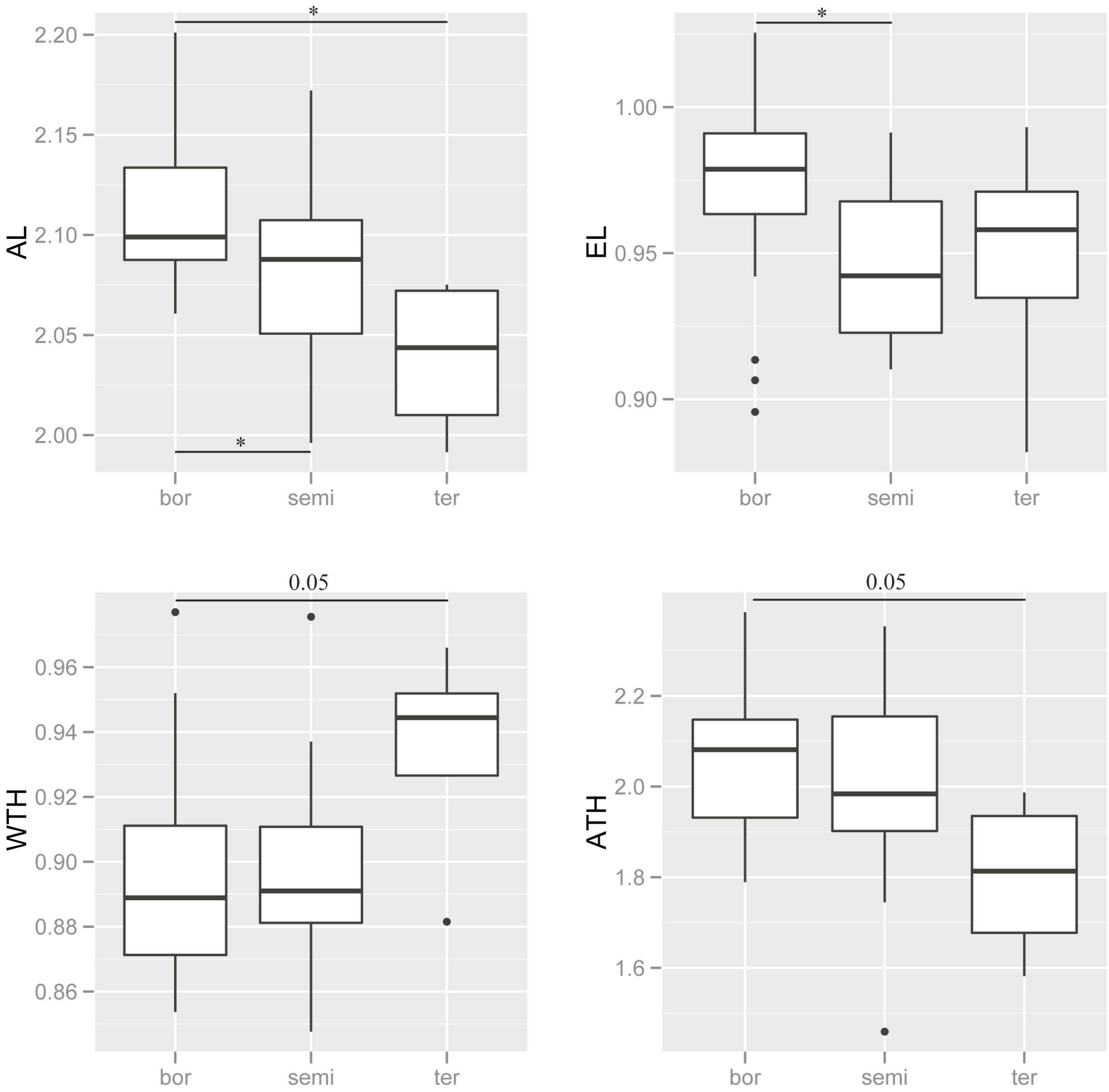


Figure 2.10b. Results for astragalus by locomotor group (Coding 2) for cercopithecoid-only sample. All results significant. bor = arboreal; ter = terrestrial; AL = length of astragalus; EL = ectal facet length; WTH = width of astragalar head; WED = trochlear wedging

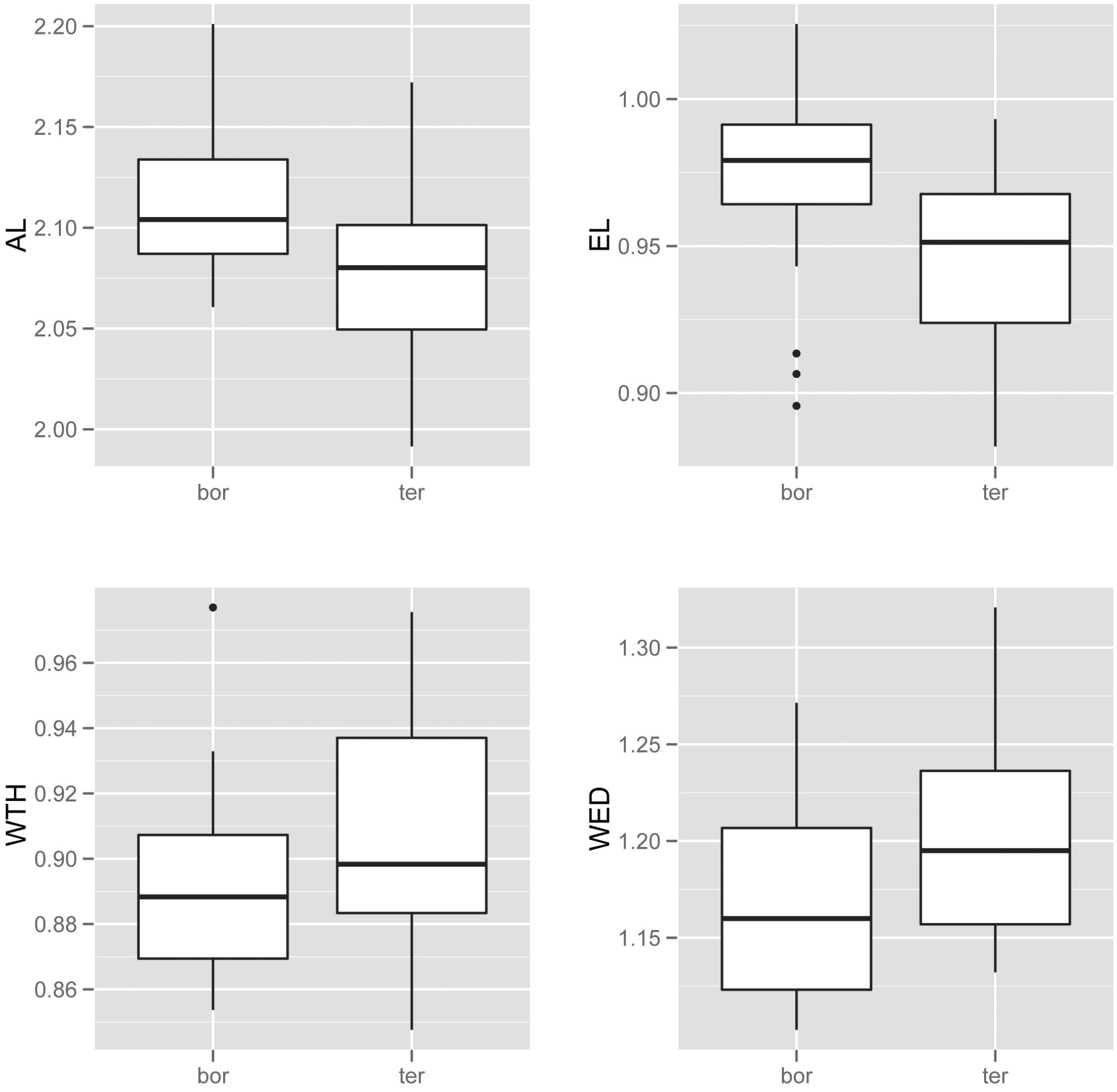


Figure 2.10c. Results for astragalus by locomotor group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. critical values. bor = arboreal; ter = terrestrial; sus = suspensory; AL = length of the astragalus; HNPD = length of head and neck; EL = ectal facet length; WTH = width of astragalar head

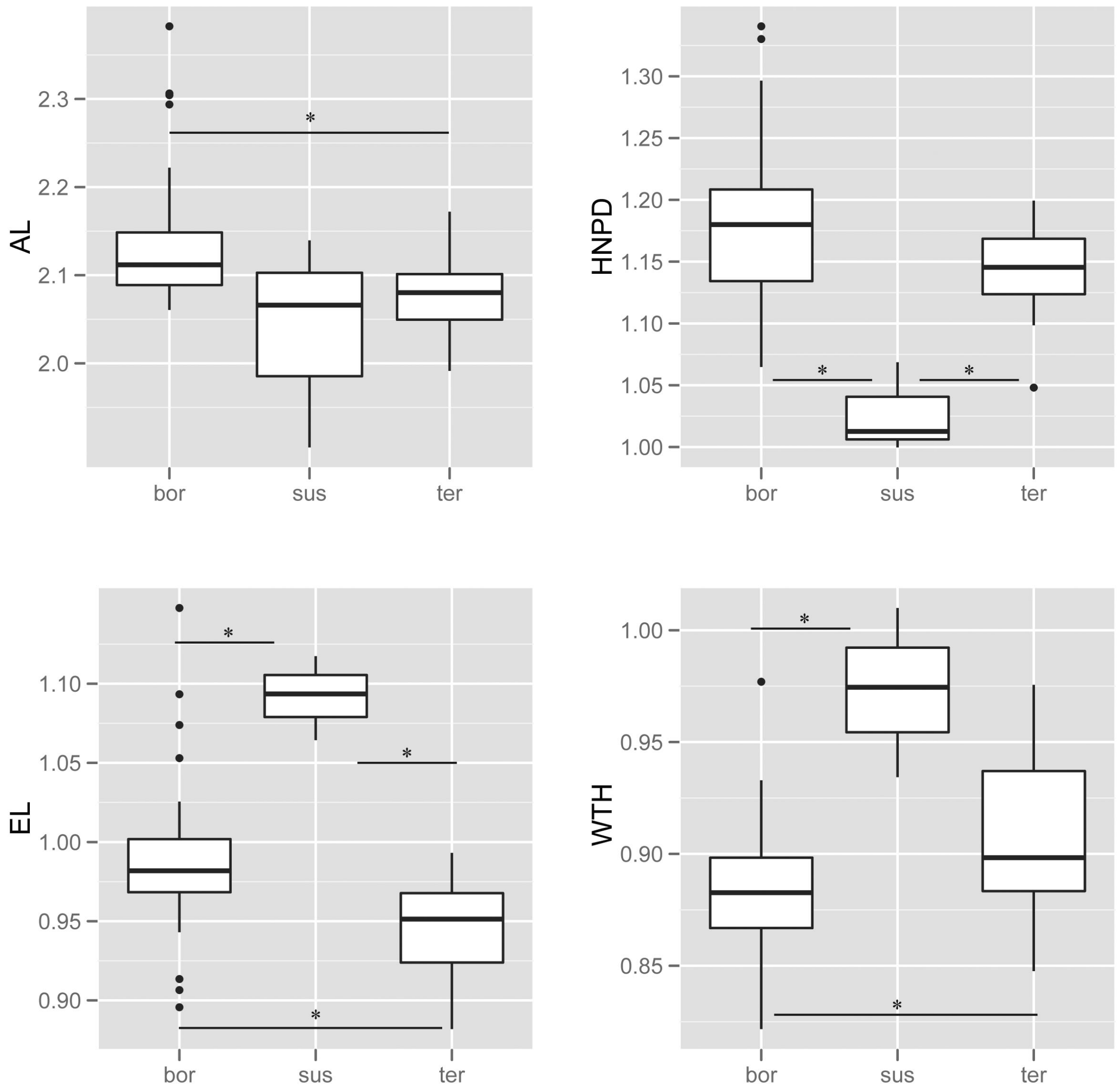
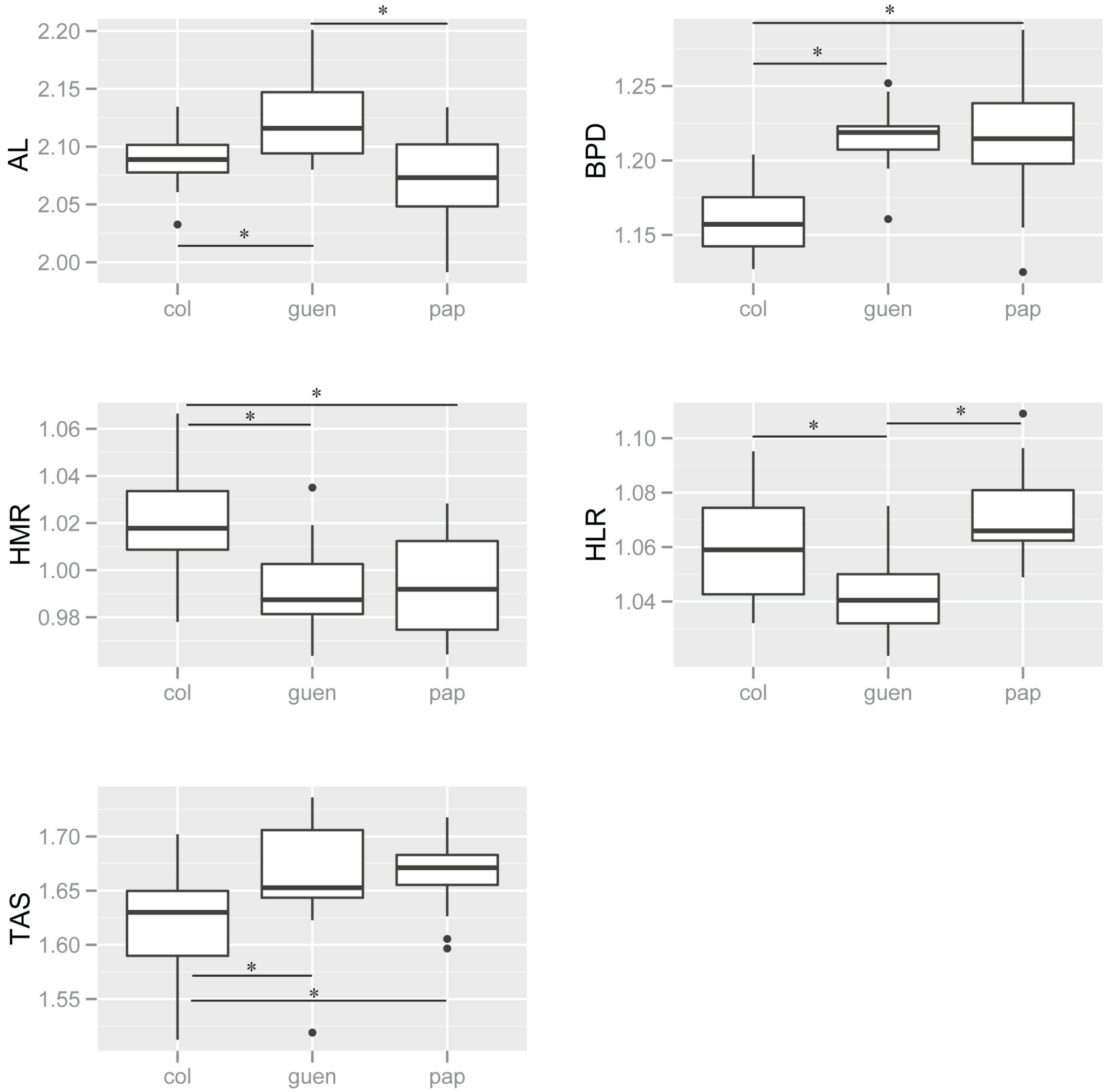


Figure 2.11a. Results for astragalus by phylogenetic group for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. col = colobine; guen = guenon; pap = papionin; AL = length of astragalus; BPD = length of body; HMR = height of medial ridge; HLR = height of lateral ridge; TAS = trochlear asymmetry; DHFF = height of fibular facet; PDFF = width of fibular facet; EW = width of ectal facet; ATH = angle of astragalar head



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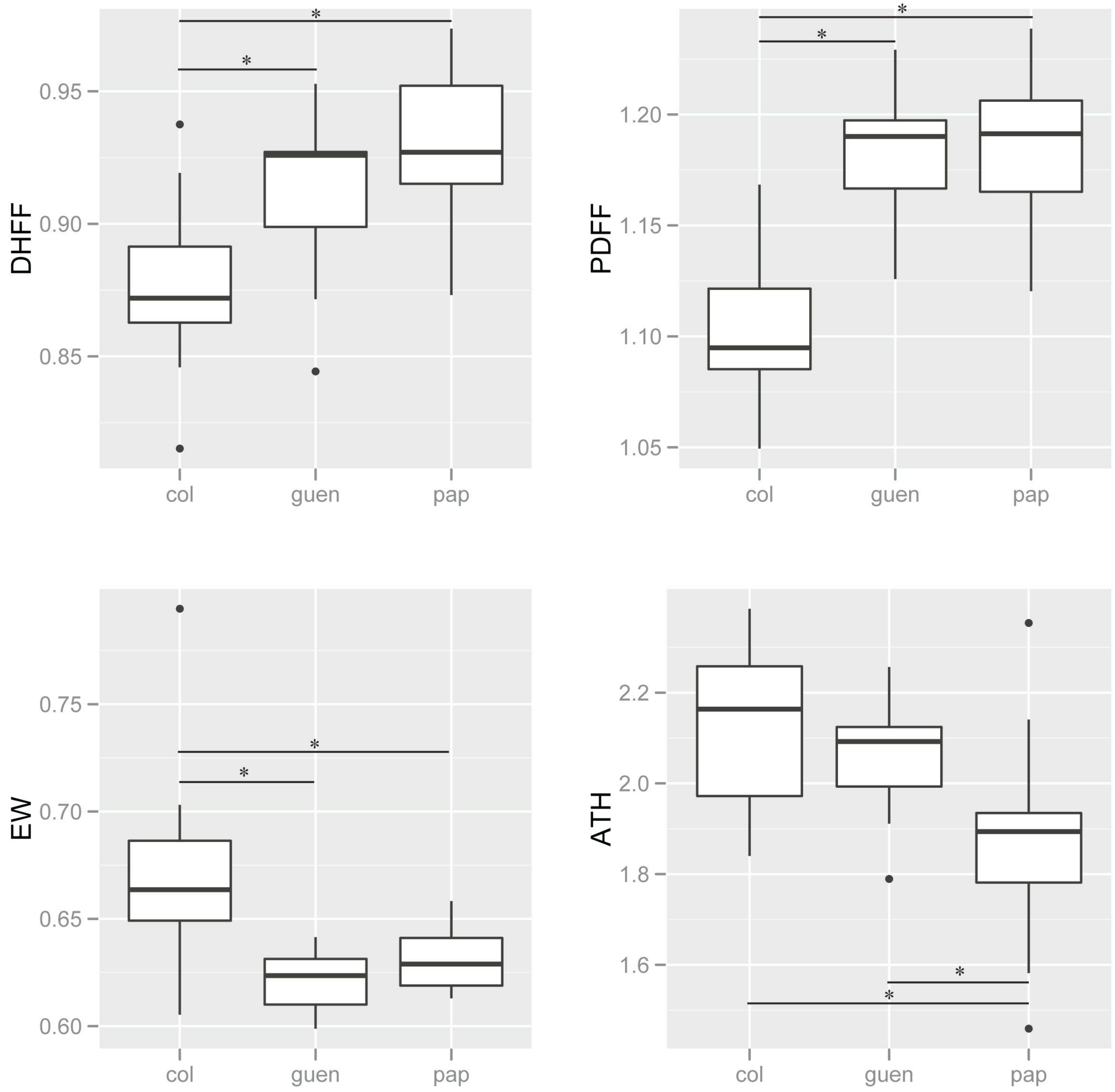
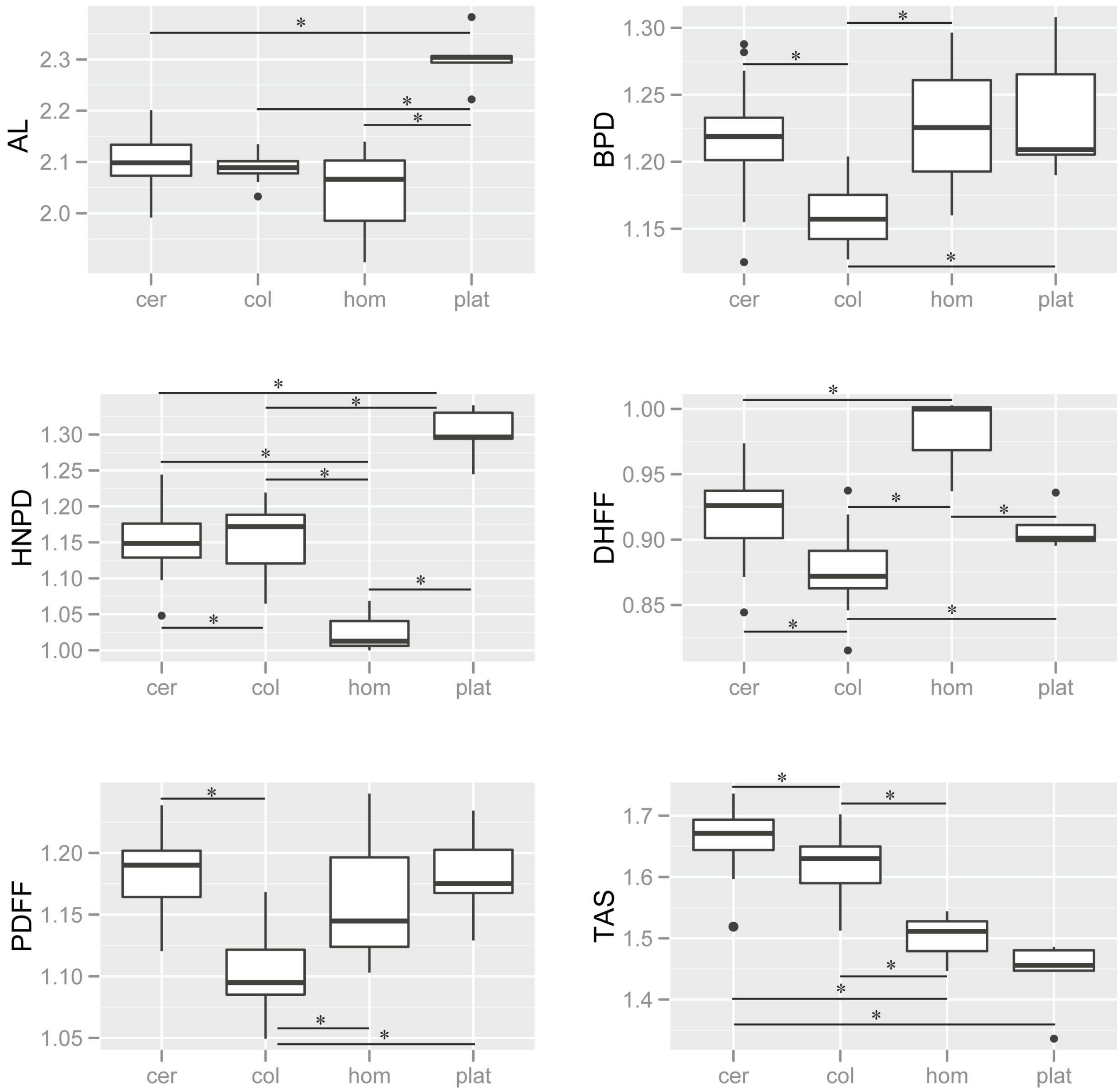


Figure 2.11b. Results for astragalus by phylogenetic group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. cer = cercopithecine; col = colobine; hom = hominoid; plat = platyrrhine; AL = length of astragalus; BPD = length of body; HNPD = length of head and neck; DHFF = height of fibular facet; PDFF = width of fibular facet; TAS = trochlear asymmetry; TW = trochlear width; EW = width of ectal facet; EL = length of ectal facet; WTH = width of astragalar head; ATH = angle of astragalar head



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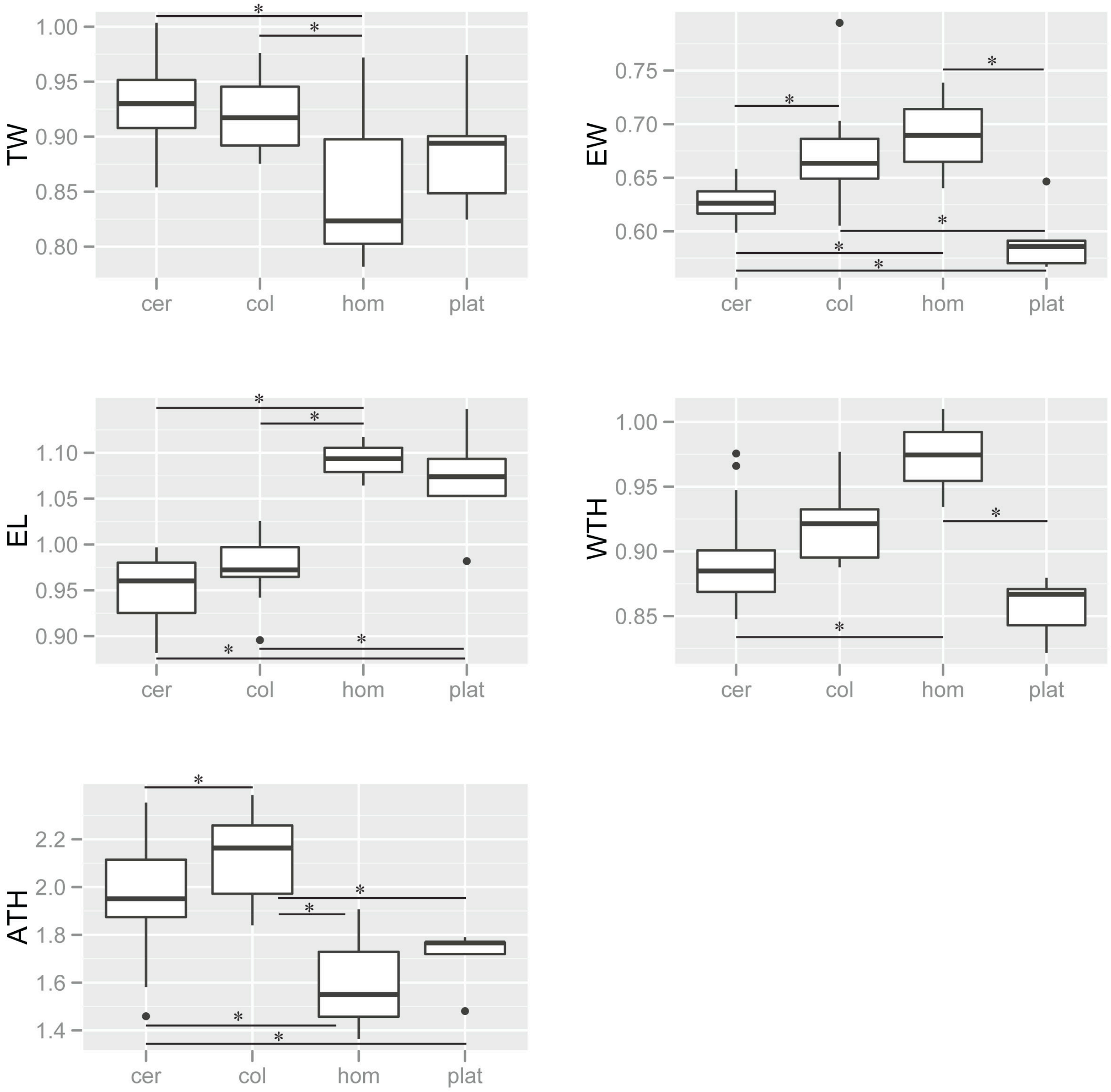


Figure 2.12. Plots of between-group PCAs on astragalus; a) cercopithecoid-only sample with species assigned using Coding 1, b) cercopithecoid-only sample with species assigned using Coding 2, c) entire anthropoid sample. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

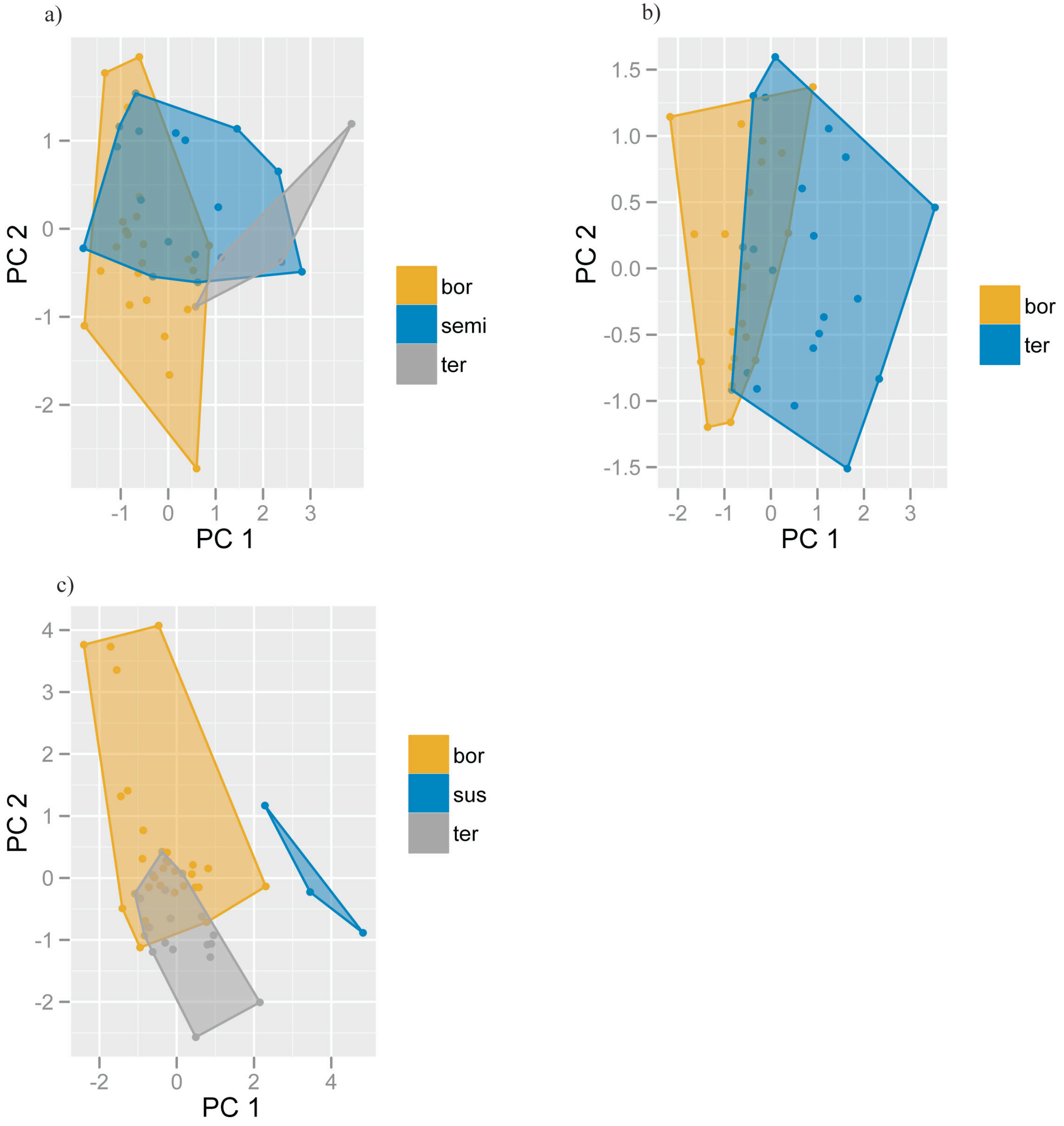


Figure 2.13. Plots of phylogenetic PCA on calcaneus; a) cercopithecoid-only sample with species labeled according to locomotor group, b) cercopithecoid-only sample with species labeled according to phylogenetic group, c) anthropoid sample with species labeled according to locomotor group, d) anthropoid sample with species labeled according to phylogenetic group. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

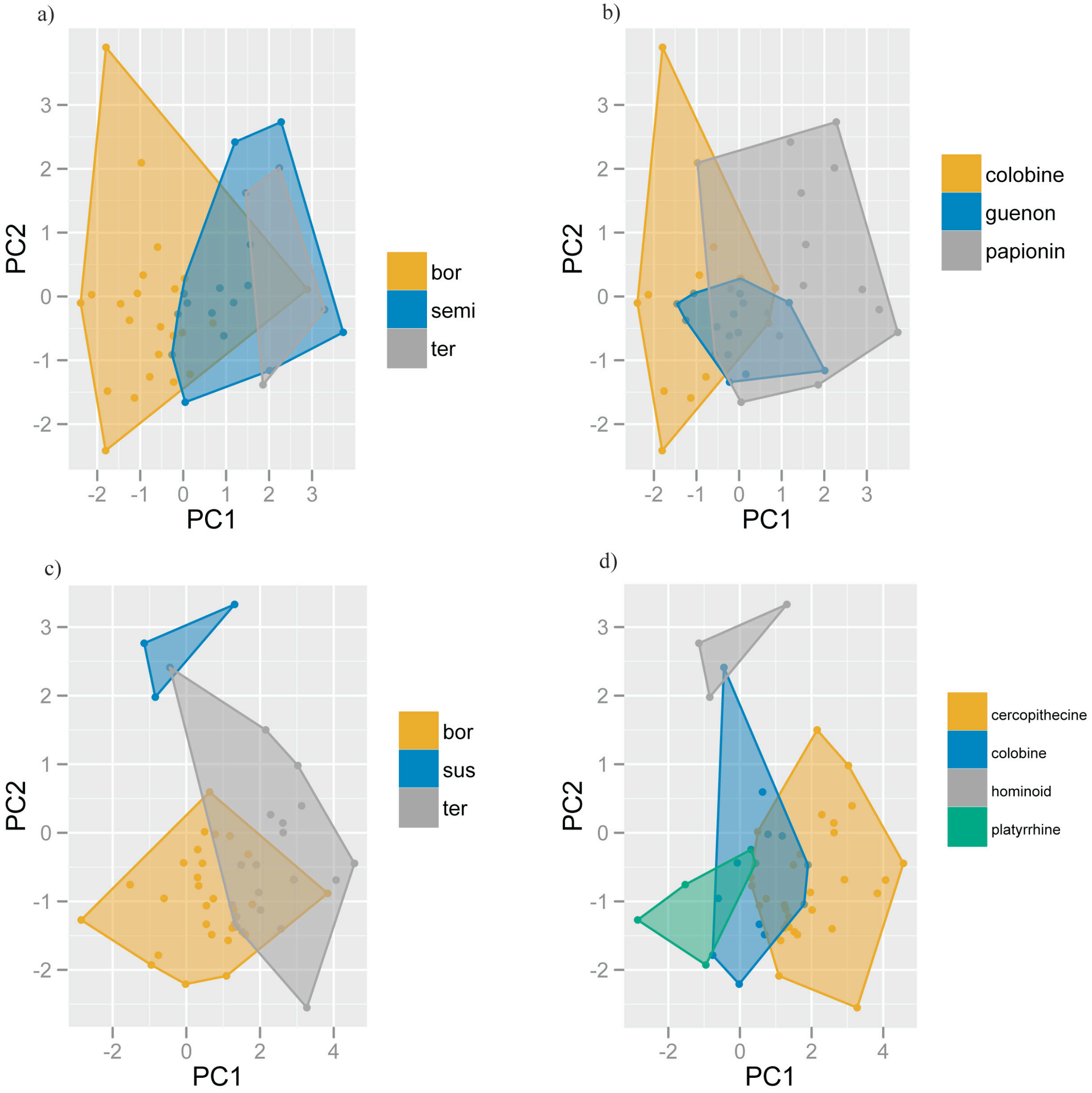


Figure 2.14a. Results for calcaneus by locomotor group (Coding 1) for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; PDA = length of distal body of calcaneus; CTL = length of calcaneal tuber; MLS = width of sustentaculum tail; HCF = height of cuboid facet

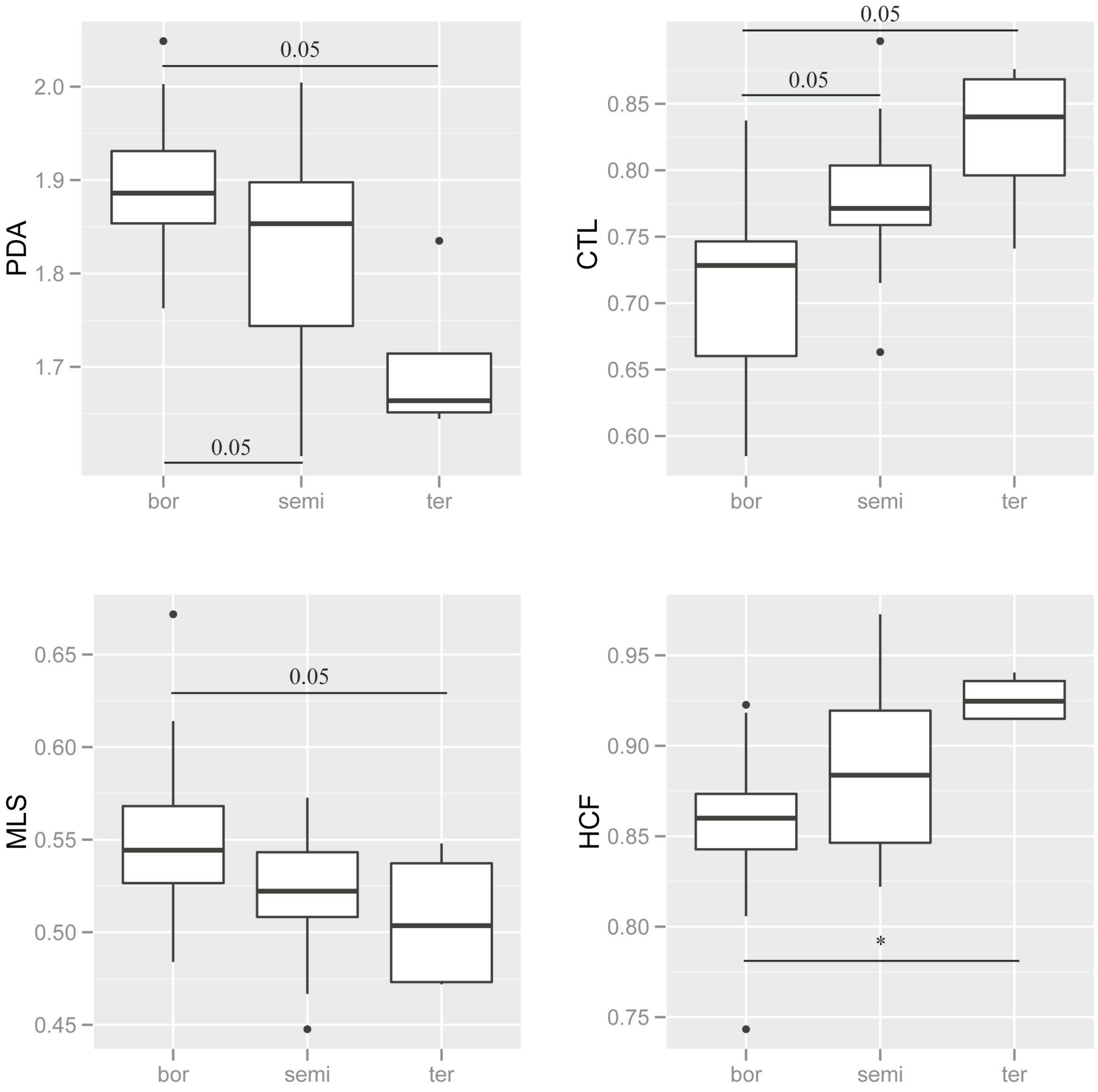


Figure 2.14b. Results for calcaneus by locomotor group (Coding 2) for cercopithecoid-only sample. All results significant. bor = arboreal; ter = terrestrial; CL = length of calcaneus; PDA = length of distal segment of body of calcaneus; HCF = height of cuboid facet

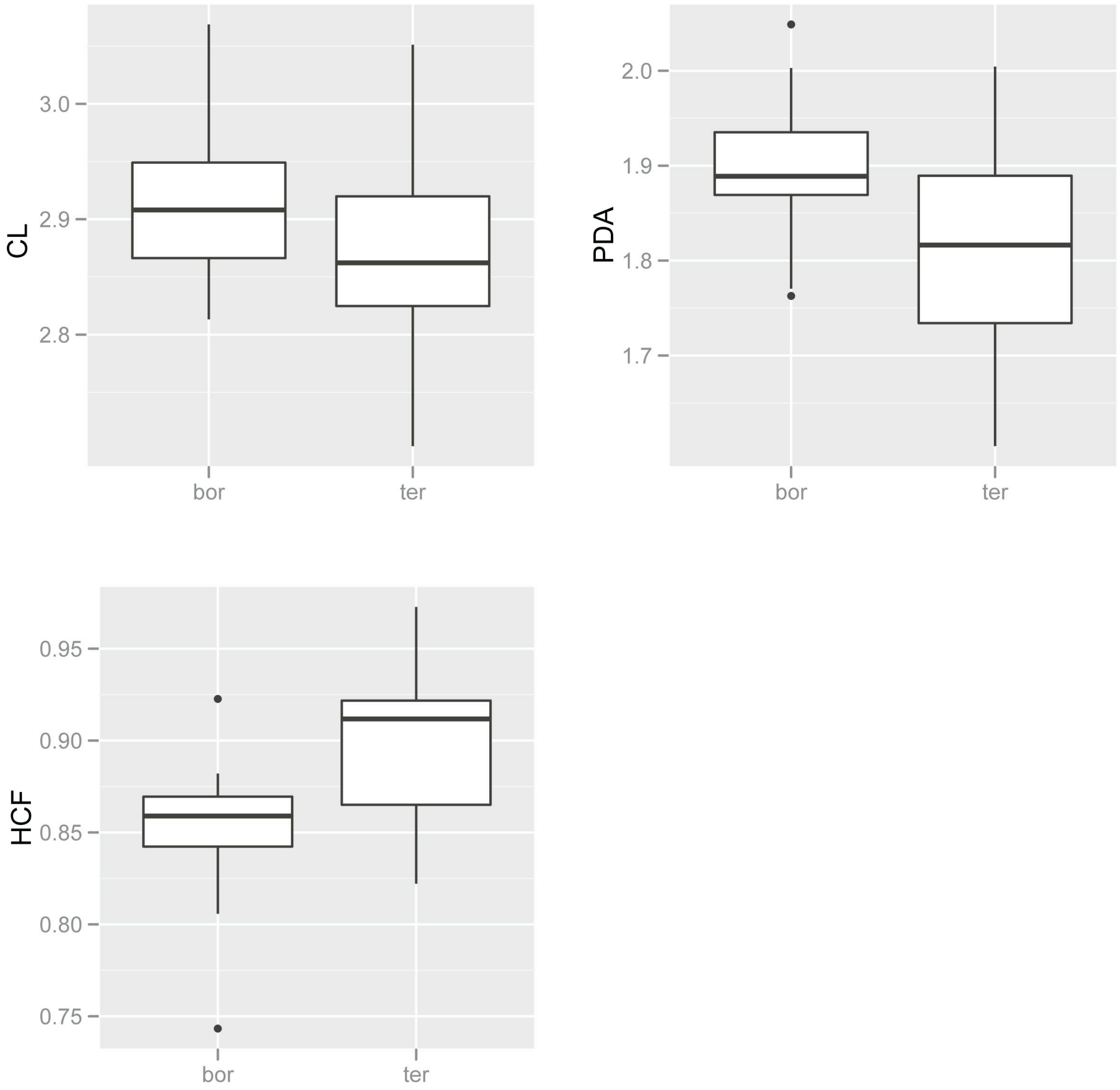


Figure 2.14c. Results for calcaneus by locomotor group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. bor = arboreal; ter = terrestrial; sus = suspensory; CL = length of calcaneus; PDA = length of distal segment of body of calcaneus; PDF = length of distal articular facet; MLS = width of sustentaculum; HDC = height of cuboid facet

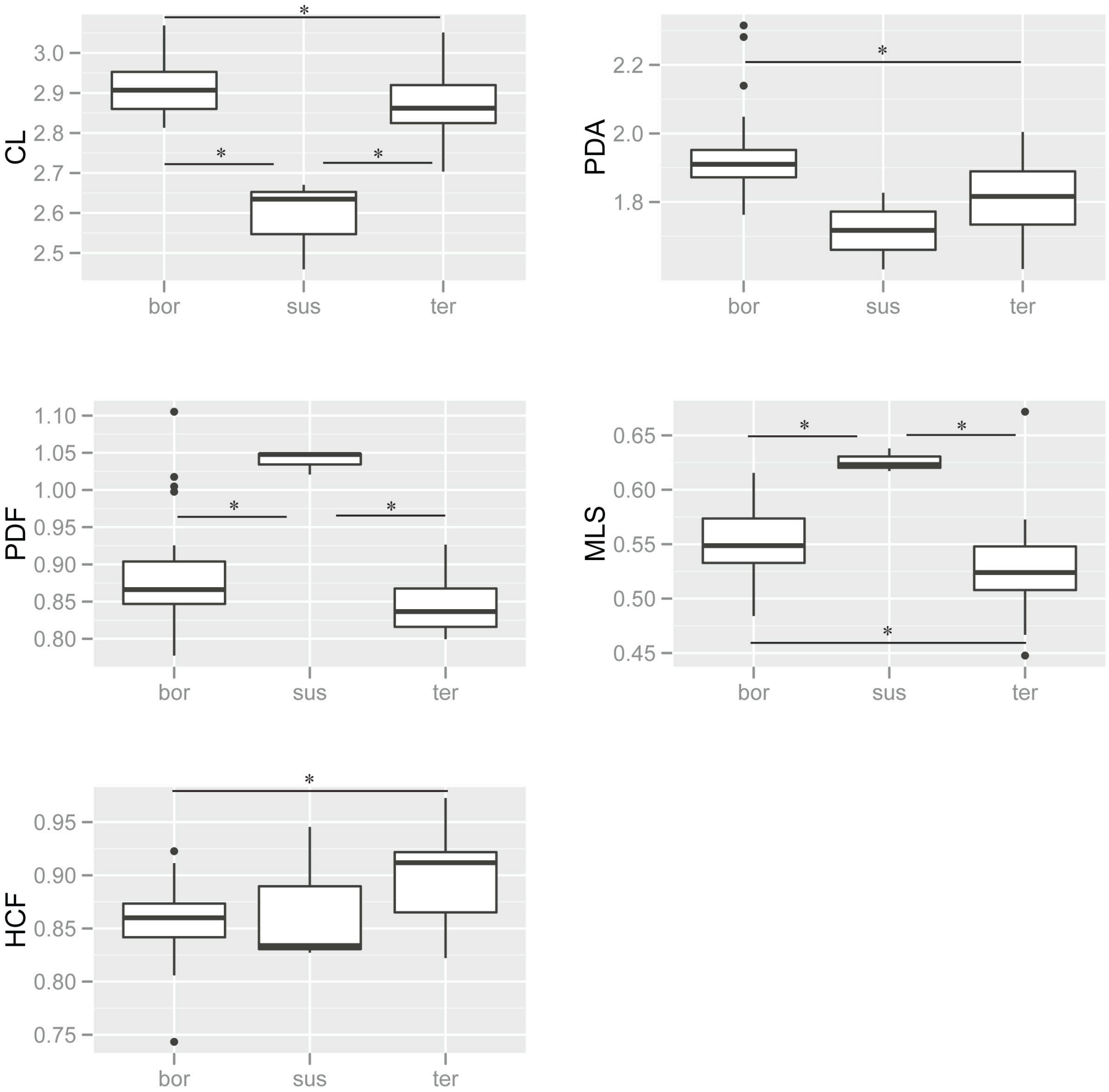
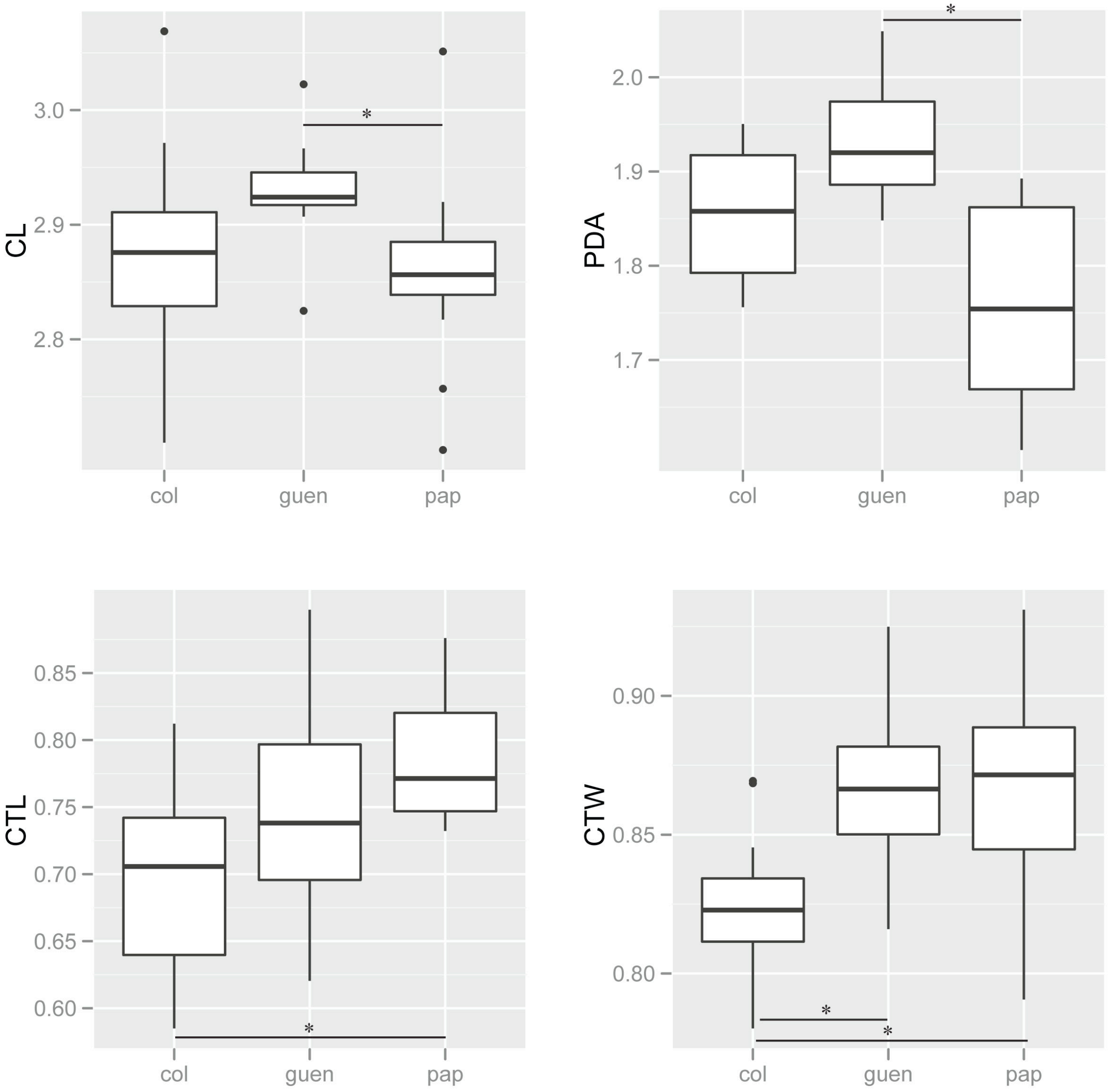


Figure 2.15a. Results for calcaneus by phylogenetic group for cercopithecoid-only sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. col = colobine; guen = guenon; pap = papionin; CL = length of calcaneus, PDA = length of distal segment; CTL = length of calcaneal tuber; CTW = width of calcaneal tuber; PDF = length of distal aritulcar facet; MLF = width of distal articular facet; HCF = height of cuboid facet



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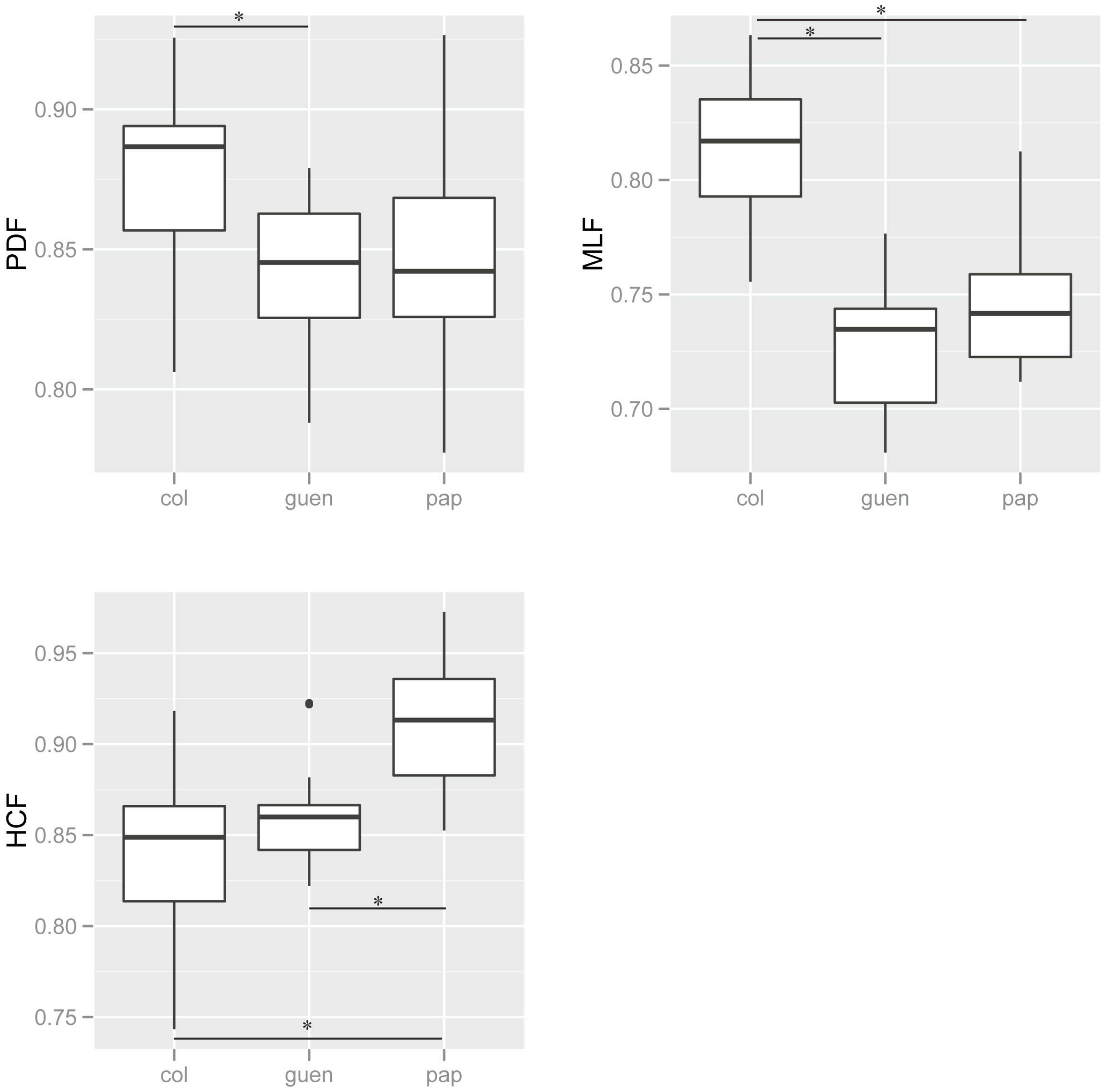


Figure 2.15b. Results for calcaneus by phylogenetic group for entire anthropoid sample. Asterisk (*) denotes comparisons that met adjusted critical values. 0.05 denotes comparisons that met significance at standard 0.05 level. cer = cercopithecine; col = colobine; hom = hominoid; plat = platyrrhine; CL = length of calcaneus; CTL = length of calcaneal tuber; PDF = length of distal articular facet; MLF = width of distal articular facet; MLS = width of sustentaculum; CTW = width of calcaneal tuber

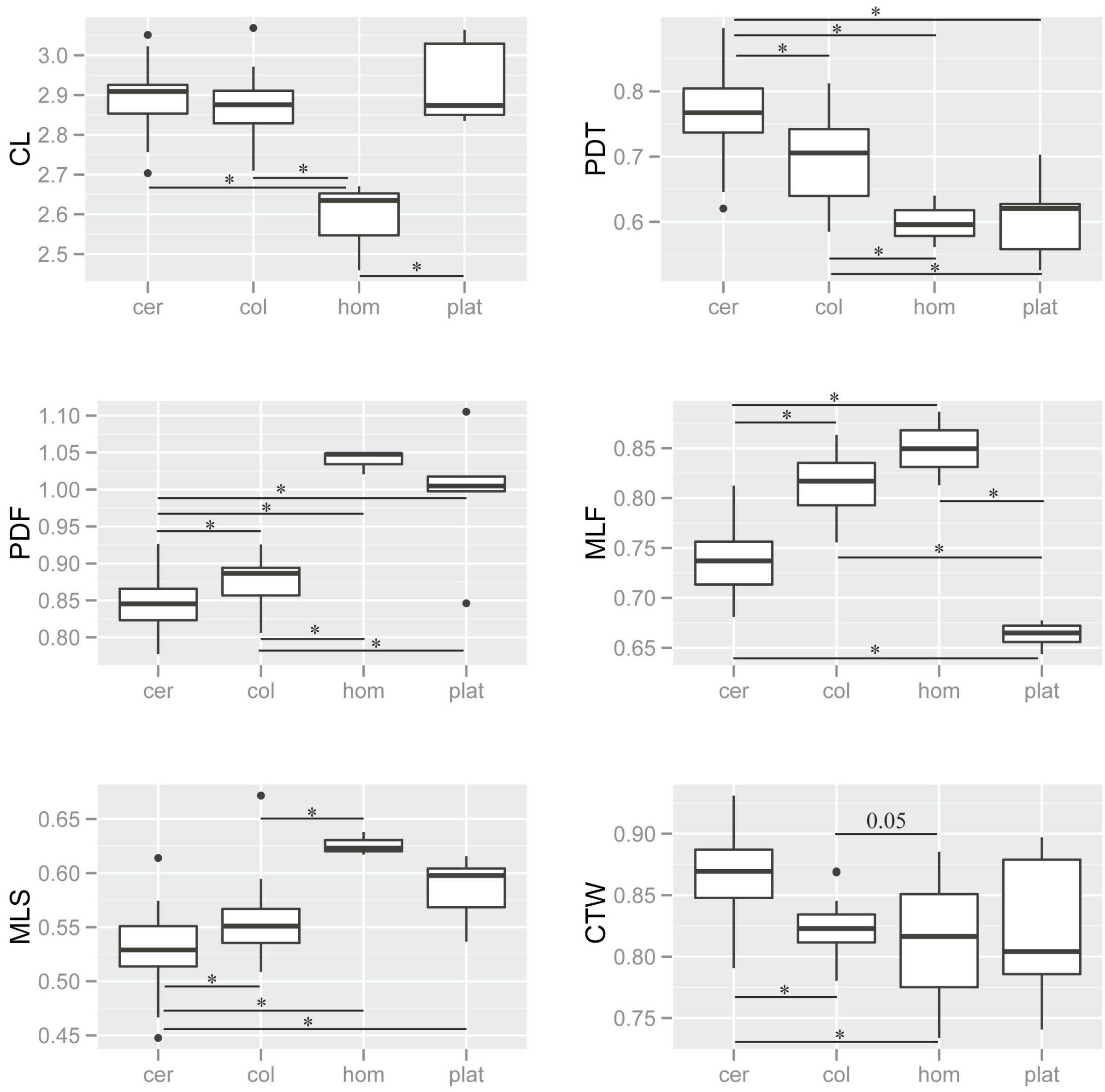


Figure 2.16. Plots of between-group PCAs on calcaneus; a) cercopithecoid-only sample with species assigned using Coding 1, b) cercopithecoid-only sample with species assigned using Coding 2, c) entire anthropoid sample. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory

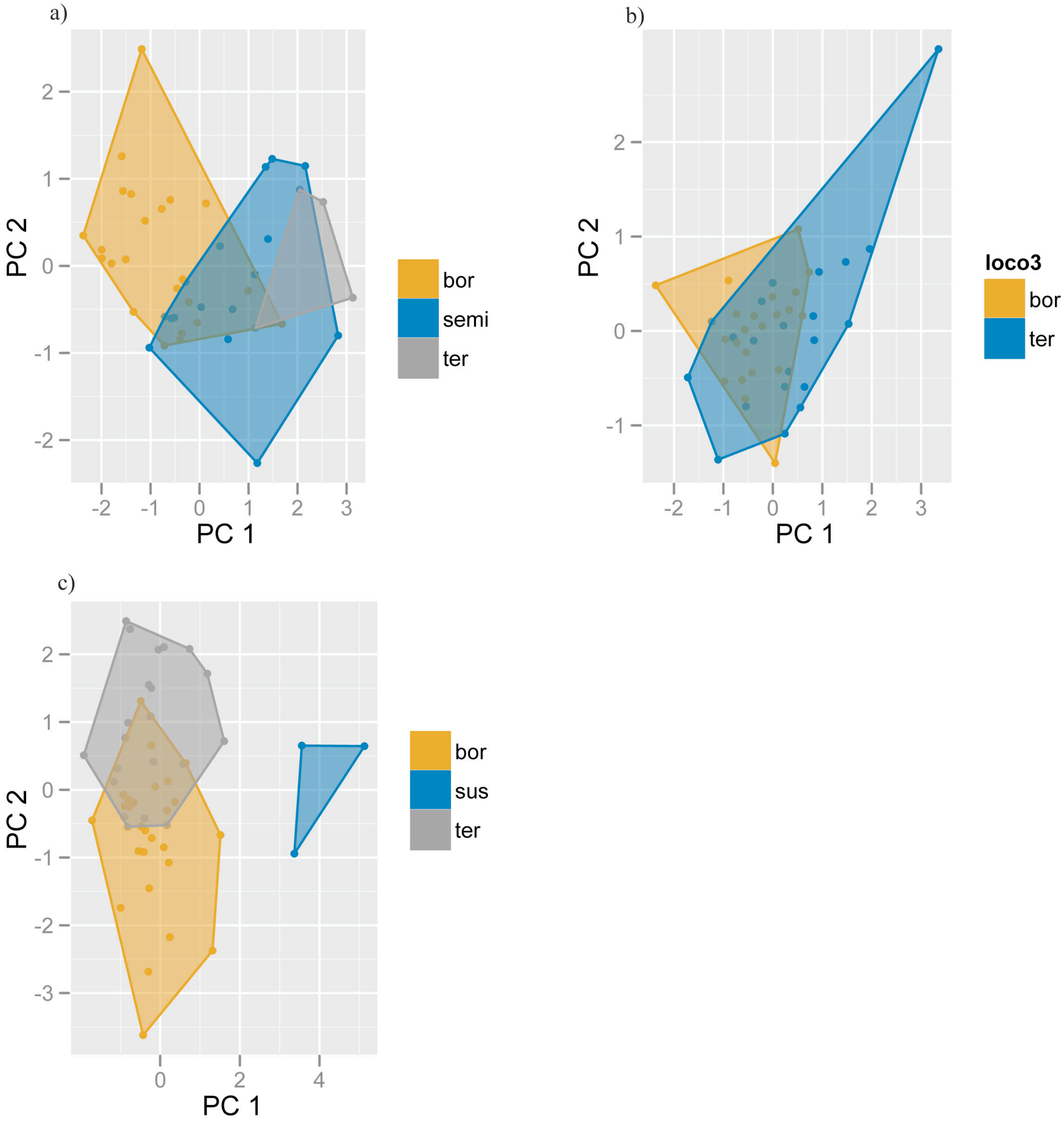
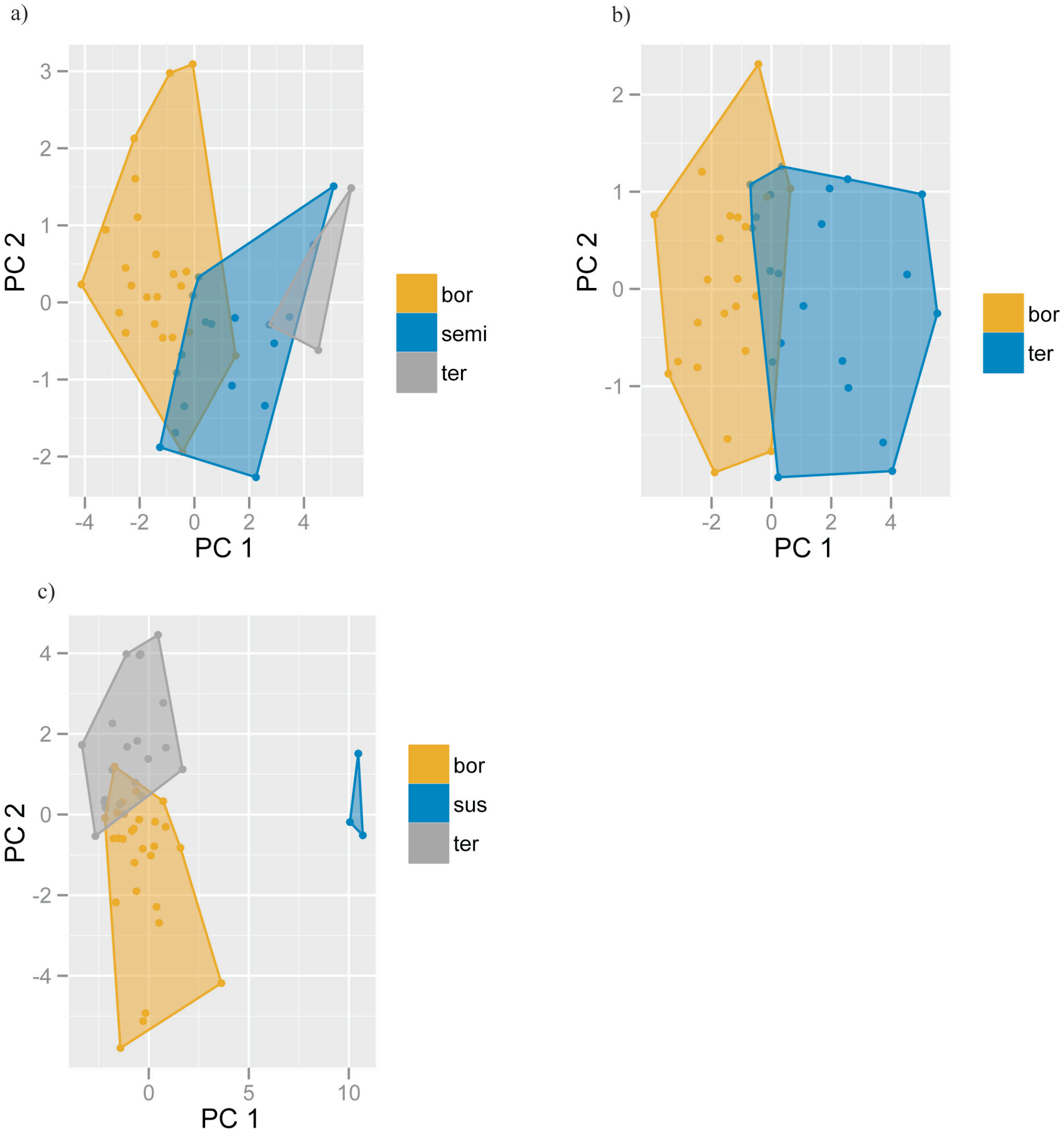


Figure 2.17. Plots of between-group PCAs on all four elements; a) cercopithecoid-only sample with species assigned using Coding 1, b) cercopithecoid-only sample with species assigned using Coding 2, c) entire anthropoid sample. bor = arboreal; semi = semi-terrestrial; ter = terrestrial; sus = suspensory



Chapter 3
Fossil Reconstructions of Extinct Cercopithecoids with Implications for Early Cercopithecoid Locomotor Evolution

Section 3.1. Introduction

Previous work on *Victoriapithecus*, a probable close sister-group of crown cercopithecoids (von Koenigswald 1969; Benefit and McCrossin 1991; Benefit 1993; Benefit and McCrossin 1993; Benefit and McCrossin 1997; Benefit 1999b; Benefit 1999a; Benefit 2000; Benefit and McCrossin 2002; Miller et al. 2009) has helped develop the hypothesis that the last common ancestor of crown cercopithecoids engaged in frequent terrestrial behavior, and that dedicated arboreality, such as that of many extant colobine and guenon species, was subsequently acquired convergently (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003). Much of this framework is based on several morphological features of *Victoriapithecus* that have been identified as possible functional correlates of a terrestrial lifestyle, including a proximally projecting humeral greater tubercle, a dorsally oriented humeral medial epicondyle, a humeral trochlear flange, a dorsally projecting ulnar olecranon process, a low femoral neck angle, and short phalanges (Harrison 1989; McCrossin et al. 1998; Benefit 1999b). Paleoenvironmental reconstructions of localities that yield *Victoriapithecus* suggest that the species lived in woodlands, wooded grasslands, and brush thickets (Wynn and Retallack 2001; Retallack et al. 2002), lending added plausibility to reconstructions of terrestrial behavior in victoriapithecids.

The hypothesis that dedicated arboreality is a derived condition within crown Cercopithecoidea is also potentially supported by reconstructions of terrestrial behavior in some extinct colobines from the Miocene of Eurasia and the Pliocene of Africa. *Dolichopithecus* and *Mesopithecus*, two colobine genera from the late Miocene of Eurasia, include species that have been interpreted as "semi-terrestrial" (Delson 1973; Youlatos 2003; Ingicco 2008; Youlatos and Koufos 2010; Youlatos et al. 2012). *Cercopithecoides*, a colobine from the Plio-Pleistocene of east Africa, includes three species (*C. williamsi*, *C. meaveae*, and *C. kimeui*) with associated postcrania that exhibit possible adaptations for terrestrial behavior (Birchette 1982; Frost and Delson 2002; Jablonski et al. 2008b). This evidence has even led some to conclude that arboreality did not evolve in colobines until the Plio-Pleistocene (Benefit 1999b; Benefit 1999a; Leakey et al. 2003). Given that molecular dating studies suggest that African and Asian colobines diverged in the late Miocene (Raaum et al. 2005; Sterner et al. 2006; Ting 2008; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012), parallel evolution of arboreality might then be required to explain the high degree of arboreal behavior in extant colobines (Leakey et al. 2003; for review also see Hlusko 2006; Hlusko 2007; Nakatsukasa et al. 2010). Unfortunately, the relationship of these potentially terrestrial fossil species to extant colobines is poorly understood, making it difficult to determine the importance of these species vis-à-vis the evolution of arboreal behavior in colobines. However it is also clear that reconstructions of the last common ancestor of crown cercopithecoids as "semi-terrestrial" hinge largely on the convincing identification of terrestrial adaptations in *Victoriapithecus,* Miocene colobines from Europe, and Pliocene colobines from Africa. Such an analysis has not yet been undertaken within the context of a large and taxonomically broad comparative sample of extant cercopithecoids.

Recent work has questioned the conclusion that the last common ancestor of colobines was semi-terrestrial and instead suggest that arboreality is the ancestral condition, based on evidence from recently discovered postcrania of fossil colobines, including *Kuseraclobus* and *Microcolobus* (Hlusko 2006; Hlusko 2007; Gilbert et al. 2010; Nakatsukasa et al. 2010). Associated postcrania of *Microcolobus* sp. come from the late Miocene site of Nakali, Kenya, which dates to 9.8-9.9 million years ago (ma). Craniodental material of *Microcolobus* is also found in the Tugen Hills at sites as old as 10.5 ma (Benefit and Pickford 1986) and colobines are now known from 12.5 ma levels in the same area (Rossie et al. 2013). The phylogenetic placement of *Microcolobus* is uncertain and known material (Benefit and Pickford 1986; Nakatsukasa et al. 2010) either predates (Ting 2008; Fabre et al. 2009; Springer et al. 2012) or postdates (Raaum et al. 2005; Sterner et al. 2006; Perelman et al. 2011) the divergence of African and Asian colobines depending on which molecular study is consulated. Therefore, *Microcolobus* could be either a crown colobine that is already on either the African or Asian colobine stem lineages, or is a stem colobine that persists close to, or beyond, the divergence of crown colobines (Nakatsuaka et al., 2010). The latter hypothesis is supported by the recent phylogenetic analysis of dental characters undertaken by Rossie et al. (2013). Either way, *Microcolobus* provides the earliest evidence of arboreality in colobines, and provides compelling new evidence for arboreality as the ancestral locomotor mode of colobines.

Hlusko (2007) identified three species of colobine at the younger (6 ma) Lemudong'o site in Kenya, including a new species of *Paracolobus, P. enkorikae.* Several postcranial bones, including humeri, ulnae, radii, femora, and manual and pedal elements, have been assigned to Colobinae with genus and species indeterminate. Hlusko (2007) interpreted several of these elements as having belonged to primarily arboreal taxa, and suggested that these specimens may represent another species of large-bodied colobine of unknown affinity. Gilbert et al. (2010) also identified colobine postcrania from the Tugen Hills in Kenya dated to 5.88 to 6.1 ma. Gilbert et al. (2010) interpreted these specimens (2010) as exhibiting adaptations for arboreal behavior.

Kuseracolobus hafu is a much larger-bodied and later-occurring colobine from Asa Issie, Ethiopia (Hlusko 2006). *Kuseracolobus* is dated to 4.4 mya and therefore predates the radiation of large-bodied African colobines during the late Pliocene. Hlukso (2006) estimated that *Kuseracolobus* was similar in size to *Paracolobus chemeroni* and was a predominantly arboreal species. Two other genera of large-bodied, possibly arboreal colobines are present in the Pliocene of Africa, *Rhinocolobus* and *Paracolobus* (Birchette 1982; Ciochon 1993; Delson et al. 2000; Frost and Delson 2002; Jablonski et al. 2008b). *Rhinocolobus* is generally considered to have been as arboreal as most extant colobines (Jablonski et al., 2008; Frost and Delson, 2002; Birchette, 1982), but *Paracolobus* exhibits a mosaic of features that have been related to both arboreal and terrestrial locomotion (Birchette 1982). Birchette (1982) found overall phenetic similarity between *P. chemeroni* and extant colobines and concluded that this species was generally arboreal but probably engaged in limited terrestrial behavior based on features such as a slightly projecting humeral head, a strong humeral trochlear flange, and a retroflexed olecranon process of the ulna (see also, Ciochon 1993).

Therefore, although the colobines clearly underwent a radiation that led to some large-bodied and terrestrial forms in the Pliocene (Frost and Delson 2002; Jablonski et al. 2008b), arboreal colobines are not absent from this geo-temporal period (Birchette 1982; Frost and Delson 2002; Hlusko 2006; Hlusko 2007; Jablonski et al. 2008b). The current fossil evidence can be used to suggest an arboreal, "semi-terrestrial", or terrestrial ancestor of crown cercopithecoids, but these competing hypotheses have not yet been investigated within an explicitly phylogenetic context that takes into account the great morphological diversity seen across cercopithecoids.

Although the previous chapter did not clearly document a complex of postcranial features that consistently characterize "semi-terrestrial" cercopithecoids, several morphological measurements were found that successfully differentiated between highly arboreal and highly terrestrial cercopithecoids. Therefore, although one may not be able to confidently predict the amount of time a fossil species spent in the trees versus the ground, it may be possible to estimate whether certain species were predominantly arboreal or terrestrial. This chapter aims to test previously published locomotor reconstructions of fossil cercopithecoids (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003; Hlusko 2006; Hlusko 2007; Gilbert et al. 2010; Nakatsukasa et al. 2010) using discriminant analysis, incorporating the morphometric variables that were applied to extant cercopithecoids in the previous chapter.

Section 3.2. Methods

The fossil sample includes sixteen fossil crown or stem cercopithecoids (Appendix G). Specimens that were damaged or distorted were not included in the sample. Some postcrania are associated with craniodental elements but some specimens are assigned to a taxon based on their locality, temporal range, size, and presence (or absence) of other primates from the locality. Specimens with relatively large samples that are given taxonomic assignments in this way include *Victoriapithecus* from Maboko Island (Kenya), *Dolichopithecus ruscinensis* from Perpignan (France), *Mesopithecus pentelicus* from Pikermi (Greece), *Theropithecus brumpti* from Shungura (Ethiopia), East Turkana, and West Turkana (Kenya), and *Theropithecus oswaldi* from East Turkana and Olorgesailie (Kenya). It should be noted that recently two associated postcrania of *T. brumpti* from West Turkana and Tugen Hills (Kenya) have been described (Jablonski et al. 2002; Gilbert et al. 2011) of which the former is included in the sample. Although no associated material of *M. pentelicus* exists, three associated skeletons of *Mesopithecus* aff. *Mesopithecus delsoni* from Hadjidimovo (Bulgaria) are described by Koufos et al. (2003). Given the taxonomic uncertainty of these specimens, the Hadjidimovo material is referred to as *Mesopithecus* sp. throughout the chapter. An associated *Microcolobus* skeleton from Nakali, Kenya is tentatively assigned by Nakatsukasa et al. (2010) and given the taxonomic uncertainty will be referred to as *Microcolobus* sp. in this chapter.

Additionally, isolated postcrania of *Parapapio jonesi, Cercopithecoides kimeui,* and *Rhinocolobus turkanensis* from Hadar are given taxonomic assignments by Frost and Delson (2002). The humeral and femoral specimens of *P. jonesi* are assigned based on their differences from other large-bodied cercopithecoids at Hadar (i.e., *Theropithecus* and *Cercopithecoides*). A.L.577-1, a distal humerus, is assigned to *C. kimeui* based on its size and overall similarity to a distal humerus of *C. meaveae* (A.L.2-64). The distal humerus of *R. turkanensis* (A.L.300-1) is assigned based on its similarity to a specimen of *R. turkanensis* from Koobi Fora and its dissimilarity to the other cercopithecoids from Hadar. Postcrania are also tentatively assigned to *Parapapio lothagamensis* by Leakey et al. (2003) based on size and morphological affinity to extant cercopithecines.

Three sets of discriminant function analyses (DFAs) were run using the comparative dataset of cercopithecoids from Chapter 2. Individuals rather than species means were used in the DFAs to account for intraspecific variation in the model, and since each fossil specimen later added as unknown to the analyses represents a single individual. In the first set of DFAs, individuals were assigned to one of three groups *a priori* using Coding 1 from Chapter 2 (i.e., arboreal, semi-terrestrial, terrestrial). In the second set of DFAs the same group assignment was used but semi-terrestrial individuals were left as unknown. Because of the large number of semi-terrestrial individuals in the sample, species means were created for later post-hoc group assignment. In the final set of DFAs, individuals were assigned to one of two groups *a priori* using Coding 2 from Chapter 2 (i.e., arboreal or terrestrial – with "semi-terrestrial" included in the terrestrial group). Leave-one-out cross validation was used in analyses to determine the correct classification rate.

For each set of DFAs, analyses are run on the complete humerus, proximal humerus, distal humerus, femur, astragalus, and calcaneus. In addition analyses are run on three combinations of elements: 1) the proximal and distal humerus, femur, astragalus, and calcaneus 2) the proximal and distal humerus, astragalus, and calcaneus, and 3) the distal humerus and astragalus. These combinations are based on the number of elements available from the fossil sample to create "composite" specimens. The variables included for each element are the same as those for the between-group principal components analyses from Chapter 2 (see Table 2.3). The four variables included for analyses of the complete humerus for Coding 1 are the humeral head index (HHI), width of lesser tubercle (MLT), height of the greater tubercle (GTH), and angle of the medial epicondyle (AME). The variables included in the analyses of the proximal humerus include the same set of variables, excluding angle of the medial epicondyle. In order to examine the distal humerus in a multivariate context, two variables were included in addition to angle of the medial epicondyle. The added variables are height of the olecranon fossa (PDOF) and height of the capitulum (PDC) and both significantly differentiate locomotor groups at the 0.05 level (Table 2.5a). Arboreal and terrestrial individuals are significantly different in PDOF and semi-terrestrial and terrestrial individuals trend towards significance. Arboreal individuals are significantly different from semi-terrestrial and terrestrial individuals in PDC. Although two variables were not significant at the Bonferroni adjusted critical value, both variables do show some ability to differentiate between groups, and when combined with the angle of the medial epicondyle may provide better separation of groups than any single variable considered in isolation. Enough variables from the proximal and distal end of the humerus significantly differentiated between locomotor groups using Coding 2, so no adjustments were needed in analyzing the proximal and distal ends of the humerus separately in DFAs using Coding 2.

Fossil specimens were added to each set of analyses as unknowns to reconstruct their most likely group assignment. Posterior probabilities were examined to determine if multiple group membership was possible. Semi-terrestrial species means were added to the second set of DFAs (i.e., with two a-priori groups) as unknown to determine if "semi-terrestrial" species would be assigned to either the one of the a-priori groups with a high posterior probability or if assignment to both groups was equally likely.

In some cases, fossil specimens were in good overall condition, but due to erosion or breaks certain features could not be measured. In these cases, a separate dataset was created for these specimens using geometric mean-based size adjustment that excluded the missing variables from each specimen individually. Specimens with missing data are marked with an asterisk (*) in Tables Tables 3.6a-i, Tables 3.7a-I, and Tables 3.8a-i. In cases where a missing variable was also a discriminating variable in the DFA, the DFA was run excluding those discriminating variables as well.

Finally, fossil specimens were entered as unknowns into multi-element DFAs using composites or associated postcrania (Table 3.1b-c). In three cases – *Microcolobus* sp., *Paracolobus chemeroni* and *Mesopithecus* sp. – associated postcrania were used. For the remaining species, *Victoriapithecus macinnesi*, *Mesopithecus pentelicus*, *Dolichopithecus* *ruscinensis, Parapapio lothagamensis, Theropithecus oswaldi,* and *Theropithecus brumpti*, composites were created using as many of the four elements as possible. When a species is represented by more than one specimen of a single element, an average was taken. Composites were only created using specimens from a single locality. For the majority of species, all postcrania are from a single locality. However, both *Theropithecus* species are represented at multiple localities. Therefore, the locality with the most elements was chosen to make the composite. The composite of *Theropithecus oswaldi* is made from elements from East Turkana and the composite of *T. brumpti* is made up of elements from West Turkana.

Paracolobus chemeroni and *Mesopithecus pentelicus* are represented by all four elements. *Victoriapithecus macinnesi*, *Mesopithecus* sp., *Parapapio lothagamensis*, and *Theropithecus oswaldi* (from East Turkana) are represented by the humerus, astragalus, and calcaneus. *Mesopithecus* sp. is missing the biepicondylar breadth measurement on the humerus (BB) and *Theropithecus oswaldi* is missing the proximal calcaneus excluding the measurements of the overall length of the calcaneus (CL), length of the tuber (CTL), and width of the tuber (CTW). As before, a separate dataset was created for these specimens using geometric mean size adjustment that excluded the missing variables. Total length of the calcaneus and length of the tuber are used as discriminators in some of the multi-element DFAs, so in the case of *Theropithecus oswaldi* these variables were also left out as discriminators.

Section 3.3. Results

Section 3.3.1: Discriminant Function Analyses – cercopithecoid sample with three *a priori* groups

In the discriminant function analysis using variables from the entire humerus, discriminant function (DF) 1 accounts for 96.9% of the variation and DF 2 accounts for 3.1% of the variation (Table 3.2a; Figure 3.1a). The variables with the highest loadings on DF 1 are angle of the medial epicondyle (-24.5) and the humeral head index (-14.6). Cross-validation shows that 74.1% of cases are correctly classified. Arboreal individuals are correctly classified in 84.3% of cases but the classification rate dropped for “semi-terrestrial” (66.2%) and terrestrial individuals (55.6%).

In the discriminant function analysis of variables from the proximal humerus, DF 1 accounts for 90.4% of the variation and DF 2 accounts for 9.6% of the variation (Table 3.2b; Figure 3.1b). Height of the greater tubercle loaded highest on DF 1 (-42.7) and humeral head index loaded highest on DF 2 (-22.6). Generally, the cross-validation showed poorer classification than when using variables from the entire humerus. Overall the correct classification is 61.3%. Arboreal individuals still had a high classification of 85.1%, but the classification rate for “semi-terrestrial” and terrestrial individuals is quite low at 34.5% and 15.6%, respectively.

In the discriminant function analyses of variables from the distal humerus, DF 1 accounts for 98.5% of the variation and DF 2 accounts for 1.5% of the variation (Table 3.2c; Figure 3.1c). Angle of the medial epicondyle has the highest loading on DF 1 (18.4). The classification rate is similar to that of the analysis that used variables from the entire humerus, with 70.6% of all individuals correctly classified. Arboreal individuals are correctly classified 83.1% of the time, while “semi-terrestrial” and terrestrial individuals are classified at 56.6% and 46.7%, respectively.

In the discriminant function analysis on the femur, DF 1 accounts for 99.3% of the variation and DF 2 accounts for 0.7% of the variation (Table 3.2d; Figure 3.1d). Overall length of the femur has the highest loadings on DF 1 (-26.9). The classification rate for cross-validation is 62% overall, but arboreal individuals have a much higher classification of 89.7%. Semi-terrestrial and terrestrial individuals are poorly classified (22.4% and 37.5%, respectively).

In the discriminant function analysis of variables from the astragalus, DF 1 accounts for 82.9% of the variation and DF 2 accounts for 17.1% of the variation (Table 3.2e; Figure 3.1e). Total length (53.8) has the highest coefficient on DF 1 and ectal facet length (36.8) has the highest coefficient on DF 2. Overall classification rate for cross-validation is 64.7%. Arboreal individuals have a high correct classification of 85.7% but "semi-terrestrial" and terrestrial individuals have low classification of 35.0% and 41.3%, respectively.

In the discriminant function analysis of variables from the calcaneus, DF 1 accounts for 91.5% of the variation and DF 2 accounts for the remaining 8.5% of the variation (Table 3.2f; Figure 3.1f). Length of the distal segment of the calcaneus has the highest coefficient on DF 1 (20.53) (Table 12a). The overall classification rate for cross-validation is 67.5% but arboreal individuals are correctly classified in 85.3% of cases. Terrestrial individuals are correctly classified 60.0% of the time but "semi-terrestrial" individuals are poorly classified at 38.0%.

In the discriminant function analysis including variables from all four elements, DF 1 accounts for 91.7% of the variation and DF 2 accounts for 8.3% of the variation (Table 3.2g; Figure 3.2a). The variables with the highest loadings on DF 1 are angle of the medial epicondyle (13.6) and overall length of the astragalus (-12.1). The total classification rate is 81.0% with arboreal individuals correctly classified at 91.2%. Semi-terrestrial and terrestrial individuals are classified lower at 62.4% and 78.4%, respectively.

In the discriminant function analysis that combined the variables from the proximal and distal humerus, astragalus, and calcaneus, DF 1 accounts for 91.7% of the variation and DF 2 accounts for 8.3% of the variation (Table 3.2h; Figure 3.2b). The variables with the highest loadings on DF 1 are angle of the medial epicondyle (13.74), height of the greater tubercle (13.3), and overall length of the astragalus (-12.9). 82.6% of individuals are correctly classified overall with 91.2% of arboreal individuals, 67.6% of "semi-terrestrial" individuals, and 78.4% of terrestrial individuals being correctly classified.

In the discriminant function analysis that combined variables from the distal humerus and astragalus, DF 1 accounts for 93.1% of the variation and DF 2 accounts for 6.9% of the variation (Table 3.2i; Figure 3.2c). The variables with the highest loadings on DF 1 are overall length of the astragalus (-25.2) and angle of the medial epicondyle (16.4). The total classification rate was 75.4% with arboreal individuals correctly classified at 87.2%, terrestrial individuals correctly classified at 69.2%, and "semi-terrestrial" individuals correctly classified at 55.6%.

Section 3.3.2: Discriminant Function Analyses – cercopithecoid sample with two *a priori* groups and "semi-terrestrialists" treated as unknowns

All analyses in this section returned a single discriminant function that accounts for 100% of the variation since only two groups were provided *a priori*. In the discriminant function analysis using variables from the entire humerus, height of the greater tubercle has the highest loading on DF 1 (13.8) (Table 3.3a; Figure 3.3a). The total classification rate for cross validation is 96.3%, with 99.2% of arboreal individuals correctly classified, and 80% of terrestrial individuals correctly classified. The variable with the highest loading for the proximal humerus is also the height of the greater tubercle (48.9) (Table 3.3b; Figure 3.3b). However, the classification rate dropped in this analysis, mainly due to incorrect classification of terrestrial individuals. The total classification rate is 87.8% with arboreal individuals classified correctly 96.4% of the time and terrestrial individuals classified correctly only 40.0% of the time. The variables with the highest loadings for the distal humerus are angle of the medial epicondyle (15.4) and height of the capitulum (14.2) (Table 3.3c; Figure 3.3c). The classification rate is better than that of the analysis of proximal humeral variables, with 94.2% of individuals correctly classified. 98.4% of the arboreal individuals are correctly classified, and 71.1% of terrestrial individuals are correctly classified.

The variable with the highest coefficient when considering the femur is overall length (-27.1) (Table 3.3d; Figure 3.3d). Both the total classification rate and the classification rate for arboreal individuals are high at 91% and 98%, respectively. However, the classification rate for terrestrial individuals is low at 56%. The variable with the highest coefficient in the analysis of astragalar variables is total length of the astragalus (-60.7) (Table 3.3e; Figure 3.3e). The total classification rate is 88.1%, with arboreal individuals classified correctly 97.1% of the time. Terrestrial individuals are correctly classified only 43.5% of the time. The variable with the highest loading in the analysis of calcaneal variables is length of the calcaneal body (-31.2) (Table 3.3f; Figure 3.3f). The classification rate improved over that of the analysis of astragalar variables, with 92.4% of individuals correctly classified. Arboreal individuals are classified correctly 96.1% of the time, and terrestrial individuals are correctly classified 73.3% of the time.

The variables with the highest loadings in the discriminant function analysis that included variables from all four elements are height of the greater tubercle (20.8) and overall length of the astragalus (-16.49) (Table 3.3g; Figure 3.3a). The overall classification rate is 97.8% with arboreal individuals correctly classified at 99.5%. Terrestrial individuals are also classified well at 89.2%. The variable with the highest loading in the discriminant function analysis that included variables from the proximal and distal humerus, astragalus, and calcaneus are height of the greater tubercle (19.5) and overall length of the astragalus (-17.9) (Table 3.3h; Figure 3.3b). The overall correct classification rate is 96.5% with arboreal individuals correctly classified 99% of the time, and terrestrial individuals correctly classified 83.8% of the time. Overall length of the astragalus has the highest loading on DF 1 (-35.0) in the discriminant function analysis that included only variables from the distal humerus and astragalus (Table 3.3i; Figure 3.3c). The overall correct classification is 95.9%, with 99% of arboreal individuals and 79.5% of terrestrial individuals correctly classified.

Section 3.3.3 Classifications for "semi-terrestrial" cercopithecoids

Seventeen "semi-terrestrial" species were treated as unknowns in the DFAs with only two *a priori* groups (arboreal and terrestrial) (Tables 3.4a-h). Of these 17 species, 12 species are classified as either the arboreal or terrestrial group by all sets of analyses. *Allenopithecus nigroviridis*, *Cercopithecus hamlyni*, *Allocrocebus lhoesti*, *Cercopithecus neglectus*, *Chlorocebus aethiops*, *Chlorocebus pygerythrus*, *Macaca arctoides*, *Macaca mulatta*, *Macaca nemestrina, Macaca thibetana*, and *Semnopithecus entellus* are classified as arboreal in each analysis, generally with high posterior probabilities (over 0.7). *Papio anubis* has a very high posterior probability of being classified as terrestrial using either the complete humerus, the distal humerus, or multiple elements together. The posterior probabilities drop to around 0.67 for the analyses based on the proximal humerus, astragalus and calcaneus.

Cercocebus torquatus, *Erythrocebus patas*, *Macaca nigra, Macaca sylvanus*, and *Macaca tonkeana* are inconsistently classified across each element. *C. torquatus* is assigned to the terrestrial group by the calcaneus, but to the arboreal group by all other single elements, and when multiple elements are combined. *Macaca nigra* is classified as terrestrial by the femur and when multiple elements are combined, but is classified as arboreal by all other single elements. *M. sylvanus* is similarly assigned to the terrestrial group by the calcaneus, and to the arboreal group by all other single elements.

M. sylvanus is assigned to the terrestrial group in the analyses that use all four elements or combine variables from the humerus, astragalus and calcaneus; but is classified as arboreal when combining only variables from the distal humerus and astragalus. *M. tonkeana* is assigned to the arboreal group based on the proximal and distal humerus and to the terrestrial group based on the complete humerus, femur, astragalus, calcaneus, and when multiple elements are combined. However, the posterior probabilities of groups assigned to the arboreal or terrestrial group are relatively similar in the analyses using the complete humerus (terrestrial: 0.53; arboreal: 0.47), astragalus (terrestrial: 0.6; arboreal 0.4), calcaneus (terrestrial: 0.56; arboreal: 0.44), and a combination of distal humerus and astragalus (terrestrial: 0.51; arboreal: 0.49). *E. patas* is assigned to the arboreal group based on the femur, astragalus, calcaneus, a combination of the humerus, astragalus, and calcaneus, and a combination of the distal humerus and astragalus. *E. patas* is assigned to the terrestrial group based on variables from the complete humerus, proximal humerus, distal humerus, and when all four elements are combined.

It is interesting that of the "semi-terrestrial" guenons, *Allochrocebus* and *Chlorocebus* are consistently classified as arboreal, but *Erythrocebus* is inconsistently assigned to the arboreal and terrestrial group. The resuts from this study along with Gebo and Sargis (1944) and Sargis et al. (2008) have shown that "semi-terrestrial" species often do not exhibit the same suite of morphological adaptations associated with terrestrial behavior. Although *Allochrocebus*, *Chlorocebus*, and *Erythrocebus* have been suggested to form a clade (Tosi et al. 2004; Tosi et al. 2005; Xing et al. 2007; Moulin et al. 2008; Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012), the results indicate that *Chlorocebus* and *Allochrocebus* can engage in a substantial amount of terrestrial behavior with a predominately "arboreal" morphotype. Given that *Erythrocebus* is assigned to the terrestrial group when using the humerus but to the arboreal group when using pedal elements, it appears that this species has the "arboreal" and "terrestrial" morphotype in different regions of the postcranium.

Section 3.3.4: Discriminant Function Analyses – cercopithecoid sample with two groups *a priori* and "semi-terrestrialists" included in the terrestrial group

All analyses in this section returned a single discriminant function that accounts for 100% of the variation because only two groups were provided *a priori* but unlike the previous set of analyses, "semi-terrestrial" individuals are included in the terrestrial group. The variables with the highest coefficients for the complete humerus are angle of the medial epicondyle (18.64), the humeral head index (14.25), and height of the greater tubercle (11.0) (Table 3.5a; Figure 3.5a). The overall classification rate is 78.4% with arboreal individuals and terrestrial individuals classified similarly (arboreal: 80%; terrestrial: 76%).

The variable with the highest loading in the analysis on the proximal humerus is height of the greater tubercle (43.9) and the overall classification rate is 68% (Table 3.5b; Figure 3.5b). Arboreal individuals are classified at 76% and terrestrial individuals are classified at 59%. The variable with the highest loading on the distal humerus is angle of the medial epicondyle (17.4) (Table 3.5c; Figure 3.5c). The total classification rate is 76% with arboreal individuals classified correctly at 79% and terrestrial individuals correctly classified at 73%.

The variable with the highest coefficient when considering the femur is length of the femur (-26.7) and the total classification rate is 70% (Table 3.5d; Figure 3.5d). Arboreal individuals are classified higher at 81% but terrestrial individuals are classified lower at 57%. The variables with the highest coefficients for the astragalus are overall length (-46.9) and length of the ectal facet (-31.0) (Table 3.5e; Figure 3.5e). The total classification rate is 71% with arboreal individuals classified at a slightly higher at 78%. Terrestrial individuals are classified lower at 63%. The length of the distal segment of the calcaneus (-23.9) and height of the cuboid facet (22.1) have the highest coefficients on DF 1 when considering the calcaneus (Table 3.5f; Figure 3.5f). The total classification rate is 68% with arboreal individuals classified at 76% and terrestrial individuals classified at 59%.

When all four elements are considered together, the variables with the highest loadings are overall length of the astragalus (-15.6), height of the greater tubercle (11.6), the humeral head index (11.4), angle of the medial epicondyle (10.9), and length of the ectal facet (-10.5) (Table 3.5g; Figure 3.6a). The overall classification rate is 81.9% with arboreal individuals classified correctly 89.1% of the time and terrestrial individuals correctly classified 72.8% of the time. When considering a combination of the proximal and distal humerus, astragalus, and calcaneus the variables with the highest loadings are overall length of the astragalus (-15.6), the humeral head index (11.9), ectal facet width (-11.3), and height of the greater tubercle (11.91) (Table 3.5h; Figure 3.6b). The total classification rate is 83% with arboreal individuals correctly classified at 91% and terrestrial individuals correctly classified at 72%. The variable with the highest loading when using a combination of the distal humerus and astragalus is overall length of the astragalus (-22.5) (Table 3.5i; Figure 3.6c). The overall classification rate is 82% with arboreal and terrestrial individuals correctly classified 88% and 74% of the time, respectively.

Section 3.3.5: Posterior Probabilities for Classification of Semi-terrestrial Species

Since semi-terrestrial individuals are assigned to the terrestrial group in the previous set of DFAs, an interesting way to consider the "degree" to which "semi-terrestrial" species engage in terrestrial behavior is to examine the posterior probabilities from leave-one-out cross-validation. Because classification of arboreal individuals is highly successful, we can consider the posterior probability of being assigned into the arboreal group as a rough numeric representation of the amount of time a species spent engaged in arboreal behavior. Posterior probabilities of extant species means are listed in Tables 3.6a-i and Figures 3.7, 3.8, and 3.9 show a color gradient from brown to green representing highly terrestrial to highly arboreal behavior with species along the gradient for analyses that combine multiple elements.

These results are not intended to provide a formal, numerical, characterization of "semi-terrestriality" among cercopithecoids; however, examining these data does provide interesting information on terrestrial behavior both between and within clades. Figures 3.7-3.9 show an overall phylogenetic signal in the posterior probability of being assigned to the arboreal group. Papionins generally have lower probabilities with almost all species below 0.5 (i.e. 50% probability of being assigned the arboreal group) belonging to this clade. Similarly, almost all species above 0.5 are guenons and colobines, although the more terrestrial representatives of these groups often fall below 0.5. *Erythrocebus patas* consistently has the lowest posterior probability of being classified as arboreal among guenons (when multiple elements are combined the posterior probabilities range from 0.19 to 0.25). The rest of the "semi-terrestrial" guenons, including *Cercopithecus hamlyni*, *Allochrocebus lhoesti*, *Cercopithecus neglectus, Chlorocebus aethiops*, and *Chlorocebus pygerythrus* generally fall between 0.4 and 0.7 while most predominately arboreal guenons fall above 0.6. These results suggest that while *Erythrocebus patas* has adaptations to facilitate frequent terrestriality that make this species more similar to papionins, such "extreme" adaptations are not found in other "semi-terrestial" guenons and are not necessary for these species to use the ground effectively(Gebo and Sargis 1994; Sargis et al. 2008).

Semnopithecus entellus has the lowest posterior probability of being assigned to the arboreal group among colobines (when multiple elements are combined the posterior probabilities range from 0.38 to 0.62) and all other colobines fall above 0.7. Interestingly, *Rhinopithecus roxellana*, which engages in terrestrial behavior more frequently than most colobines, has similar posterior probabilities to *Pygathrix nemeaus* (when all four or three elements are combined) and *Trachypithecus obscurus* (when two elements are combined). This result suggests that colobines with a morphology generally adapted to arboreal behavior can still use the ground effectively.

Section 3.3.5: Fossil Reconstructions

Each element and composite specimen that is classified using the analyses described above is assigned to locomotor groups based on a) DFAs including three *a priori* groups (i.e. arboreal, semi-terrestrial, and terrestrial) (Tables 3.7a-i), b) DFAs including two *a priori* groups with "semi-terrestrialists" treated as unknowns (Tables 3.8a-i), and c) DFAs including two *a priori groups* with "semi-terrestrialists" included in the terrestrial group (Tables 3.9a-i). No fossil reconstructions were performed using the femur alone because the two features associated with terrestrial *versus* arboreal locomotor behavior are overall length of the femur and height of the patellar groove. Given that most fossil femora are fragmentary, these specimens could not be included in an analysis that uses overall length as a discriminator. Locomotor assignments based on three *a priori* groupings will be discussed first, followed by assignments based on two *a priori* groupings.

Victoriapithecus macinnesi

Both proximal humeri of *Victoriapithecus* (KNM-MB 2044 and 21809) are classified as arboreal with posterior probabilities of 0.91 and 0.69. Five of the six distal humeri of *Victoriapithecus* (KNM-MB 19, 21207, 21818, 21822, and 34712) are classified as semi-terrestrial with posterior probabilities of over 0.61. One distal humerus (KNM-MB 3) is classified as arboreal with a posterior probability of 0.85. KNM-MB 3 appears to have post-mortem abrasion on the distal articular surface, specifically on the medial trochlear margin and the lateral aspect of the capitulum. This abrasion may have affected measurements of the capitulum and trochlea and consequently this reconstruction should be considered with more caution. Of seven astragali, six (KNM-MB 4814, 12013, 34364, 34810, 34809, 34812) are classified as arboreal with posterior probabilities ranging from 0.51 to 0.88. One astragalus (KNM-MB 34816) is classified as semi-terrestrial with a posterior probability of 0.56. Of ten calcanei, seven (KNM 12006, 21208, 21209, 21211, 35571, 35573, and 46664) are classified as arboreal with posterior probabilities ranging from 0.67 to 0.9. One calcaneus is placed in the arboreal (0.49) or semi-terrestrial group (0.48) with equal likelihood. The remaining two calcanei of KNM-MB 14375 and 34821 are classified as semi-terrestrial with posterior probabilities of 0.49. KNM-MB 34821 is also likely to be placed in the arboreal group (0.41) and KNM-MB 14375 is also likely to be placed in the terrestrial group (0.43). A composite specimen of *Victoriapithecus* including the proximal and distal ends of the humerus, astragalus, and calcaneus is classified as arboreal with a posterior probability of 0.88.

Almost all elements of *Victoriapithecus* are classified as arboreal with generally high posterior probabilities (above 0.75) based on analyses using the two *a priori* locomotor groups when "semi-terrestrialists" are treated as unknown. One astragalus (KNM-MB 34816) is classified as arboreal with a lower posterior probability of 0.54. One distal humerus (KNM-MB 19) and one calcaneus (KNM-MB 14375) are classified as terrestrial with posterior probabilities of 0.78 and 0.82, respectively. A composite specimen of *Victoriapithecus* including the proximal and distal ends of the humerus, astragalus, and calcaneus is classified as arboreal with a posterior probability of 0.99.

More variation in classification exists when considering *Victoriapithecus* using two *a priori* locomotor groups with "semi-terrestrialists" included in the terrestrial group. Both proximal humeri (KNM-MB 21809 and 2044) are classified as arboreal with posterior probabilites of 0.76 and 0.96. One distal humerus (KNM-MB 3) is reconstructed as arboreal (0.8) but the remaining five humeri (KNM-MB 21207, 21818, 21822, 19, and 34712) are classified as terrestrial with posterior probabilities ranging from 0.65 to 0.88. Three astragali (KNM-MB 34814, 34810, and 34812) are classified as arboreal with posterior probabilities ranging from 0.61 to 0.87 and two astragali (KNM-MB 34816 and 34809) are classified as terrestrial with posterior probabilities of 0.73 and 0.8. Two astragali are classified as arboreal and terrestrial with equal likelihood (KNM-MB 34364: arboreal = 0.53, terrestrial = 0.47; KNM-MB 12013: arboreal = 0.5, terrestrial = 0.5). Five calcanei (KNM-MB 34820, 12006, 21211, 46664, and 35571) are classified as arboreal with posterior probabilities ranging from 0.61 to 0.89 and one calcaneus (KNM-MB 34821) is classified as terrestrial with a posterior probability of 0.71.

Microcolobus sp.

The distal humerus and astragalus (KNM-NA 47915K and KNM-NA 47916A) of *Microcolobus* are classified as arboreal using any of the three *a priori* groupings (posterior probabilities ranging from 0.63 – 0.96). *Microcolobus* is also classified as arboreal when considering a combination of the distal humerus and the astragalus with any of the three *a priori* groupings (posterior probabilities ranging from 0.83 to 0.99.)

Kuseracolobus hafu

The distal humerus of *Kuseracolobus hafu* (ASI VP 2-59c) is classified as terrestrial using either *a priori* grouping (posterior probabilities of and 0.49 and 0.89).

Paracolobus chemeroni

The humerus of *Paracolobus chemeroni* (KNM-BC 3B S) is classified with equal probability as arboreal (0.54) or semi-terrestrial (0.44). The astragalus (KNM-BC 3 AQ) is classified as arboreal with a posterior probability of 0.7. The calcaneus (KNM-BC 3 R) is classified as semi-terrestrial with a posterior probability of 0.55. When all elements of *P. chemeroni* were considered together, this specimen is classified as semi-terrestrial with a posterior probability of 0.49 and as arboreal with a posterior probability of 0.42.

When all elements of *P. chemeroni* are considered individually and together in analyses using two groups *a priori* and "semi-terrestrialists" treated as unknown, all assignments are to the arboreal group (posterior probabilities ranging from 0.82 - 0.98). When considering *P. chemeroni* using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group, isolated elements are generally classified with low posterior probabilities indicating that assignment to either the arboreal or terrestrial group is equally likely. The humerus (KNM-BC 3B) is classified as terrestrial with a posterior probability of 0.58. The astragalus (KNM-BC 3AQ) and calcaneus (KNM-BC 3R) are classified as arboreal with posterior probabilities of 0.63 and 0.59. With all elements combined, *P. chemeroni* is classified as arboreal with a posterior probability of 0.79.

Rhinocolobus turkanensis

Two humeri, a complete specimen (KNM-ER 15420) and a distal specimen (AL300-1), are both classified as arboreal using any of the *a priori* groupings (posterior probabilities ranging from 0.85 - 0.99).

Cercopithecoides

The humerus of *Cercopithecoides williamsi* (KNM-ER 4420C), the humerus of *C. meaveae* (AL2-63/64), and the proximal humerus of *C. kimeui* (KNM-ER 176G) are all classified as semi-terrestrial with posterior probabilities around 0.69 when using three *a priori* groups. All elements are classified as arboreal when using two *a priori* groups with "semi-terrestrialists" treated as unknown. The posterior probability for *C. meaveae* is relatively high at 0.92 but the posterior probabilities for *C. williamsi* and *C kimeui* are lower at 0.71 and 0.62, respectively. *C. meavae* and *C. williamsi* are classified as terrestrial when using two *a priori* groups with "semi-terrestrialists" included in the terrestrial group with posterior probabilities of 0.71 and 0.76. *C. kimeui* is classified as the arboreal and terrestrial with about equal likelihood (arboreal: 0.53; terrestrial: 0.47).

Mesopithecus

Of three *Mesopithecus* sp. humeri, two are classified as arboreal (HD 916 and 1004) and one is classified as semi-terrestrial (HD 1610) with posterior probabilities above 0.82. The proximal humerus of *Mesopithecus* sp. (HD 417) is classified as arboreal with a posterior probability of 0.79. Of three distal humeri, two (HD 1611 and 1612) are classified as arboreal with posterior probabilites above 0.82 and one (HD 1625) is classified as semi-terrestrial with a relatively low posterior probability of 0.55. The astragalus of *Mesopithecus* sp. (HD 1025) is classified as semi-terrestrial but the posterior probabilities were spread relatively equally across all three locomotor groups (arboreal: 0.31; semi-terrestrial: 0.46; terrestrial: 0.23). Of three calcanei, two (HD 408 and 1023) are classified as arboreal and one (HD 1569) is classified as semi-terrestrial (posterior probabilites above 0.75). One composite of *Mesopithecus* sp. including the proximal and distal ends of the humerus, astragalus, and calcaneus is classified as arboreal with a posterior probability of 0.56 and as semi-terrestrial with a posterior probability of 0.43.

All specimens of *Mesopithecus* sp. are classified as arboreal when using two groups *a priori* with "semi-terrestrialists" treated as unknown. Generally, the posterior probabilities are above 0.9. One humerus (HD 1610) and one astragalus (HD 1025) have lower posterior probabilities of 0.73 and 0.6, respectively. The composite specimen is assigned to the arboreal group with a posterior probability of 0.99.

Almost all specimens of *Mesopithecus* sp. are classified as arboreal when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group (posterior probabilities ranging from 0.71 to 0.97. One complete humerus (HD 1610) and one astragalus (1025) are classified as terrestrial with posterior probabilities of 0.86 and 0.74. One distal humerus (HD 1625) and one calcaneus (HD 1569) have relatively equally likelihood of being placed in either group (distal humerus: arboreal = 0.43, terrestrial = 0.57; calcaneus: arboreal = 0.54, terrestrial = 0.46). The composite is classified as arboreal with a posterior probability of 0.61.

Of three *Mesopithecus pentelicus* humeri, two are classified as arboreal (Pik 355 and 244) and one is classified as semi-terrestrial (Pik 1727). Pik 355 and 1727 have lower posterior probabilites of 0.58 and 0.6, respectively, while Pik 244 has a posterior probability of 0.9. The proximal humerus of *M. pentelicus* (Pik 298) is classified as arboreal with a posterior probability of 0.68. Of three distal humeri, one (Pik 245) is classified as arboreal, one (Pik 356) is classified as semi-terrestrial, and one (Pik 419) is classified as terrestrial. Pik 245 and Pik 419 have low posterior probabilities for their most likely classifications (of 0.54 and 0.53), while Pik 356 has a relatively higher posterior probability of 0.68. Of four astragali, two (Pik 368 and 238) are classified as arboreal with low posterior probabilities of 0.62 and 0.56, respectively. One astragalus (Pik 237) is classified as semi-terrestrial and another (Pik 256) is classified as terrestrial, both with relatively low posterior probabilities of 0.47 and 0.44, respectively. Of four calcanei, three (Pik 266, 1746, and 239) are classified as arboreal and one (Pik 240) is classified as terrestrial. Only Pik 266 has a high posterior probability of 0.93, while the other three specimens have posterior probabilities ranging from 0.46 to 0.59. A composite specimen of *M. pentelicus*, including the proximal and distal ends of the humerus, distal femur, astragalus, and calcaneus, is classified as arboreal with a posterior probability of 0.72.

Almost all *M. pentelicus* specimens are classified as arboreal when using two groups *a priori* with "semi-terrestrialists" treated as unknown. Generally posterior probabilities are over 0.9, but Pik 1727 (humerus), 356 (distal humerus), and 237 (astragalus) are exceptions with posterior probabilities of 0.65, 0.51, 0.6, respectively. One distal humerus (Pik 419), one astragalus (Pik 256), and one calcaneus (Pik 240) are classified as terrestrial with posterior probabilities of 0.94, 0.61, and 0.81. The composite specimen of *M. pentelicus* is classified as arboreal with a posterior probability of 0.99.

More variation in classification exists when considering *M. pentelicus* using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. Two complete humeri (Pik 355 and 244) are classified as arboreal with posterior probabilities of 0.7 and 0.88 and the other complete humerus (Pik 1727) is classified as terrestrial with a posterior probability of 0.68. The proximal humerus (Pik 298) is classified as arboreal with a posterior probability of 0.7. Two distal humeri (Pik 356 and 419) are classified as terrestrial with posterior probabilities of 0.77 and 0.95. The other distal humerus (Pik 245) is equally likely to be classified as arboreal or terrestrial (arboreal = 0.56, terrestrial = 0.46). Three astragali (Pik 237, 256, and 238) are classified as terrestrial with posterior probabilities ranging from 0.63 to 0.79. The other astragalus (Pik 368) is classified as arboreal or terrestrial with equal likelihood (arboreal = 0.5, terrestrial = 0.5). One calcaneus (Pik 266) is classified as arboreal with a posterior probability of 0.79 and one calcaneus (Pik 240) is classified as terrestrial with a posterior probability of 0.82. Two calcanei (Pik 1746 and 239) are about equally likely to be classified into either group (1746: arboreal = 0.55, terrestrial = 0.45; 239: arboreal = 0.46, terrestrial = 0.54). The composite specimen of *M. pentelicus* is reconstructed as arboreal with a posterior probability of 0.75.

Dolichopithecus ruscinensis

Of the three *D. ruscinensis* distal humeri, one (Per 011) is classified as semi-terrestrial with posterior probability of 0.5. The other two distal humeri (Per 010 and 012) are classified as arboreal with posterior probabilities of 0.61 and 0.77. Both astragali of *D. ruscinensis* (Pp 20a and Pp 20b) are classified as arboreal with posterior probabilities of 0.49 and 0.88. The composite specimen of *D. ruscinensis*, including the distal humerus and astragalus, is classified as arboreal with a posterior probability of 0.62.

All specimens of *D. ruscinensis* (with one exception) are classified as arboreal with posterior probabilities generally over 0.75 when using two *a priori* groups with "semi-terrestrialists" treated as unknown. One distal humerus (Per 011) is classified as terrestrial with a posterior probability of 0.82. The composite specimen of *D. ruscinensis* is classified as arboreal with a posterior probability of 0.93.

One humerus (Per 012) of *D. ruscinensis* is classified as arboreal with a posterior probability of 0.73 and one humerus (Per 011) is classified as terrestrial with posterior probability of 0.86 using two *a priori* groups with "semi-terrestrialists" included in the terrestrial group. Another humerus (Per 010) is classified into either the arboreal (0.59) or terrestrial group (0.41) with relatively high posterior probabilities. One astragalus (Pp 20b) is classified as arboreal with a posterior probability of 0.9. The other astragalus (Pp 20a) is classified with about equal probability into either group (arboreal = 0.56, terrestrial = 0.44). The composite specimen of *D. ruscinensis* is classified as arboreal with a posterior probability of 0.7.

Parapresbytis eohanuman

The distal humerus of *Parapresbytis* is classified as arboreal using any of the *a priori* groupings with posterior probabilities ranging from 0.72 and 0.99.

Theropithecus

Two humeri of *Theropithecus oswaldi* (KNM-ER 18917 and 5491) are classified as terrestrial with posterior probabilities of 0.72 and 0.83. Based on two proximal humeri, *T. oswaldi* (KNM-ER 567 and 13) is classified as arboreal based on two specimens with relatively low posterior probabilities of 0.55 and 0.59. A third proximal humerus (KNM-ER 601C) is classified as semi-terrestrial with a posterior probability of 0.49 and as terrestrial with a posterior probability of 0.41. One distal humerus (KNM-ER 3876) is classified as arboreal with a posterior probability of 0.53 and a second distal humerus (KNM-ER 13B) is classified as semi-terrestrial with a posterior probability of 0.72. All five astragali (KNM-ER 3876, KNM-OG 948, 950, 1188, 1580) are classified as arboreal with posterior probabilities ranging from 0.46 to 0.7. Of seven calcanei, four (KNM-OG 1192, 484, 1138, and 472) are classified as arboreal with posterior probabilities ranging from 0.53 to 0.89. Two calcanei (KNM-OG 475 and 958) are classified as terrestrial with posterior probabilities of 0.48 and 0.62. The final calcaneus (KNM-ER 3878) is classified as semi-terrestrial with a posterior probability of 0.43. The composite specimen of *T. oswaldi*, including the proximal and distal ends of the humerus, astragalus, and calcaneus is classified as semi-terrestrial with a posterior probability of 0.58 and as terrestrial with a posterior probability of 0.41.

Both complete humeri (KNM-ER 18917 and 5491), one proximal humerus (KNM-ER 601 C), and three calcanei (KNM-OG 475 and 958) are classified as terrestrial with posterior probabilities above 0.74 when using two groups *a priori* with "semi-terrestrialists" as unknown.

All other elements are classified as arboreal with posterior probabilities above 0.68. The composite specimen of *T. oswaldi* is classified as terrestrial with a posterior probability of 0.98.

The complete humeri (KNM-ER 18917 and 5491) of *T. oswaldi* are classified as terrestrial with posterior probabilities of 0.97 when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. One proximal humerus (KNM-ER 567) is classified as arboreal with a posterior probability of 0.69 and one proximal humerus (KNM-ER 601 C) is classified as terrestrial with a posterior probability of 0.88. A third proximal humerus (KNM-ER 13) is about equally likely to be placed in either the arboreal (0.46) or terrestrial (0.54) group. One distal humerus (KNM-ER 13B) is classified as terrestrial with a posterior probability of 0.83 and the other distal humerus (KNM-ER 3876) is about equally likely to be placed in the arboreal (0.55) or terrestrial group (0.45). Three astragali (KNM-OR 1580, 948, and 950) are classified as arboreal with posterior probabilities ranging from 0.61 to 0.7. The other two astragali (KNM-ER 3876 and KNM-OR 1188) are classified as terrestrial with posterior probabilities of 0.61 and 0.69. Four calcanei (KNM-OG 475, 958, and 484, and KNM-ER 3878) are classified as terrestrial with posterior probabilities ranging from 0.6 to 0.85. Two calcanei (KNM-OG 1192 and 1138) are classified as arboreal with posterior probabilities of 0.65 and 0.81. The final calcaneus (KNM-OG 472) is likely to be placed in either the arboreal (0.56) or terrestrial group (0.44). The composite specimen of *T. oswaldi* is classified as terrestrial with a posterior probability of 0.98

The humerus of *T. brumpti* (KNM-WT 38738) is classified as semi-terrestrial with a posterior probability of 0.55. The next likely locomotor group was arboreal with a posterior probability of 0.43. Based on the distal humerus alone, *T. brumpti* (KNM-ER 3013) is likely to be classified as arboreal (0.52) or semi-terrestrial (0.46). Both astragali (KNM-WT 17544D and L865-1t) are classified as semi-terrestrial with posterior probabilities of 0.55 and 0.62, respectively. The calcaneus (L865-1r) is classified as semi-terrestrial with a posterior probability of 0.48. The composite specimen of *T. brumpti*, including distal humerus and astragalus is classified as semi-terrestrial with a posterior probability of 0.7.

When using two groups *a priori* with "semi-terrestrialists" treated as unknown, the humerus (KNM-WT 38738), distal humerus (KNM-ER 3013), and one astragalus (KNM-WT 17544) of *T. brumpti* are classified as arboreal with posterior probabilities over 0.68. The other astragalus (L865-1t) is classified as terrestrial with a posterior probability of 0.94. The calcaneus (L865-1r) is classified as being arboreal (0.51) or terrestrial (0.49) with equal likelihood. The composite specimen of *T. brumpti* is classified as arboreal with a posterior probability of 0.71.

All specimens of *T. brumpti* are classified as terrestrial (with one exception) with posterior probabilities ranging from 0.59 to 0.99, when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. One distal humerus (KNM-ER 3013) is assigned to either group with equal likelihood (arboreal = 0.51, terrestrial = 0.49). The composite specimen of *T. brumpti* is classified as terrestrial with a posterior probability of 0.8.

Parapapio jonesi

The distal humerus of *Parapapio jonesi* (AL363-12) is classified as semi-terrestrial with a posterior probability of 0.59 using three groups *a priori*. This element is classified as arboreal with a posterior probability of 0.9 when using two groups *a priori* with "semi-terrestrialists" as unknown but as terrestrial with a posterior probability of 0.66 when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

<u>*Parapapio lothagamensis*</u>

The proximal humerus of *Parapapio lothagamensis* (KNM-LT 28769) is classified as arboreal with a posterior probability of 0.92. The distal humerus (KNM-LT 23074) is classified as semi-terrestrial with a posterior probability 0.74. The astragalus (KNM-LT 23081) is reconstructed as classified with a posterior probability of 0.5 and as arboreal with a posterior probability of 0.43. Both calcanei (KNM-LT 28575 and 24125) are classified as arboreal with posterior probabilities of 0.6 and 0.59. The composite specimen of *P. lothagamensis* including the proximal and distal humerus, astragalus, and calcaneus is classified as semi-terrestrial with a posterior probability of 0.85.

When using two groups *a priori* with "semi-terrestrialists" as unknown, all specimens except one distal humerus (KNM-LT 23074) are classified as arboreal with posterior probabilities above 0.86. KNM-LT 23074 is classified as terrestrial with a posterior probability of 0.65. The composite specimen of *P. lothagamensis* is classified as arboreal with a posterior probability of 0.99.

When using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group a proximal humerus (KNM-LT 28769), and two calcanei (KNM-LT 28575 and 24125) are classified as arboreal with posterior probabilities ranging from 0.72 to 0.94. One distal humerus (KNM-LT 23074) and one astragalus (KNM-LT 23081) are classified as terrestrial with posterior probabilities of 0.94 and 0.76. The composite specimen of *P. lothagamensis* is equally likely to be classified as arboreal (0.52) or terrestrial (0.48).

Section 3.4.1: Discussion of Multivariate Techniques for Predicting Locomotor Behavior

When using a multivariate approach to examine morphological differences among arboreal, semi-terrestrial, and terrestrial cercopithecoids, the DFAs presented generally show that arboreal and terrestrial individuals are well-separated in the morphospace, but semi-terrestrial individuals overlap substantially with both groups. When examining single elements, the humerus performs best in cross-validation with an overall correct classification rate of 74.1%. Across all single elements, arboreal individuals are consistently well-classified in cross-validation (>80% correctly classified). However, semi-terrestrial and terrestrial individuals are not assigned to their *a priori* groups with high posterior probabilities in cross-validation. The humerus had the highest classification rate for these individuals with 64.4% of semi-terrestrial and 51.1% of terrestrial individuals correctly classified.

The cross-validation rate improves for arboreal and terrestrial individuals when using a combination of elements. The highest classification rates are achieved when using a combination of four elements or a combination of three elements (the proximal and distal humerus, astragalus, and calcaneus). Arboreal individuals are correctly classified over 90% of the time and terrestrial individuals are correctly classified over 76% of the time. Over 62% of semi-terrestrial individuals are correctly classified, which is about the same rate as when using the humerus alone (64.4%). When combining the distal humerus and astragalus, the classification rates are slightly lower, with arboreal individuals correctly classified 85.8% of the time and terrestrial individuals correctly classified 69.2% of the time. However, the classification rate for semi-terrestrial individuals (56.9%) was lower than when using the humerus alone (64.4%).

When semi-terrestrial individuals are left as unknowns, arboreal and terrestrial individuals continue to be well-separated in the morphospace and the rate of correct classification is generally higher than when semi-terrestriality individuals are included as an *a* *priori* group. When examining single elements, the humerus has the highest rate of correct classification (96.3%). Arboreal individuals are consistently correctly classified by all single elements (>95% correctly classified). Terrestrial individuals have the highest classification rates when using the humerus (80%), calcaneus (73.9%) and the distal humerus (71.1%). However shape variables from the proximal humerus and calcaneus have very poor classification rates of 41.3% and 31.1%, respectively. The multi-element models have the best classification rates, although their improvement over using the humerus alone is only slight. In all multi-element analyses, arboreal individuals are correctly classified 99% of the time. Terrestrial individuals are correctly classified over 84% of the time.

Overall, when left unassigned, "semi-terrestrial" individuals are placed consistently into either the arboreal or terrestrial group by single elements and combinations of elements. *Allenopithecus nigroviridis*, *Cercopithecus hamlyni*, *A. lhoesti*, *C. neglectus*, *Chlorocebus aethiops*, *Ch. pygerythrus*, *Macaca. arctoides*, *M. mulatta*, *M. nemestrina, M. thibetana*, and *Semnopitheus. entellus* are assigned to the arboreal group and *P. anubis* is assigned to the terrestrial group in all set of analyses. These results suggest that adaptations to arboreal behavior in the postcranium of cercopithecoids do not preclude them from engaging in a substantial amount of terrestrial behavior. Likewise, although *P. anubis* is morphologically similar to the most committed terrestrial cercopithecoids, this species is adept at climbing and arboreal locomotion. Gebo and Sargis (1994) also documented similar morphologies between arboreal and semi-terrestrial guenons, making associations between morphology and behavior in this clade difficult.

Other "semi-terrestrial" cercopithecoids are exceptions to this pattern and show assignment to different locomotor groups based on which elements are examined. If we consider just the humerus and calcaneus, which have the best classification rates of single elements, we see that *Cercocebus torquatus* and *Macaca sylvanus* are classified as "arboreal" by the humerus and "terrestrial" by the calcaneus and that these assignments are reversed for *Erythrocebus patas*. These results suggest that some "semi-terrestrial" species show different sets of adaptations in different elements or among different regions of the body (Gebo and Sargis 1994; Sargis et al. 2008). The differences may be the results of the habitat of each species, how frequently each species engages in terrestrial behavior, and what behaviors are most frequently used on the ground (i.e. travelling, feeding, social, etc.). In most analyses *Macaca tonkeana* is assigned to the arboreal or terrestrial group with about equal likelihood, suggesting this taxon does have an "intermediate" morphology that shares similarities with both locomotor extremes. These results suggest that morphological features associated with terrestrial behavior are not the same across all species that engage in terrestrial behavior and cast doubt on the idea that these adaptations to terrestriality are inherited from a common ancestor (Gebo and Sargis 1994; Sargis et al. 2008).

As would be expected, classification rates for terrestrial individuals are higher for some elements when considering two groups *a priori* with "semi-terrestrialists" as unknown, and Figure 3.2 shows that overlap between locomotor groups was less than when considering three groups *a priori*. The complete humerus (80%), distal humerus (71.1%), and calcaneus (73.9%) performed much better when this set of two *a priori* groups is used, making the elements more useful when considering "extremes" in locomotor behavior. Shape variables from the proximal humerus and astragalus performed poorly (41.3% and 31.1%, respectively). A combination of variables from the humerus, astragalus, and calcaneus performed best at classifying individuals as in the other sets of analyses. Arboreal individuals are correctly classified at least 88% of the time and terrestrial individuals are correctly classified at least 73% of the time.

Classification rates when considering two groups *a priori* with "semi-terrestrialists" *included* in the terrestrial group are similar to other DFAs in that the total correct classification rate for the humerus (0.78), distal humerus (0.76), and a combination of elements (four elements = 0.82; three elements = 0.83; two elements = 0.82) have the highest classification rates. Also similar to other analyses, arboreal individuals are correctly classified at a consistently higher rate than terrestrial individuals with correct classification rates ranging from 0.76 to 0.91. Terrestrial individuals have the best classification rates when using the humerus (0.76), distal humerus (0.73), a combination of two elements (0.74), four elements (0.73) or three elements (0.72). Classification rate for terrestrial individuals drops for the proximal humerus (0.59), astragalus (0.63), and calcaneus (0.59).

The posterior probabilities of being assigned to the arboreal group in these sets of analyses suggest that postcranial morphology has a strong phylogenetic signal. Within each clade, papionins, guenons, and colobines generally have similar posterior probabilities of being assigned to the arboreal group (see Figure 3.7 – 3.9), although species that engage in terrestrial behavior have lower posterior probabilities for their clade. These results demonstrate that while all clades have terrestrial members, the morphology of these species is influenced by the ancestral condition for each clade. For example, the "semi-terrestrial" guenons (excluding *Erythrocebus patas*) are more similar in morphology to the arboreal guenons than to *Erythrocebus patas*. *E. patas* may be more morphologically specialized than other "semi-terrestrial" guenons but that does not preclude other species from engaging in terrestrial behavior (Gebo and Sargis 1994; Sargis et al. 2008). *Macaca fascicularis*, an arboreal macaque has posterior probabilities of being assigned to the arboreal group ranging from 0.63 to 0.74 and falls near *Pygathrix nemaeus* and *Rhinopithecus roxellana* (when three or four elements are combined; Figure 3.7 and 3.8) or *Cercopithecus cephus* (when two elements are combined; Figure 3.9). But *Macaca arctoides*, another arboreal macaque, has a range of posterior probabilities from 0.45 to 0.55 and falls near the semi-terrestrial guenons. Given that *M. fascicularis* and *M. arctoides* are not especially closely related among macaques (e.g. Springer et al. 2012), these results again suggest that the ancestral condition combined with difference in habitat and behavior can produce different morphologies even among arboreal species of the same clade (Sargis et al. 2008).

When considering two groups *a priori* with "semi-terrestrialists" included in the terrestrial group, fossil species typically had variation both between and within elements in classification to the arboreal or terrestrial group. This is not surprising given that all "semi-terrestrial" individuals were included in the terrestrial group and substantial overlap exists between the arboreal and terrestrial groups (Figure 3.3 and 3.4). When "semi-terrestrial" individuals are left as unknown, fossil species must be placed into one of two "extreme" locomotor categories and this often led to a majority of elements within a fossil species being placed in the arboreal group. Given that many of the fossil species are considered "semi-terrestrial" by previous work and that substantial overlap exists between arboreal and semi-terrestrial individuals, the frequent classification of fossil elements to the arboreal group is expected. But, when "semi-terrestrial" individuals are included in the terrestrial group, the terrestrial group contains a considerable amount of variation in morphologies associated with terrestrial behavior. Since many fossil species are similar to extant species in having overlapping morphologies with both an arboreal and terrestrial "extreme," it is also expected that in this set of analyses fossil species would not be consistently classified into either the arboreal or terrestrial group.

Section 3.4.2: Discussion of Fossil Reconstructions

Previous work on *Victoriapithecus* (Harrison 1989; McCrossin et al. 1998; Benefit 1999b) has demonstrated that this species likely engaged in some amount of terrestrial behavior. The results presented here support this conclusion but also suggest that *Victoriapithecus* may have been more adept at arboreal locomotion than previously thought. Figure 3.8 shows that a composite specimen of *Victoriapithecus* is most similar to arboreal guenons such as, *Cercopithecus mona, C. ascanius,* and *C. cephus* when examining the posterior probability of being assigned to the arboreal group. Figure 3.5 shows variation in direction of the medial epicondyle of *Victoriapithecus*. Some specimens, such as KNM-MB 19, have a medial epicondyle that is dorsally oriented to the same extent as *Erythrocebus patas* (Figure 3.3), but other specimens, such as KNM-MB 21822, have projection more similar to *Colobus guereza* (Figure 3.3). This variation explains why some of the distal humeri from *Victoriapithecus* are classified as arboreal by the DFAs.

Additionally, both proximal humeri (KNM-MB 12044 and 21809) are assigned to the arboreal group. As can be seen in Figure 3.5, the humeral head of *Victoriapithecus* is at the same level as (or projects above) the greater tubercle, which is a morphology seen in arboreal anthropoids (Figure 3.4 and see previous chapter; Harrison 1989; contra McCrossin et al. 1998). In addition, most astragali and calcanei are classified as arboreal, although one astragalus and two calcanei are classified as semi-terrestrial. Finally, the composite specimen of *Victoriapithecus* is classified as arboreal, although this may be driven by the morphology of the astragalus given its high loadings in the multi-element DFA. Based on this evidence, *Victoriapithecus* probably resembled many extant cercopithecoids that transition easily between the ground and above-ground substrates. The orientation of the medial epicondyle was shown in the previous chapter to be highly associated with locomotor preference and thus the morphology of the distal humerus of *Victoriapithecus* would lead to the conclusion that this species utilized the ground for some behaviors. However, most other elements document adaptations to arboreality, and therefore, this species was likely to be very active in arboreal environments as well. Previous work on the postcranium of *Victoriapithecus* (Harrison 1989; McCrossin et al. 1998; Benefit 1999b) has been based on a limited sample and over the past two decades Benefit and her colleagues have increased the sample of *Victoriapithecus* tremendously (Benefit and McCrossin 2002). The reconstruction provided here is based on the most comprehensive taxonomic sample of extant cercopithecoids and a larger sample of *Victoriapithecus* than has been previously studied, which may explain why the results of this study differ from previous work.

This study also supports previous work on *Microcolobus* (Nakatsukasa et al. 2010), which suggests that this early colobine was primarily arboreal. The distal humerus and astragalus of *Microcolobus* are assigned to the arboreal group in all analyses. Figure 3.9 shows that *Microcolobus* is similar to other colobines in its posterior probability of being assigned to the arboreal group. Much of the debate concerning when and if arboreality re-evolved (Hlusko 2006; Hlusko 2007; Nakatsukasa et al. 2010) has pointed to evidence of early adaptations for arboreal behavior in the colobine lineage as evidence for arboreality in the last common ancestor of colobines rather than parallel evolution as was suggested by Leakey et al. (2003).

The reconstructions presented in this study of later occurring colobines - *Mesopithecus*, *Dolichopithecus*, *Parapresbytis, Paracolobus*, *Kuseracolobus, Rhinocolobus* and *Cercopithecoides* - generally support previous research on these species as well. Previous work on *Mesopithecus* describes this species as semi-terrestrial and having a mosaic of arboreal and terrestrial features (Delson 1973; Youlatos 2003; Ingicco 2008; Youlatos and Koufos 2010; Youlatos et al. 2012). This mosaic can be seen in the reconstructions with humeri, astragali, and calcanei of *Mesopithecus* sp. from Bulgaria and *M. pentelicus* from Greece being assigned to either the arboreal group or the semi-terrestrial group with equal likelihood. Delson (1973) previously suggested that *Dolichopithecus* was highly terrestrial, but the results of this study, along with that of Ciochon (1993) and Ingicco (2008), suggest that *Dolichopithecus* was probably more similar to *Mesopithecus* in its locomotor repitoire. Figures 3.7 – 3.9 show that *Mesopithecus* and *Dolichopithecus* are like other colobines in having a posterior probability of being assigned to the arboreal group above 0.5. Although *Dolichopithecus* and *M. pentelicus* fall near arboreal guenons and colobines along the color gradient, *Mesopithecus* sp. is most similar to "semi-terrestrial" species such as, *Cercopithecus hamlyni* and *Semnopithecus entellus.* Although previous work on *Mesopithecus* has suggested The final Eurasian colobine, *Parapresbytis*, is classified as arboreal, supporting the conclusion of Egi et al. (2007).

Previous work on *Paracolobus chemeroni* has described this species as having a mosaic of arboreal and terrestrial features, but that it most likely spent more time engaged in arboreal behavior (Birchette 1982; Ciochon 1993). The present study supports these findings, with the humerus of *P. chemeroni* classified as equally likely to fall in the arboreal or semi-terrestrial group. The astragalus is classified as arboreal, but the calcaneus is classified as terrestrial. *Paracolobus* is most similar to arboreal guenons in its posterior probability of being assigned to the arboreal group (Figure 3.7). Although the locomotor reconstruction previously proposed by Birchette (1982) is supported by this study, many of the comparisons he made were phenetic in nature. He accurately described a mosaic of arboreal and terrestrial features, especially in the humerus, and suggested that *P. chemeroni* was capable of limited terrestrial behavior. However, he concluded that the overall signal from the postcranium of *P. chemeroni* was that of an arboreal quadruped based on several phenetic similarities of the clavicle, scapula, and ulna between *P. chemeroni* and extant colobines. Such comparisons should be read with caution as the previous chapter has shown that examinations of associations between morphology and behavior (or phylogeny) outside the context of a broad comparative sample and phylogenetically informed analytical models may produce results that inflate differences between groups.

Rhinocolobus turkanensis is not known from many postcranial elements. This species has been described as arboreal in having a greater tubercle that projects only slightly above the humeral head and a medially projecting medial condyle (Frost and Delson 2002; Jablonski et al. 2008b). The three humeri of *R. turkanensis* are classified as arboreal in the present study. Hlusko (2006) described a postcranium of *Kuseracolobus*, which includes a distal humerus. The present study classified this element as terrestrial when using either two or three groups *a priori*. Hlukso (2006) interpreted *Kuseracolobus* as having been arboreal, and based on personal observations the medial epicondyle does not appear to be as dorsally projecting as that of *T. gelada* or *P. cynocephalus* (Figures 3.3 and 3.6), but the medial epicondyle of this specimen is also more dorsally oriented than that of *Microcolobus* (Figure 3.6) When using the three group *a priori* model, *Kuseracolobus* is about equally likely to fall in the semi-terrestrial (43.9%) or the terrestrial groups (48%). DFAs that incorporate variables from the complete humerus had better classification rates of semi-terrestrial and terrestrial individuals, and future discoveries of more complete postcrania of this taxon could alter the current reconstructions.

All species of *Cercopithecoides* have been described previously as having been terrestrial (Birchette 1982; Frost and Delson 2002; Jablonski et al. 2008b). In the present study, only humeral elements of this genus were considered because no astragali or calcanei are known. *C. williamsi* and *C. meaveae* are represented by proximal and distal ends of the humerus and *C. kimeui* is represented by the proximal and distal humerus from two separate elements. *C. williamsi* and *C. meaveae* are classified as semi-terrestrial when using three groups *a priori* but both are classified as arboreal when using only two groups *a priori*. The proximal humerus of *C. kimeui* is classified as semi-terrestrial when using three groups *a priori* but is classified as arboreal when using two groups *a priori*. Given, the low cross-validation rate for terrestrial individuals in the model using only shape variables from the proximal humerus and two groups *a priori* (41.3%), it would seem unlikely for unknowns to be assigned to the terrestrial group, even if their morphology reflects "terrestriality" and additional postcranial material for this species may alter the reconstructions presented here. The distal humerus of *C. kimeui* is classified as arboreal when using either two or three groups *a priori*.

Although *C. meaveae* and *C. williamsi* are quite large in body size, previous research has noted that the greater tubercle in both of these species projects only slightly above the humeral head (Frost and Delson 2002; Jablonski et al. 2008b). Figures 3.4 and 3.7 show that the greater tubercles *C. kimeui* and *C. meaveae* are either at the level of, or below, the humeral head and that these species are more similar to *Colobus guereza* and *Cercopithecus mitis*. *C. williamsi* has a remarkably large greater tubercle, but the actual *projection* above the humeral head is similar to that of *Cercocebus torquatus* (Figures 3.4 and 3.7). Frost and Delson (2002) described the medial epicondyle of *C. kimeui* and *C. meaveae* as oriented dorsally, while Jablonski et al. (2008) described the medial epicondyle of *C. williamsi* as projecting medially. The relative medial projection of *C. williamsi* relative to that of *C. meaveae* and *C. kimeui* can be seen in Figure 3.7. Although the medial epicondyles of *C. meaveae* and *C. kimeui* are large, they are not as dorsally projecting as those of *Theropithecus gelada* or *Papio cynocephalus* and are more similar to those of *Erythrocebus patas* (Figure 3.3). As can be seen in Figure 3.3, the medial epicondyle of *T. gelada* is so dorsally reflected that the epicondyle is directly underneath the trochlea when examining the humerus in distal view. In *E. patas*, the medial epicondyle is positioned more medially, reflecting a less dorsally oriented morphology. Given the subtle differences between *Cercopithecoides* and *T. gelada* or *P. cynocephalus* in morphology of the greater tubercle and the medial epicondyle (which have the highest loadings in DFAs) it seems reasonable that these species would not be classified as committed terrestrialists. The assignment to the semi-terrestrial category of *C. meaveae*, *C. williamsi*, and the proximal humerus of *C. kimeui* implies that these species may have been more similar *E. patas* in their behavior than to *T. gelada*. The assignment of the distal humerus of *C. kimeui* to the arboreal group even when using two groups *a priori* is unexpected. The DFA using the complete humerus does have a better classification rate than when using the distal humerus alone and these results could change if a complete humerus of *C. kimeui* is discovered.

The reconstructions for the four papionin species examined in this study are in general agreement with previous research. Frost and Delson (2002) describe *Parapapio jonesi* as engaging in more arboreal behavior than is typical for extant *Papio, Theropithecus*, and *Mandrillus*. Based on the distal humerus, *P. jonesi* is classified as semi-terrestrial when using three groups *a priori* and as arboreal when using two groups *a priori*. *Parapapio lothagamensis* is described by Leakey et al. (2003) as terrestrial but the locomotor reconstruction in this chapter suggests this species was also adept at arboreal behavior. The composite specimen of *P. lothagamensis* is reconstructed as semi-terrestrial when using three groups *a priori* and as arboreal when using two groups *a priori* with "semi-terrestrial" individuals as unknown. The composite is reconstructed with equal likelihood as arboreal or terrestrial when using two groups *a priori* with "semi-terrestrial" individuals included in the terrestrial group and Figure 3.8 shows *P. lothagamensis* in the middle of the color gradient among other "semi-terrestrial" species such as, *Cercopithecus neglectus* and *Lophocebus albigena*. The greater tubercle of *P. lothagamensis* does not project above the humeral head (Figure 3.16; Leakey et al., 2003) and although the medial epicondyle is dorsally oriented (Figure 3.16), the dorsal projection is not as extreme as in *Theropithecus gelada* or *Papio cynocephalus* (Figure 3.10).

T. oswaldi and *T. brumpti* have generally been accepted as highly terrestrial cercopithecoids (Gilbert et al. 2011; Guthrie 2011; Jablonski et al. 2008; Jablonski 2002; Ciochon 1993; Krentz 1993), although these species are considered to have preferred different habitats. The habitat of *T. oswaldi* is likely to have been open grasslands (Eck 1987) but *T. brumpti* has been found in habitats reconstructed as woodland (Eck and Jablonski 1987). Previous work has suggested that *T. brumpti* may have been less committed to the ground than extant geladas and may have engaged in limited arboreal behavior (Gilbert et al. 2010; Guthrie, 2011; Jablonski et al. 2008; Jablonski 2002; Ciochon, 1993; Krentz, 1993). Two complete humeri of *T. oswaldi* are classified as terrestrial, but other elements of the postcranium are assigned inconsistently to the arboreal and semi-terrestrial group. When using a composite, *T. oswaldi* is classified as semi-terrestrial with three groups *a priori* but there is also a high probability of this composite being assigned to the terrestrial group (0.43). When using only two-groups *a priori*, this composite is assigned to the terrestrial group. When examining single elements of *T. brumpti*, this species is assigned with equal likelihood to the arboreal and semi-terrestrial groups. A composite specimen of *T. brumpti* is assigned to the semi-terrestrial group when using two groups *a priori* and to the terrestrial group when using three groups *a priori*.

These results generally reconstruct *T. oswaldi* and *brumpti* as having engaged in more arboreal behavior than previously discussed, although both of these species are considered morphologically more similar to *Mandrillus sphinx, T. gelada*, and *P. cynocephalus* when assignment is limited to the arboreal and terrestrial groups. Figure 3.8 shows that *T. oswaldi* has a very low posterior probability of being assigned to the arboreal group (0.02) falling with the most terrestrial cercopithecoid, which supports previous work that *T. oswaldi* was highly terrestrial (Ciochon 1993; Krentz 1993). Figure 3.9 shows that *T. brumpti* has a higher posterior probability of being assigned to the arboreal group (0.2) and is closer to *Macaca nigra, Macaca sylvanus*, and *Erythrocebus patas* then the most committed terrestrial cercopithecoids. Figures 3.7 and 3.8 show variation in greater tubercle projection and the angle of the medial epicondyle in *T. brumpti* and *T. oswaldi*. Most specimens are more similar to *Cercopithecus mitis* in projection of the greater tubercle (Figure 3.4) and to *E. patas* and *C. torquatus* in orientation of the medial epicondyle (Figure 3.3) than to the most committed terrestrial primates. *T. brumpti* also is more similar to *Cercopithecoides* (Figure 3.15) in the degree of retroflexion of the medial epicondyle while *T. oswaldi* is most similar to extant terrestrial taxa.

Section 3.5: Conclusions

The multivariate analyses were moderately successful at predicting locomotor mode among cercopithecoids using a combination of features that are well-associated with behavior. The discriminant functions were highly successful at predicting membership in the arboreal group, indicating that arboreal individuals were not often mistaken for semi-terrestrial or terrestrial individuals. However, the correct classification of semi-terrestrial and terrestrial individuals varies widely depending on which element(s) were used, suggesting that semi-terrestrial and terrestrial individuals were often misclassified (see also, Elton 2002). Figures 3.1 and 3.2 show that semi-terrestrial individuals overlap substantially with both arboreal and terrestrial individuals. Arboreal and terrestrial individuals also overlap modestly, with the most overlap occurring in the proximal humerus and astragalus.

The DFAs on single elements produced the best classification for terrestrial individuals when using the entire humerus (64.4%) and for semi-terrestrial indviduals when using the distal humerus (58.2%). Shape variables from the proximal humerus alone had poor classification rates for semi-terrestrial (32.9%) and terrestrial taxa (15.6%), suggesting that, despite a high loading for height of the greater tubercle, an isolated proximal humerus may not be as reliable for locomotor reconstruction. It is surprising that the proximal humerus perfomed poorly in classification analyses given the significant relationship between height of the greater tubercle and the humeral head index and locomotor behavior found in Chapter 2. It is possible that these features are more variable among "semi-terrestrial" and terrestrial species than angle of the medial epicondyle making them less useful in a predictive model. A univariate approach considering these features in isolation may yield better results. The astragalus and calcaneus also had poor classification rates (below 45% with two groups *a priori*) suggesting that even the best associations between morphology and behavior in these elements may not be adequate for determining the relative amount of terrestrial behavior in which an individual engages.

Given the limitations of this multivariate approach, fossil reconstructions presented here should not be considered final. More confidence can be assumed in reconstructions that include a complete humerus, a distal humerus, a calcaneus, or a combination of multiple elements. Although assignment to the arboreal group may also be accepted with some confidence given the success of cross-validation of demonstrably arboreal individuals, taxa that have often been thought of as "terrestrial" may not be assigned as such given the lower cross-validation rate of this locomotor category. Given the high classification rates of arboreal species, it appears that there may be less variation in the arboreal morphotype than in the "semi-terrestrial" or terrestrial morphotypes. The "semi-terrestrial" species included in these analyses vary widely in the amount of time spent in terrestrial behavior whereas arboreal species are predominately engaged in arboreal behavior. Additionally, results from Chapter 2 show that "semi-terrestrial" species cannot be united by a suite of common features. Therefore, it is possible that arboreal species share many morphological features that lead to high classification rates, while "semi-terrestrial" species are misclassified frequently due to their variation in morphology.

This study also demonstrates that posterior probabilities should be inspected in order to determine whether the discriminant function has assigned group membership definitively or if an individual is likely to be assigned to multiple groups. Finally, this study did not include other elements of the postcranium that may show associations between morphology and behavior, such as the ulna and scapula. As this chapter has shown, including more elements improves classification rates in the DFAs and considering other elements in the future may change fossil reconstructions presented here.

Given the reconstructions of *Victoriapithecus* presented in this study, I would argue that while cercopithecoid evolution included multiple transitions to terrestrial behavior in varying degrees, the earliest cercopithecoids were most likely capable of efficient arboreal locomotion with a few adaptations to facilitate terrestrial behavior. Therefore, colobines did not *secondarily* evolve arboreality but rather inherited a morphology from the last common ancestor of cercopithecoids that maintained an ability to utilize arboreal substrates while also evolving traits that enabled terrestrial locomotion. Early cercopithecoids may have emphasized a greater or lesser commitment to arboreal behavior and consequently evolved subtle differences in morphology to accommodate different habitats. Clearly, *Microcolobus* is well adapted for arboreal behavior and, as illustrated in Figure 3.9, *Microcolobus* has a high posterior probability of being assigned to the arboreal. However, adaptations to arboreal behavior in *Microcolobus* would not have required a major reorganization of the *Bauplan*, given many of the arboreal adaptations in *Victoriapithecus*, which supports previous research that has suggested that colobines are ancestrally arboreal (Hlusko 2006; Hlusko 2007; Gilbert et al. 2010; Nakatsukasa et al. 2010). One morphological feature that appears to have changed in *Microcolobus* relative to stem cercopithecoids is the angle of the medial epicondyle. The medial epicondyle is relatively dorsally oriented in *Victoriapithecus* (see Figure 3.5) and the last common ancestor of cercopithecoids likely inherited this feature. In *Microcolobus*, the medial epicodyle is the more medially oriented (see Figure 3.6) and this may reflect an increased commitment to arboreal behavior in stem colobines.

Although convergent evolution has often been suggested for arboreal behavior in cercopithecoids (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003), it seems more likely that terrestrial behavior has arisen independently multiple times in cercopithecoid evolution. There are three main lines of evidence to support this idea. First, as stated above, *Victoriapithecus* probably engaged in much more arboreal behavior than previously suggested (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a) and features associated with arboreality, such as low greater tubercle, was retained in the last common ancestor of crown cercopithecoids. Given the difference in direction of the medial epicondyle in *Victoriapithecus* and *Microcolobus*, it is possible that a more dorsally oriented medial epicondyle was retained in the cercopithecine radiation while a more medially oriented medially epicondyle was revolved in stem colobines as they increased commitment to an arboreal lifestyle. Second, many of the crown cercopithecoid fossil specimens studied suggest that arboreality was an important component of their behavior even if some species exhibit some adaptations to terrestriality. Finally, the extant data overwhelmingly show that adaptations to terrestriality are varied within and between clades, which make inheriting a “terrestrial morphology” from a common ancestor unlikely. The extant data demonstrate that many species engage in both arboreal and terrestrial behavior without much alteration to the general cercopithecoid body plan. The major modifications to this body plan occur in species that are highly committed to terrestrial behavior, such as *Theropithecus gelada* and *Papio cynocephalus*. However, these behavioral and morphological specializations seem to be unique to the papionins as many of the large-bodied colobines exhibit morphologies more associated with the frequent use of *both* arboreal and terrestrial behavior. Therefore, cercopithecoid locomotor evolution involved several transitions to terrestrial behavior, with adaptations to terrestriality varying across clades and habitats. The pattern and timing of locomotor transitions in the cercopithecoid clade is the subject of Chapter 4.

Table 3.1a. Fossil composites created

Species	**Composite or Associated**	**Locality**	**Elements Included**
Victoriapithecus macinnesi	Composite	Maboko Island, Kenya	humerus, astragalus, calcaneus
Microcolobus sp.	Associated	Nakali, Kenya	distal humerus, astragalus
Paracolobus chemeroni	Associated	Tugen Hills, Kenya	humerus, distal femur astragalus, calcaneus
Mesopithecus pentelicus	Composite	Pikermi, Greece	humerus, distal femur, astragalus, calcaneus
Mesopithecus sp.	Composite	Hadjidimovo, Bulgaria	humerus, astragalus, calcaneus
Dolichopithecus ruscinensis	Composite	Perpignan, France	distal humerus, astragalus
Parapapio lothagamensis	Composite	Lothagam, Kenya	humerus, astragalus, calcaneus
Theropithecus oswaldi	Composite	East Turkana, Kenya	humerus, astragalus, calcaneus
Theropithecus brumpti	Composite	West Turkana, Kenya	distal humerus, astragalus

Table 3.1b. Specimens used in composites

Species	**Specimen #**
Victoriapithecus macinnesi	Humerus: KNM-MB 21809, 12044, 21207, 21818, 21822, 19, 3, 34712; Astragalus: KNM-MB 34818, 34810, 34364, 34812, 34816, 34809, 12013; Calcaneus: KNM-MB 35573, 34820, 12006, 21208, 21209, 21211, 35571, 46664, 34821, 14375
Microcolobus sp.	Humerus: KNM-NA 47916A, Astragalus: KNM-NA 47915K
Paracolobus chemeroni	KNM BC3 B (Humerus), AR (Femur), AQ (Astragalus), R (Calcaneus)
Mesopithecus pentelicus	Humerus: Pik 355, 244, 1727, 298, 356 Femur: Pik 024, 1731, 287, 1735, 1733 Astragalus: Pik 237, 368, 256, 238 Calcaneus: Pik 240, 266, 1746, 239
Mesopithecus sp.	Humerus: HD 1610, 916, 1004, 417, 1612, 1611, 1625 Astragalus: HD 1025 Calcaneus: HD 1569, 408, 1023
Dolichopithecus ruscinensis	Humerus: Per 010, 011, 012 Astragalus: Pp20a, Pp20b
Parapapio lothagamensis	Humerus: KNM-LT 28769, 23074 Astragalus: KNM-LT 23081 Calcaneus: KNM-LT 28575, 24125
Theropithecus oswaldi	Humerus: KNM-ER 18917, 5491, 567, 13, 601, 13 3876 Astragalus: KNM-ER 3876 Calcaneus: KNM-ER 30878
Theropithecus brumpti	Humerus: KNM-WT 38738 Astragalus: KNM-WT 17544

Table 3.2a. Discriminant function analysis on the humerus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.969	0.031
Coefficients		
Width of lesser tubercle	-1.12	-2.47
Height of greater tubercle	-7.92	-26.56
Humeral head index	-14.64	19.98
Angle of medial epicondyle	-24.45	-16.82
Classification	**Correct**	**Misclassified**
Total	0.754	0.246
Arboreal	0.843	0.157
Semi-terrestrial	0.662	0.338
Terrestrial	0.556	0.444

Table 3.2b. Discriminant function analysis on the proximal humerus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.904	0.096
Coefficients		
Width of lesser tubercle	-15.69	-1.2
Height of greater tubercle	-42.71	31.4
Humeral head index	-22.64	-29.84

Classification	**Correct**	**Misclassified**
Total	0.613	0.387
Arboreal	0.851	0.149
Semi-terrestrial	0.345	0.655
Terrestrial	0.156	0.844

Table 3.2c. Discriminant function analysis on the distal humerus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.985	0.015
Coefficients		
Height of olecranon fossa	-2.25	1.23
Height of capitulum	7.99	37.73
Angle of medial epicondyle	18.38	-11.21

Classification	**Correct**	**Misclassified**
Total	0.706	0.294
Arboreal	0.831	0.169
Semi-terrestrial	0.566	0.434
Terrestrial	0.467	0.533

Table 3.2d. Discriminant function analysis on the femur using three groups a priori

	DF1	**DF 2**
Proportion of Variation	0.9925	0.0075
Coefficients		
Length of the femur	-26.909	-22.984
Height of the patellar groove	-17.713	24.834
Classification	**Correct**	**Misclassified**
Total	0.620	0.380
Arboreal	0.897	0.103
Semi-terrestrial	0.224	0.776
Terrestrial	0.375	0.625

Table 3.2e. Discriminant function analysis on the astragalus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.829	0.171
Coefficients		
Overall length of the astragalus	53.78	4.96
Ectal facet length	19.39	36.84
Width of astragalar head	-14.15	25.21
Angle of astragalar head	6.49	-5.86
Classification	**Correct**	**Misclassified**
Total	0.647	0.353
Arboreal	0.857	0.143
Semi-terrestrial	0.35	0.65
Terrestrial	0.413	0.587

Table 3.2f. Discriminant function analysis on the calcaneus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.915	0.085
Coefficients		
Length of distal segment of the calcaneus	20.53	-38.3
Length of tuber	-6.6	-16.75
Width of sustentaculum	5.18	1.17
Height of cuboid facet	-17.76	-9.58
Classification	**Correct**	**Misclassified**
Total	0.675	0.325
Arboreal	0.853	0.147
Semi-terrestrial	0.38	0.621
Terrestrial	0.6	0.4

Table 3.2g. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using three groups a priori

	DF 1	**DF 2**
Proportion of Variation	0.9167	0.0833
Coefficients		
Width of lesser tubercle	0.89	3.95
Height of greater tubercle	13.38	16.24
Humeral head index	10.52	-12.52
Angle of medial epicondyle	13.64	-5.69
Overall length of the astragalus	-12.13	13.38
Ectal facet length	-0.72	16.39
Width of astragalar head	5.67	4.80
Angle of astragalar head	-1.74	-6.15
Length of the distal segment of the calcaneus	-7.21	-24.00
Length of tuber	1.79	-7.40
Width of sustentaculum	-4.94	1.61
Height of cuboid facet	3.81	-5.07
Height of patellar groove	-3.28	-0.93
Classification	**Correct**	**Misclassified**
Total	0.810	0.190
Aboreal	0.912	0.088
Semi-terrestrial	0.624	0.376
Terrestrial	0.784	0.216

Table 3.2h. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using three groups a priori

	DF1	**DF 2**
Proportion of Variation	0.917	0.083
Coefficients		
Width of lesser tubercle	1.01	4.35
Height of greater tubercle	13.25	16.85
Humeral head index	10.89	-12.73
Angle of medial epicondyle	13.74	-5.67
Overall length of the astragalus	-12.91	-11.87
Ectal facet length	-1.39	16.75
Width of astragalar head	6.3	5.23
Angle of astragalar head	-1.6	-5.43
Length of the distal segment of the calcaneus	-7.18	-23.57
Length of tuber	2.2	-7.29
Width of sustentaculum	-4.91	1.76
Height of cuboid facet	4.37	-4.51
Classification	**Correct**	**Misclassified**
Total	0.826	0.174
Arboreal	0.912	0.088
Semi-terrestrial	0.676	0.324
Terrestrial	0.784	0.216

Table 3.2i. Discriminant function analysis based on a combination of the distal humerus and astragalus using three groups a priori

	DF1	**DF 2**
Proportion of Variation	0.931	0.069
Coefficients		
Height of the olecranon fossa	-0.82	0.06
Height of the capitulum	9.0	17.32
Angle of medial epicondyle	16.36	-8.28
Overall length of the astragalus	-25.24	-11.7
Ectal facet length	-5.55	21.69
Width of astragalar head	8.66	19.48
Angle of astragalar head	-2.68	-8.34

	Correct	**Misclassified**
Total	0.754	0.246
Arboreal	0.872	0.128
Semi-terrestrial	0.556	0.444
Terrestrial	0.692	0.308

Table 3.3a. Discriminant function analysis on the humerus using two groups a priori (“semi-terrestrialist” as unknown)

	DF 1	
Proportion of Variation	100	
Coefficients		
Width of lesser tubercle	3.84	
Height of greater tubercle	26.9	
Humeral head index	13.77	
Angle of medial epicondyle	11.75	
Classification	**Correct**	**Misclassified**
Total	0.963	0.037
Arboreal	0.992	0.008
Terrestrial	0.800	0.200

Table 3.3b Discriminant function analysis on the proximal humerus using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1	
Proportion of Variation	100	
Coefficients		
Width of lesser tubercle	17.05	
Height of greater tubercle	48.86	
Humeral head index	21.14	
Classification	**Correct**	**Misclassified**
Total	0.878	0.122
Arboreal	0.964	0.036
Terrestrial	0.4	0.6

Table 3.3c. Discriminant function analysis on the distal humerus using two groups a priori (“semi-terrestrialist” as unknown)

	DF1	
Proportion of Variation	100	
Coefficients		
Height of olecranon fossa	-2.71	
Height of capitulum	14.19	
Angle of medial epicondyle	15.42	
Classification	**Correct**	**Misclassified**
Total	0.942	0.058
Arboreal	0.984	0.016
Terrestrial	0.711	0.289

Table 3.3d. Discriminant function analysis on the femur using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1
Proportion of Variation	1
Coefficient	
Length of femur	-27.125
Height of the patellar groove	-19.272

Classification	**Correct**	**Misclassified**
Total	0.913	0.087
Arboreal	0.980	0.020
Terrestrial	0.563	0.438

Table 3.3e. Discriminant function analysis on the astragalus using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1	
Proportion of Variation	100	
Coefficients		
Overall length of the astragalus	-60.68	
Ectal facet length	-12.73	
Width of astragalar head	13.95	
Angle of astragalar head	-7.48	
Classification	**Correct**	**Misclassified**
Total	0.8807	0.113
Arboreal	0.971	0.029
Terrestrial	0.435	0.565

Table 3.3f. Discriminant function analysis on the calcaneus using two groups a priori (“semi-terrestrialist” as unknown)

	DF 1	
Proportion of Variation	100	
Coefficients		
Length of the distal segment of the calcaneus	-31.17	
Length of tuber	1.99	
Width of sustentaculum	-5.52	
Height of cuboid facet	15.99	
Classification	**Correct**	**Misclassified**
Total	0.924	0.076
Arboreal	0.961	0.039
Terrestrial	0.733	0.267

Table 3.3g. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1	
Proportion of Variation	1	
Coefficients		
Width of lesser tubercle	1.89	
Height of greater tubercle	20.78	
Humeral head index	12.13	
Angle of medial epicondyle	10.36	
Overall length of the astagalus	-16.49	
Ectal facet length	0.75	
Width of astragalar head	6.25	
Angle of astragalar head	-2.79	
Length of the distal segment of the calcaneus	-14.38	
Length of tuber	-1.25	
Width of sustentaculum	-5.87	
Height of cuboid facet	1.35	
Height of patellar groove	-7.63	
Classification	**Correct**	**Misclassified**
Total	0.978	0.022
Arboreal	0.995	0.005
Terrestrial	0.892	0.108

Table 3.3h. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1	
Proportion of Variation	100	
Coefficients		
Width of lesser tubercle	2.45	
Height of greater tubercle	19.54	
Humeral head index	12.74	
Angle of medial epicondyle	10.69	
Overall length of the astragalus	-17.92	
Ectal facet length	0.15	
Width of astragalar head	6.99	
Angle of astragalar head	-2.39	
Length of distal segment of the calcaneu	-14.39	
Length of tuber	-0.31	
Width of sustentaculum	-5.46	
Height of cuboid facet	2.11	
Classification	**Correct**	**Misclassified**
Total	0.965	0.035
Arboreal	0.990	0.010
Terrestrial	0.838	0.162

Table 3.3i. Discriminant function analysis based on a combination of the distal humerus and astragalus using two groups a priori ("semi-terrestrialist" as unknown)

	DF 1
Proportion of Variation	100
Coefficients	
Height of olecranon fossa	-1.05
Height of the capitulum	14.25
Angle of medial epicondyle	13.55
Overall length of the astragalus	-35.0
Ectal facet length	-2.83
Width of astragalar head	12.84
Angle of astragalar head	-3.42

Classification	**Correct**	**Misclassified**
Total	0.959	0.041
Arboreal	0.990	0.010
Terrestrial	0.795	0.205

Table 3.4a. Classification for semi-terrestrial cercopithecoids based on the humerus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.994	0.006
Cercocebus torquatus	arboreal	0.897	0.103
Cercopithecus hamlyni	arboreal	0.985	0.015
Cercopithecus lhoesti	arboreal	0.963	0.037
Cercopithecus neglectus	arboreal	0.926	0.074
Chlorocebus aethiops	arboreal	0.792	0.208
Chlorocebus pygerythrus	arboreal	0.804	0.196
Erythrocebus patas	terrestrial	0.176	0.824
Macaca arctoides	arboreal	0.954	0.046
Macaca mulatta	arboreal	0.956	0.044
Macaca nemestrina	arboreal	0.939	0.061
Macaca nigra	arboreal	0.847	0.153
Macaca sylvanus	arboreal	0.771	0.229
Macaca thibetana	arboreal	0.734	0.266
Macaca tonkeana	terrestrial	0.474	0.526
Papio anubis	terrestrial	0.027	0.973
Semnopithecus entellus	arboreal	0.915	0.085

Table 3.4b. Classification for semi-terrestrial cercopithecoids based on the proximal humerus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.935	0.065
Cercocebus torquatus	arboreal	0.915	0.085
Cercopithecus hamlyni	arboreal	0.929	0.071
Cercopithecus lhoesti	arboreal	0.916	0.084
Cercopithecus neglectus	arboreal	0.902	0.098
Chlorocebus aethiops	arboreal	0.840	0.160
Chlorocebus pygerythrus	arboreal	0.752	0.248
Erythrocebus patas	terrestrial	0.303	0.697
Macaca arctoides	arboreal	0.958	0.042
Macaca mulatta	arboreal	0.939	0.061
Macaca nemestrina	arboreal	0.967	0.033
Macaca nigra	arboreal	0.825	0.175
Macaca sylvanus	arboreal	0.871	0.129
Macaca thibetana	arboreal	0.689	0.311
Macaca tonkeana	arboreal	0.736	0.264
Papio anubis	terrestrial	0.278	0.722
Semnopithecus entellus	arboreal	0.910	0.090

Table 3.4c. Classification for semi-terrestrial cercopithecoids based on the distal humerus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.997	0.003
Cercocebus torquatus	arboreal	0.853	0.147
Cercopithecus hamlyni	arboreal	0.994	0.006
Cercopithecus lhoesti	arboreal	0.819	0.181
Cercopithecus neglectus	arboreal	0.950	0.050
Chlorocebus aethiops	arboreal	0.880	0.120
Chlorocebus pygerythrus	arboreal	0.866	0.134
Erythrocebus patas	terrestrial	0.319	0.681
Macaca arctoides	arboreal	0.966	0.034
Macaca mulatta	arboreal	0.954	0.046
Macaca nemestrina	arboreal	0.853	0.147
Macaca nigra	arboreal	0.878	0.122
Macaca sylvanus	arboreal	0.763	0.237
Macaca thibetana	arboreal	0.856	0.144
Macaca tonkeana	arboreal	0.813	0.187
Papio anubis	terrestrial	0.084	0.916
Semnopithecus entellus	arboreal	0.845	0.155

Table 3.4d. Classification for semi-terrestrial cercopithecoids based on the femur

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.876	0.124
Cercocebus torquatus	arboreal	0.966	0.034
Cercopithecus hamlyni	arboreal	0.980	0.020
Cercopithecus lhoesti	arboreal	0.974	0.026
Cercopithecus neglectus	arboreal	0.974	0.026
Chlorocebus aethiops	arboreal	0.984	0.016
Chlorocebus pygerythrus	arboreal	0.981	0.019
Erythrocebus patas	arboreal	0.885	0.115
Macaca arctoides	arboreal	0.556	0.444
Macaca mulatta	arboreal	0.773	0.227
Macaca nemestrina	arboreal	0.922	0.078
Macaca nigra	terrestrial	0.422	0.578
Macaca sylvanus	arboreal	0.632	0.368
Macaca tonkeana	terrestrial	0.331	0.669
Papio anubis	terrestrial	0.274	0.726
Semnopithecus entellus	arboreal	0.982	0.018

Table 3.4e. Classification for semi-terrestrial cercopithecoids based on the astragalus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.964	0.036
Cercocebus torquatus	arboreal	0.902	0.098
Cercopithecus hamlyni	arboreal	0.892	0.108
Cercopithecus lhoesti	arboreal	0.975	0.025
Cercopithecus neglectus	arboreal	0.955	0.045
Chlorocebus aethiops	arboreal	0.994	0.006
Chlorocebus pygerythrus	arboreal	0.983	0.017
Erythrocebus patas	arboreal	0.973	0.027
Macaca arctoides	arboreal	0.950	0.050
Macaca mulatta	arboreal	0.895	0.105
Macaca nemestrina	arboreal	0.951	0.049
Macaca nigra	arboreal	0.647	0.353
Macaca sylvanus	arboreal	0.762	0.238
Macaca tonkeana	terrestrial	0.403	0.597
Papio anubis	terrestrial	0.326	0.674
Semnopithecus entellus	arboreal	0.871	0.129

Table 3.4f. Classification for semi-terrestrial cercopithecoids based on the calcaneus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.994	0.006
Cercocebus torquatus	arboreal	0.911	0.089
Cercopithecus hamlyni	arboreal	0.975	0.025
Cercopithecus lhoesti	arboreal	0.998	0.002
Cercopithecus neglectus	arboreal	0.994	0.006
Chlorocebus aethiops	arboreal	0.987	0.013
Chlorocebus pygerythrus	arboreal	0.995	0.005
Erythrocebus patas	arboreal	0.970	0.030
Macaca arctoides	arboreal	0.956	0.044
Macaca mulatta	arboreal	0.578	0.422
Macaca nemestrina	arboreal	0.930	0.070
Macaca nigra	arboreal	0.761	0.239
Macaca sylvanus	terrestrial	0.176	0.824
Macaca tonkeana	terrestrial	0.437	0.563
Papio anubis	terrestrial	0.342	0.658
Semnopithecus entellus	arboreal	0.898	0.102

Table 3.4g. Classification for semi-terrestrial cercopithecoids based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	0.999	3.049E-04
Cercocebus torquatus	arboreal	0.993	0.007
Cercopithecus hamlyni	arboreal	0.998	0.002
Cercopithecus lhoesti	arboreal	0.999	1.174E-04
Cercopithecus neglectus	arboreal	0.993	0.007
Chlorocebus aethiops	arboreal	0.998	0.002
Chlorocebus pygerythrus	arboreal	0.999	0.001
Erythrocebus patas	terrestrial	0.477	0.523
Macaca arctoides	arboreal	0.996	0.004
Macaca mulatta	arboreal	0.974	0.026
Macaca nemestrina	arboreal	0.984	0.016
Macaca nigra	terrestrial	0.047	0.953
Macaca sylvanus	terrestrial	0.133	0.867
Macaca tonkeana	terrestrial	0.061	0.939
Papio anubis	terrestrial	1.176E-04	0.999
Semnopithecus entellus	arboreal	0.991	0.009

Table 3.4h. Classification for semi-terrestrial cercopithecoids based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	1.000	0.000
Cercocebus torquatus	arboreal	0.987	0.013
Cercopithecus hamlyni	arboreal	0.997	0.003
Cercopithecus lhoesti	arboreal	1.000	0.000
Cercopithecus neglectus	arboreal	0.978	0.022
Chlorocebus aethiops	arboreal	0.996	0.004
Chlorocebus pygerythrus	arboreal	0.997	0.003
Erythrocebus patas	arboreal	0.545	0.455
Macaca arctoides	arboreal	0.994	0.006
Macaca mulatta	arboreal	0.967	0.033
Macaca nemestrina	arboreal	0.984	0.016
Macaca nigra	terrestrial	0.150	0.850
Macaca sylvanus	terrestrial	0.140	0.860
Macaca tonkeana	terrestrial	0.163	0.837
Papio anubis	terrestrial	0.001	0.999
Semnopithecus entellus	arboreal	0.980	0.020

Table 3.4i. Classification for semi-terrestrial cercopithecoids based on a combination of the distal humerus and astragalus

Species	**Classification**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	arboreal	1.000	0.000
Cercocebus torquatus	arboreal	0.906	0.094
Cercopithecus hamlyni	arboreal	0.997	0.003
Cercopithecus lhoesti	arboreal	0.986	0.014
Cercopithecus neglectus	arboreal	0.986	0.014
Chlorocebus aethiops	arboreal	0.995	0.005
Chlorocebus pygerythrus	arboreal	0.990	0.010
Erythrocebus patas	arboreal	0.759	0.241
Macaca arctoides	arboreal	0.993	0.007
Macaca mulatta	arboreal	0.987	0.013
Macaca nemestrina	arboreal	0.935	0.065
Macaca nigra	terrestrial	0.313	0.687
Macaca sylvanus	arboreal	0.661	0.339
Macaca tonkeana	terrestrial	0.492	0.508
Papio anubis	terrestrial	0.006	0.994
Semnopithecus entellus	arboreal	0.853	0.147

Table 3.5a. Discriminant function analysis on the humerus using two groups a priori (“semi-terrestrialist” included in terrestrial group)

	DF 1	
Proportion of Variation	1	
Coefficients		
Width of greater tubercle	-5.16	
Width of lesser tubercle	-0.19	
Height of capitulum	-2.52	
Height of greater tubercle	11.01	
Humeral head index	14.25	
Angle of medial epicondyle	18.64	
Classification	**Correct**	**Misclassified**
Total	0.784	0.216
Arboreal	0.804	0.196
Terrestrial	0.759	0.241

Table 3.5b Discriminant function analysis on the proximal humerus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation	100	
Coefficients		
Width of greater tubercle	-12.5	
Width of lesser tubercle	12.74	
Height of greater tubercle	43.85	
Humeral head index	24.42	
Classification	**Correct**	**Misclassified**
Total	0.681	0.319
Arboreal	0.758	0.242
Terrestrial	0.588	0.412

Table 3.5c. Discriminant function analysis on the distal humerus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF1	
Proportion of Variation	100	
Coefficients		
Height of capitulum	4.79	
Angle of medial epicondyle	17.4	
Classification	**Correct**	**Misclassified**
Total	0.763	0.237
Arboreal	0.792	0.208
Terrestrial	0.729	0.271

Table 3.5d. Discriminant function analysis on the femur using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation	1	
Coefficeints		
Length of the femur	-26.66	
Height of the patellar groove	-16.14	
Classification	**Correct**	**Misclassified**
Total	0.700	0.300
Arboreal	0.814	0.186
Terrestrial	0.566	0.434

Table 3.5e. Discriminant function analysis on the astragalus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation	1	
Coefficients		
Overall length of the astragalus	-46.92	
Ectal facet length	-31.03	
Width of astragalar head	10.53	
Trochlear wedge index	12.24	
Classification	**Correct**	**Misclassified**
Total	0.708	0.292
Arboreal	0.775	0.225
Terrestrial	0.629	0.371

Table 3.5f. Discriminant function analysis on the calcaneus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation	1	
Coefficients		
Total length of the calcaneus	-2.45	
Length of the distal segment of the calcaneus	-23.90	
Height of cuboid facet	22.06	
Classification	**Correct**	**Misclassified**
Total	0.682	0.318
Arboreal	0.757	0.243
Terrestrial	0.592	0.408

Table 3.5g. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation	1	
Coefficients		
Width of the greater tubercle	4.04	
Width of lesser tubercle	-1.32	
Height of capitilum	0.12	
Height of greater tubercle	11.58	
Humeral head index	11.41	
Angle of medial epicondyle	10.90	
Overall length of the astragalus	-15.61	
Ectal facet length	-10.46	
Width of astragalar head	5.64	
Trochlear wedge index	3.55	
Overall length of calcaneus	-3.72	
Length of distal segment of the calcaneus	-1.25	
Height of cuboid facet	8.33	
Height of patellar groove	-2.88	
Classification	**Correct**	**Misclassified**
Total	0.819	0.181
Arboreal	0.891	0.109
Terrestrial	0.728	0.272

Table 3.5h. Discriminant function analysis based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using two groups a priori (“semi-terrestrialist” included in terrestrial group)

	DF1	
Proportion of Variation	100	
Coefficients		
Width of greater tubercle	3.72	
Width of lesser tubercle	-1.18	
Heigh of capitulum	0.69	
Height of greater tubercle	11.31	
Humeral head index	11.92	
Angle of medial epicondyle	10.98	
Overall length of the astragalus	-15.63	
Ectal facet length	-11.32	
Width of astragalar head	5.97	
Trochlear wedge index	3.65	
Overall length of calcaneus	-3.79	
Length of the distal segment of the calcaneus	-1.95	
Height of cuboid facet	8.60	
Classification	**Correct**	**Misclassified**
Total	0.826	0.174
Arboreal	0.908	0.092
Terrestrial	0.723	0.277

Table 3.5i. Discriminant function analysis based on a combination of the distal humerus and astragalus using two groups a priori ("semi-terrestrialist" included in terrestrial group)

	DF 1	
Proportion of Variation		
Coefficients		
Height of capitulum	4.35	
Angle of medial epicondyle	14.03	
Overall length of the astragalus	-22.46	
Ectal facet length	-13.66	
Width of astragalar head	7.63	
Tochlear wedge index	8.08	
Classification	**Correct**	**Misclassified**
Total	0.817	0.183
Arboreal	0.876	0.124
Terrestrial	0.744	0.256

Table 3.6a. Posterior probabilities from the analysis on the humerus of extant species for being classified to the arboreal or terrestrial group using two groups a priori (“semi-terrestrialists” included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.670	0.330	*Macaca nigra*	0.354	0.646
Cercocebus torquatus	0.422	0.578	*Macaca sinica*	0.224	0.776
Cercopithecus ascanius	0.686	0.314	*Macaca sylvanus*	0.303	0.697
Cercopithecus cephus	0.620	0.380	*Macaca thibetana*	0.381	0.619
Cercopithecus diana	0.458	0.542	*Macaca tonkeana*	0.124	0.876
Cercopithecus hamlyni	0.632	0.368	*Mandrillus sphinx*	0.074	0.926
Cercopithecus lhoesti	0.455	0.545	*Miopithecus talapoin*	0.623	0.377
Cercopithecus mitis	0.548	0.452	*Nasalis larvatus*	0.931	0.069
Cercopithecus mona	0.645	0.355	*Papio anubis*	0.071	0.929
Cercopithecus neglectus	0.457	0.543	*Papio cynocephalus*	0.039	0.961
Cercopithecus nictitans	0.675	0.325	*Piliocolobus badius*	0.876	0.124
Cercopithecus pogonias	0.726	0.274	*Piliocolobus foai*	0.898	0.102
Chlorocebus aethiops	0.353	0.647	*Piliocolobus kirkii*	0.663	0.337
Chlorocebus pygerythrus	0.355	0.645	*Presbytis comata*	0.959	0.041
Colobus guereza	0.909	0.091	*Presbytis melalophos*	0.794	0.206
Erythrocebus patas	0.168	0.832	*Pygathrix nemaeus*	0.886	0.114
Lophocebus albigena	0.432	0.568	*Rhinopithecus roxellana*	0.832	0.168
Macaca arctoides	0.443	0.557	*Semnopithecus entellus*	0.400	0.600
Macaca assamensis	0.657	0.343	*Theropithecus gelada*	0.073	0.927
Macaca fascicularis	0.595	0.405	*Trachypithecus cristata*	0.823	0.177
Macaca mulatta	0.495	0.505	*Trachypithecus obscurus*	0.797	0.203
Macaca nemestrina	0.372	0.628	*Trachypithecus phrayei*	0.951	0.049

Table 3.6b. Posterior probabilities from the analysis on the proximal humerus of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.649	0.351
Cercocebus torquatus	0.582	0.418
Cercopithecus ascanius	0.626	0.374
Cercopithecus cephus	0.671	0.329
Cercopithecus diana	0.559	0.441
Cercopithecus hamlyni	0.601	0.399
Cercopithecus lhoesti	0.617	0.383
Cercopithecus mitis	0.518	0.482
Cercopithecus mona	0.684	0.316
Cercopithecus neglectus	0.537	0.463
Cercopithecus nictitans	0.713	0.287
Cercopithecus pogonias	0.688	0.312
Chlorocebus aethiops	0.483	0.517
Chlorocebus pygerythrus	0.401	0.599
Colobus guereza	0.712	0.288
Erythrocebus patas	0.254	0.746
Lophocebus albigena	0.530	0.470
Macaca arctoides	0.662	0.338
Macaca assamensis	0.551	0.449
Macaca fascicularis	0.684	0.316
Macaca mulatta	0.615	0.385
Macaca nemestrina	0.639	0.361
Macaca nigra	0.420	0.580
Macaca sinica	0.543	0.457
Macaca sylvanus	0.483	0.517
Macaca thibetana	0.379	0.621
Macaca tonkeana	0.355	0.645
Mandrillus sphinx	0.337	0.663
Miopithecus talapoin	0.774	0.226
Nasalis larvatus	0.519	0.481
Papio anubis	0.181	0.819
Papio cynocephalus	0.266	0.734
Piliocolobus badius	0.537	0.463
Piliocolobus foai	0.480	0.520
Piliocolobus kirkii	0.564	0.436
Presbytis comata	0.713	0.287
Presbytis melalophos	0.546	0.454
Pygathrix nemaeus	0.559	0.441
Rhinopithecus roxellana	0.492	0.508
Semnopithecus entellus	0.555	0.445
Theropithecus gelada	0.315	0.685
Trachypithecus cristata	0.651	0.349
Trachypithecus obscurus	0.640	0.360
Trachypithecus phrayei	0.709	0.291

Table 3.6c. Posterior probabilities from the analysis on the distal humerus of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.640	0.360	*Macaca nigra*	0.418	0.582
Cercocebus torquatus	0.357	0.643	*Macaca sinica*	0.360	0.640
Cercopithecus ascanius	0.651	0.349	*Macaca sylvanus*	0.319	0.681
Cercopithecus cephus	0.577	0.423	*Macaca thibetana*	0.437	0.563
Cercopithecus diana	0.451	0.549	*Macaca tonkeana*	0.226	0.774
Cercopithecus hamlyni	0.656	0.344	*Mandrillus sphinx*	0.154	0.846
Cercopithecus lhoesti	0.356	0.644	*Miopithecus talapoin*	0.650	0.350
Cercopithecus mitis	0.584	0.416	*Nasalis larvatus*	0.894	0.106
Cercopithecus mona	0.606	0.394	*Papio anubis*	0.115	0.885
Cercopithecus neglectus	0.500	0.500	*Papio cynocephalus*	0.053	0.947
Cercopithecus nictitans	0.594	0.406	*Piliocolobus badius*	0.826	0.174
Cercopithecus pogonias	0.681	0.319	*Piliocolobus foai*	0.920	0.080
Chlorocebus aethiops	0.404	0.596	*Piliocolobus kirkii*	0.683	0.317
Chlorocebus pygerythrus	0.406	0.594	*Presbytis comata*	0.938	0.062
Colobus guereza	0.874	0.126	*Presbytis melalophos*	0.798	0.202
Erythrocebus patas	0.215	0.785	*Pygathrix nemaeus*	0.873	0.127
Lophocebus albigena	0.432	0.568	*Rhinopithecus roxellana*	0.852	0.148
Macaca arctoides	0.458	0.542	*Semnopithecus entellus*	0.358	0.642
Macaca assamensis	0.707	0.293	*Theropithecus gelada*	0.058	0.942
Macaca fascicularis	0.538	0.462	*Trachypithecus cristata*	0.794	0.206
Macaca mulatta	0.519	0.481	*Trachypithecus obscurus*	0.743	0.257
Macaca nemestrina	0.333	0.667	*Trachypithecus phrayei*	0.929	0.071

Table 3.6d. Posterior probabilities from the analysis on the femur of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.482	0.518	*Macaca nigra*	0.245	0.755
Cercocebus torquatus	0.633	0.367	*Macaca sinica*	0.500	0.500
Cercopithecus ascanius	0.654	0.346	*Macaca sylvanus*	0.317	0.683
Cercopithecus cephus	0.661	0.339	*Macaca thibetana*	0.127	0.873
Cercopithecus diana	0.624	0.376	*Macaca tonkeana*	0.218	0.782
Cercopithecus hamlyni	0.686	0.314	*Mandrillus sphinx*	0.510	0.490
Cercopithecus lhoesti	0.652	0.348	*Miopithecus talapoin*	0.720	0.280
Cercopithecus mitis	0.515	0.485	*Nasalis larvatus*	0.586	0.414
Cercopithecus mona	0.652	0.348	*Papio anubis*	0.211	0.789
Cercopithecus neglectus	0.653	0.347	*Papio cynocephalus*	0.410	0.590
Cercopithecus nictitans	0.610	0.390	*Piliocolobus badius*	0.447	0.553
Cercopithecus pogonias	0.687	0.313	*Piliocolobus foai*	0.647	0.353
Chlorocebus aethiops	0.700	0.300	*Piliocolobus kirkii*	0.640	0.360
Chlorocebus pygerythrus	0.678	0.322	*Presbytis comata*	0.858	0.142
Colobus guereza	0.530	0.470	*Presbytis melalophos*	0.723	0.277
Erythrocebus patas	0.488	0.512	*Pygathrix nemaeus*	0.712	0.288
Lophocebus albigena	0.670	0.330	*Rhinopithecus roxellana*	0.426	0.574
Macaca arctoides	0.283	0.717	*Semnopithecus entellus*	0.670	0.330
Macaca assamensis	0.321	0.679	*Theropithecus gelada*	0.180	0.820
Macaca fascicularis	0.573	0.427	*Trachypithecus cristatus*	0.702	0.298
Macaca mulatta	0.387	0.613	*Trachypithecus obscurus*	0.702	0.298
Macaca nemestrina	0.540	0.460	*Trachypithecus phayrei*	0.670	0.330

Table 3.6e. Posterior probabilities from the analysis on the astragalus of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.307	0.693	*Macaca nigra*	0.342	0.658
Cercocebus torquatus	0.341	0.659	*Macaca sinica*	0.648	0.352
Cercopithecus ascanius	0.593	0.407	*Macaca sylvanus*	0.393	0.607
Cercopithecus cephus	0.564	0.436	*Macaca thibetana*	0.589	0.411
Cercopithecus diana	0.589	0.411	*Macaca tonkeana*	0.254	0.746
Cercopithecus hamlyni	0.533	0.467	*Mandrillus sphinx*	0.158	0.842
Cercopithecus lhoesti	0.591	0.409	*Miopithecus talapoin*	0.832	0.168
Cercopithecus mitis	0.651	0.349	*Nasalis larvatus*	0.745	0.255
Cercopithecus mona	0.654	0.346	*Papio anubis*	0.218	0.782
Cercopithecus neglectus	0.597	0.403	*Papio cynocephalus*	0.421	0.579
Cercopithecus nictitans	0.634	0.366	*Piliocolobus badius*	0.667	0.333
Cercopithecus pogonias	0.773	0.227	*Piliocolobus foai*	0.589	0.411
Chlorocebus aethiops	0.647	0.353	*Presbytis comata*	0.606	0.394
Chlorocebus pygerythrus	0.540	0.460	*Presbytis melalophos*	0.801	0.199
Colobus guereza	0.614	0.386	*Pygathrix nemaeus*	0.498	0.502
Erythrocebus patas	0.506	0.494	*Rhinopithecus roxellana*	0.395	0.605
Lophocebus albigena	0.396	0.604	*Semnopithecus entellus*	0.455	0.545
Macaca arctoides	0.649	0.351	*Theropithecus gelada*	0.294	0.706
Macaca assamensis	0.723	0.277	*Trachypithecus cristatus*	0.627	0.373
Macaca fascicularis	0.635	0.365	*Trachypithecus obscurus*	0.666	0.334
Macaca mulatta	0.418	0.582	*Trachypithecus phrayrei*	0.589	0.411
Macaca nemestrina	0.578	0.422			

Table 3.6f. Posterior probabilities from the analysis on the calcaneus of extant species for being classified to the arboreal or terrestrial group using two groups a priori (“semi-terrestrialists” included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.639	0.361	*Macaca nigra*	0.329	0.671
Cercocebus torquatus	0.532	0.468	*Macaca sinica*	0.402	0.598
Cercopithecus ascanius	0.662	0.338	*Macaca sylvanus*	0.207	0.793
Cercopithecus cephus	0.763	0.237	*Macaca thibetana*	0.419	0.581
Cercopithecus diana	0.709	0.291	*Macaca tonkeana*	0.195	0.805
Cercopithecus hamlyni	0.651	0.349	*Mandrillus sphinx*	0.153	0.847
Cercopithecus lhoesti	0.738	0.262	*Miopithecus talapoin*	0.677	0.323
Cercopithecus mitis	0.653	0.347	*Nasalis larvatus*	0.714	0.286
Cercopithecus mona	0.638	0.362	*Papio anubis*	0.254	0.746
Cercopithecus neglectus	0.745	0.255	*Papio cynocephalus*	0.220	0.780
Cercopithecus nictitans	0.642	0.358	*Piliocolobus badius*	0.467	0.533
Cercopithecus pogonias	0.770	0.230	*Piliocolobus foai*	0.758	0.242
Chlorocebus aethiops	0.667	0.333	*Presbytis comata*	0.895	0.105
Chlorocebus pygerythrus	0.724	0.276	*Presbytis melalophos*	0.590	0.410
Colobus guereza	0.469	0.531	*Pygathrix nemaeus*	0.561	0.439
Erythrocebus patas	0.658	0.342	*Rhinopithecus roxellana*	0.356	0.644
Lophocebus albigena	0.570	0.430	*Semnopithecus entellus*	0.504	0.496
Macaca arctoides	0.520	0.480	*Theropithecus gelada*	0.170	0.830
Macaca assamensis	0.605	0.395	*Trachypithecus cristatus*	0.805	0.195
Macaca fascicularis	0.650	0.350	*Trachypithecus obscurus*	0.640	0.360
Macaca mulatta	0.292	0.708	*Trachypithecus phrayei*	0.809	0.191
Macaca nemestrina	0.469	0.531			

Table 3.6g. Posterior probabilities from the analysis on all four elements of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.392	0.608	*Macaca nigra*	0.095	0.905
Cercocebus torquatus	0.461	0.539	*Macaca sinica*	0.365	0.635
Cercopithecus ascanius	0.752	0.248	*Macaca sylvanus*	0.138	0.862
Cercopithecus cephus	0.780	0.220	*Macaca thibetana*	0.375	0.625
Cercopithecus diana	0.670	0.330	*Macaca tonkeana*	0.036	0.964
Cercopithecus hamlyni	0.612	0.388	*Mandrillus sphinx*	0.021	0.979
Cercopithecus lhoesti	0.645	0.355	*Miopithecus talapoin*	0.788	0.212
Cercopithecus mitis	0.658	0.342	*Nasalis larvatus*	0.950	0.050
Cercopithecus mona	0.766	0.234	*Papio anubis*	0.016	0.984
Cercopithecus neglectus	0.571	0.429	*Papio cynocephalus*	0.028	0.972
Cercopithecus nictitans	0.804	0.196	*Piliocolobus badius*	0.845	0.155
Cercopithecus pogonias	0.905	0.095	*Piliocolobus foai*	0.882	0.118
Chlorocebus aethiops	0.690	0.310	*Piliocolobus kirkii*	0.894	0.106
Chlorocebus pygerythrus	0.479	0.521	*Presbytis melalophos*	0.844	0.156
Colobus guereza	0.854	0.146	*Presbytis rubicunda*	0.980	0.020
Erythrocebus patas	0.193	0.807	*Pygathrix nemaeus*	0.728	0.272
Lophocebus albigena	0.475	0.525	*Rhinopithecus roxellana*	0.723	0.277
Macaca arctoides	0.452	0.548	*Semnopithecus entellus*	0.617	0.383
Macaca assamensis	0.605	0.395	*Theropithecus gelada*	0.026	0.974
Macaca fascicularis	0.735	0.265	*Trachypithecus cristata*	0.916	0.084
Macaca mulatta	0.317	0.683	*Trachypithecus obscurus*	0.829	0.171
Macaca nemestrina	0.387	0.613	*Trachypithecus phayrei*	0.974	0.026

Table 3.6h. Posterior probabilities from the analysis on the humerus, astragalus, and calcaneus of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.445	0.555	*Macaca nigra*	0.114	0.886
Cercocebus torquatus	0.461	0.539	*Macaca sinica*	0.378	0.622
Cercopithecus ascanius	0.766	0.234	*Macaca sylvanus*	0.139	0.861
Cercopithecus cephus	0.772	0.228	*Macaca thibetana*	0.410	0.590
Cercopithecus diana	0.679	0.321	*Macaca tonkeana*	0.044	0.956
Cercopithecus hamlyni	0.600	0.400	*Mandrillus sphinx*	0.019	0.981
Cercopithecus lhoesti	0.649	0.351	*Miopithecus talapoin*	0.767	0.233
Cercopithecus mitis	0.656	0.344	*Nasalis larvatus*	0.948	0.052
Cercopithecus mona	0.764	0.236	*Papio anubis*	0.020	0.980
Cercopithecus neglectus	0.548	0.452	*Papio cynocephalus*	0.028	0.972
Cercopithecus nictitans	0.803	0.197	*Piliocolobus badius*	0.837	0.163
Cercopithecus pogonias	0.911	0.089	*Piliocolobus foai*	0.879	0.121
Chlorocebus aethiops	0.674	0.326	*Piliocolobus kirkii*	0.880	0.120
Chlorocebus pygerythrus	0.455	0.545	*Presbytis comata*	0.980	0.020
Colobus guereza	0.864	0.136	*Presbytis melalophos*	0.827	0.173
Erythrocebus patas	0.209	0.791	*Pygathrix nemaeus*	0.712	0.288
Lophocebus albigena	0.494	0.506	*Rhinopithecus roxellana*	0.709	0.291
Macaca arctoides	0.462	0.538	*Semnopithecus entellus*	0.602	0.398
Macaca assamensis	0.602	0.398	*Theropithecus gelada*	0.026	0.974
Macaca fascicularis	0.716	0.284	*Trachypithecus cristatus*	0.922	0.078
Macaca mulatta	0.310	0.690	*Trachypithecus obscurus*	0.824	0.176
Macaca nemestrina	0.399	0.601	*Trachypithecus phayrei*	0.971	0.029

Table 3.6i. Posterior probabilities from the analysis on the distal humerus and astragalus of extant species for being classified to the arboreal or terrestrial group using two groups a priori ("semi-terrestrialists" included in the terrestrial group)

Species	**PP Arboreal**	**PP Terrestrial**	**Species**	**PP Arboreal**	**PP Terrestrial**
Allenopithecus nigroviridis	0.522	0.478	*Macaca nigra*	0.241	0.759
Cercocebus torquatus	0.276	0.724	*Macaca sinica*	0.584	0.416
Cercopithecus ascanius	0.673	0.327	*Macaca sylvanus*	0.240	0.760
Cercopithecus cephus	0.624	0.376	*Macaca thibetana*	0.552	0.448
Cercopithecus diana	0.665	0.335	*Macaca tonkeana*	0.110	0.890
Cercopithecus hamlyni	0.571	0.429	*Mandrillus sphinx*	0.075	0.925
Cercopithecus lhoesti	0.519	0.481	*Miopithecus talapoin*	0.871	0.129
Cercopithecus mitis	0.671	0.329	*Nasalis larvatus*	0.917	0.083
Cercopithecus mona	0.739	0.261	*Papio anubis*	0.046	0.954
Cercopithecus neglectus	0.503	0.497	*Papio cynocephalus*	0.050	0.950
Cercopithecus nictitans	0.689	0.311	*Piliocolobus badius*	0.831	0.169
Cercopithecus pogonias	0.857	0.143	*Piliocolobus foai*	0.887	0.113
Chlorocebus aethiops	0.529	0.471	*Piliocolobus kirkii*	0.811	0.189
Chlorocebus pygerythrus	0.435	0.565	*Presbytis comata*	0.957	0.043
Colobus guereza	0.865	0.135	*Presbytis melalophos*	0.888	0.112
Erythrocebus patas	0.249	0.751	*Pygathrix nemaeus*	0.694	0.306
Lophocebus albigena	0.350	0.650	*Rhinopithecus roxellana*	0.737	0.263
Macaca arctoides	0.550	0.450	*Semnopithecus entellus*	0.384	0.616
Macaca assamensis	0.822	0.178	*Theropithecus gelada*	0.028	0.972
Macaca fascicularis	0.635	0.365	*Trachypithecus cristatus*	0.856	0.144
Macaca mulatta	0.456	0.544	*Trachypithecus obscurus*	0.716	0.284
Macaca nemestrina	0.367	0.633	*Trachypithecus phayrei*	0.945	0.055

Table 3.7a. Fossil reconstructions based on entire humerus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi-terrestrial**	**PP Terrestrial**
Cercopithecoides meavae	AL2-63/64	semi-terrestrial	0.236	0.680	0.084
*Cercopithecoides williamsi**	KNM-ER 4420C	semi-terrestrial	0.213	0.692	0.094
Mesopithecus pentelicus	Pik 355	arboreal	0.580	0.411	0.009
Mesopithecus pentelicus	Pik 244	arboreal	0.904	0.096	7.60E-04
Mesopithecus pentelicus	Pik 1727	semi-terrestrial	0.344	0.598	0.058
Mesopithecus sp.	HD 1610	semi-terrestrial	0.076	0.819	0.105
Mesopithecus sp.	HD 916	arboreal	0.961	0.038	2.08E-04
Mesopithecus sp.*	HD 1004	arboreal	0.893	0.107	4.85E-04
Paracolobus chemeroni	KNM-BC 3B	arboreal	0.535	0.435	0.030
*Rhinocolobus turkanensis**	KNM-ER 15420	arboreal	0.871	0.128	0.001
*Theropithecus brumpti**	KNM-WT 38738	semi-terrestrial	0.426	0.548	0.026
Theropithecus oswaldi	KNM-ER 18917	terrestrial	0.011	0.274	0.715
*Theropithecus oswaldi**	KNM-ER 5491	terrestrial	0.010	0.156	0.834

Table 3.7b. Fossil reconstructions based on proximal humerus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi-terrestrial**	**PP Terrestrial**
*Cercopithecoides kimeui**	KNM-ER 176G	semi-terrestrial	0.222	0.678	0.100
Mesopithecus pentelicus	Pik 298	arboreal	0.678	0.291	0.031
Mesopithecus sp.	HD 417	arboreal	0.787	0.208	0.005
Parapapio lothagamensis	KNM-LT 28769	arboreal	0.922	0.077	0.001
Theropithecus oswaldi	KNM-ER 567	arboreal	0.548	0.429	0.024
Theropithecus oswaldi	KNM-ER 13	arboreal	0.586	0.360	0.053
*Theropithecus oswaldi**	KNM-ER 601 C	semi-terrestrial	0.098	0.490	0.413
Victoriapithecus macinnesi	KNM-MB 21809	arboreal	0.694	0.252	0.053
Victoriapithecus macinnesi	KNM-MB 2044	arboreal	0.907	0.092	0.001

Table 3.7c. Fossil reconstructions based on distal humerus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi-terrestrial**	**PP Terrestrial**
Cercopithecoies kimeui	AL577-1	arboreal	0.699	0.297	0.004
Dolichopithecus ruscinensis	Per010	arboreal	0.614	0.350	0.036
Dolichopithecus ruscinensis	Per011	semi-terrestrial	0.097	0.500	0.403
Dolichopithecus ruscinensis	Per012	arboreal	0.774	0.220	0.006
Kuseracolobus hafu	ASI VP 2-59c	terrestrial	0.080	0.432	0.488
Mesopithecus pentelicus	Pik419	terrestrial	0.019	0.456	0.525
Mesopithecus pentelicus	Pik245	arboreal	0.544	0.442	0.014
*Mesopithecus pentelicus**	Pik356	semi-terrestrial	0.159	0.682	0.159
Mesopithecus sp.	HD 1625	semi-terrestrial	0.424	0.546	0.030
Mesopithecus sp.	HD 1612	arboreal	0.915	0.083	0.002
Mesopithecus sp.	HD 1611	arboreal	0.819	0.173	0.008
Microcolobus sp.	KNM-NA 47916	arboreal	0.630	0.354	0.016
Parapapio jonesi	AL363-12	semi-terrestrial	0.362	0.585	0.054
Parapapio lothagamensis	KNM-LT 23074	semi-terrestrial	0.040	0.742	0.218
Parapresbytis eohanuman	PIN 3381-210	arboreal	0.747	0.249	0.004
Rhinocolobus turkanesis	AL300-1	arboreal	0.991	0.009	5.37E-06
Theropithecus brumpti	KNM-ER 3013	arboreal	0.515	0.458	0.027
Theropithecus oswaldi	KNM-ER 13B	semi-terrestrial	0.155	0.721	0.124
*Theropithecus oswaldi**	KNM-ER 3876	arboreal	0.525	0.468	0.007
Victoriapithecus macinnesi	KNM-MB 21207	semi-terrestrial	0.224	0.726	0.051
Victoriapithecus macinnesi	KNM-MB 21818	semi-terrestrial	0.231	0.692	0.078
Victoriapithecus macinnesi	KNM-MB 21822	semi-terrestrial	0.193	0.697	0.110
Victoriapithecus macinnesi	KNM-MB 19	semi-terrestrial	0.047	0.690	0.263
Victoriapithecus macinnesi	KNM-MB 3	arboreal	0.847	0.152	0.001
*Victoriapithecus macinnesi**	KNM-MB 34712	semi-terrestrial	0.309	0.609	0.082

Table 3.7d. Fossil reconstructions based on astragalus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi-terrestrial**	**PP Terrestrial**
Dolichopithecus ruscinensis	Pp20a	arboreal	0.494	0.451	0.055
Dolichopithecus ruscinensis	Pp20b	arboreal	0.875	0.100	0.025
Mesopithecus pentelicus	Pik237	semi-terrestrial	0.311	0.471	0.218
Mesopithecus pentelicus	Pik368	arboreal	0.624	0.356	0.021
Mesopithecus pentelicus	Pik256	terrestrial	0.303	0.253	0.444
Mesopithecus pentelicus	Pik238	arboreal	0.562	0.243	0.195
Mesopithecus sp.	HD 1025	semi-terrestrial	0.306	0.461	0.233
Microcolobus sp.	KNM-NA 47915K	arboreal	0.761	0.197	0.042
Paracolobus chemeroni	KNM-BC 3 AQ	arboreal	0.700	0.201	0.099
Parapapio lothamensis	KNM-LT 23081	semi-terrestrial	0.431	0.504	0.065
Theropithecus brumpti	KNM-WT 17544 D	semi-terrestrial	0.317	0.545	0.138
Theropithecus brumpti	L865-1t	semi-terrestrial	0.017	0.620	0.363
Theropithecus oswaldi	KNM-ER 3876	arboreal	0.590	0.358	0.052
Theropithecus oswaldi	KNM-OG 1580	arboreal	0.696	0.212	0.092
Theropithecus oswaldi	KNM-OG 948	arboreal	0.688	0.270	0.042
*Theropithecus oswaldi**	KNM-OG 950	arboreal	0.699	0.291	0.010
*Theropithecus oswaldi**	KNM-OG 1188	arboreal	0.464	0.383	0.153
Victoriapithecus macinnesi	KNM-MB 34814	arboreal	0.549	0.421	0.030
Victoriapithecus macinnesi	KNM-MB 34810	arboreal	0.667	0.300	0.032
Victoriapithecus macinnesi	KNM-MB 34364	arboreal	0.514	0.302	0.185
Victoriapithecus macinnesi	KNM-MB 34812	arboreal	0.882	0.114	0.003
Victoriapithecus macinnesi	KNM-MB 34816	semi-terrestrial	0.250	0.558	0.192
Victoriapithecus macinnesi	KNM-MB 34809	arboreal	0.510	0.401	0.090
Victoriapithecus macinnesi	KNM-MB 12013	arboreal	0.644	0.339	0.018

Table 3.7e. Fossil reconstructions based on the calcaneus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi-terrestrial**	**PP Terrestrial**
Mesopithecus pentelicus	Pik240	terrestrial	0.130	0.412	0.458
Mesopithecus pentelicus	Pik266	arboreal	0.932	0.065	0.003
Mesopithecus pentelicus	Pik1746	arboreal	0.594	0.359	0.047
Mesopithecus pentelicus	Pik239	arboreal	0.485	0.369	0.146
Mesopithecus sp.	HD 1569	semi-terrestrial	0.210	0.757	0.033
Mesopithecus sp.	HD 408	arboreal	0.795	0.197	0.007
Mesopithecus sp.	HD 1023	arboreal	0.749	0.231	0.021
Paracolobus chemeroni	KNM-BC 3 R	semi-terrestrial	0.345	0.552	0.103
Parapapio lothagamensis	KNM-LT 28575	arboreal	0.600	0.384	0.016
Parapapio lothagamensis	KNM-LT 24125	arboreal	0.585	0.403	0.013
Theropithecus brumpti	L865-1r	semi-terrestrial	0.280	0.478	0.242
Theropithecus oswaldi	KNM-OG 475	terrestrial	0.291	0.229	0.481
Theropithecus oswaldi	KNM-OG 1192	arboreal	0.889	0.095	0.016
Theropithecus oswaldi	KNM-OG 958	terrestrial	0.104	0.281	0.615
Theropithecus oswaldi	KNM-OG 484	arboreal	0.525	0.385	0.091
*Theropithecus oswaldi**	KNM-ER 3878	semi-terrestrial	0.176	0.426	0.398
*Theropithecus oswaldi**	KNM-OG 1138	arboreal	0.875	0.112	0.014
*Theropithecus oswaldi**	KNM-OG 472	arboreal	0.565	0.373	0.062
Victoriapithecus macinnesi	KNM-MB 35573	arboreal	0.695	0.277	0.028
Victoriapithecus macinnesi	KNM-MB 34820	arboreal	0.491	0.480	0.029
Victoriapithecus macinnesi	KNM-MB 12006	arboreal	0.802	0.197	0.001
*Victoriapithecus macinnesi**	KNM-MB 21211	arboreal	0.901	0.098	7.39E-04
*Victoriapithecus macinnesi**	KNM-MB 46664	arboreal	0.674	0.319	0.007
*Victoriapithecus macinnesi**	KNM-MB 34821	semi-terrestrial	0.414	0.485	0.101
*Victoriapithecus macinnesi**	KNM-MB 21208	arboreal	0.790	0.181	0.029
*Victoriapithecus macinnesi**	KNM-MB 21209	arboreal	0.815	0.162	0.024
*Victoriapithecus macinnesi**	KNM-MB 14375	semi-terrestrial	0.085	0.485	0.430
*Victoriapithecus macinnesi**	KNM-MB 35571	arboreal	0.864	0.133	0.003

Table 3.7f. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi**	**PP Terrestrial**
Paracolobus chemeroni	KNM-BC 3B	semi-terrestrial	0.416	0.486	0.098
Mesopithecus pentelicus	composite	arboreal	0.715	0.283	0.001

Table 3.7g. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using three groups a-priori. Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi**	**PP Terrestrial**
Victoriapithecus macinnesi	composite	arboreal	0.883	0.116	2.507E-04
*Theropithecus oswaldi**	composite	semi-terrestrial	0.013	0.581	0.406
Parapapio lothagamensis	composite	semi-terrestrial	0.154	0.845	8.45E-01
Mesopithecus sp.	composite	arboreal	0.568	0.431	0.001

Table 3.7h. Fossil reconstructions based on a combination of the distal humerus and astragalus using three groups a-priori.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Semi**	**PP Terrestrial**
Microcolobus sp.	KNM-NA 47915/6	arboreal	0.825	0.170	0.005
Theropithecus brumpti	composite	semi-terrestrial	0.220	0.700	0.080
Dolichopithecus ruscinensis	composite	arboreal	0.620	0.341	0.039

Table 3.8a. Fossil reconstructions based on the humerus using two groups a-priori ("semi-terrestriralists" as unknown). Asterisk (*) denotes specimens that have missing data.

Specimen	Specimen #	Classification	PP Arboreal	PP Terrestrial
*Cercopithecoides meavae**	AL2-63/64	arboreal	0.923	0.077
*Cercopithecoides williamsi**	KNM-ER 4420C	arboreal	0.707	0.293
Mesopithecus pentelicus	Pik 355	arboreal	0.996	0.004
Mesopithecus pentelicus	Pik 244	arboreal	0.999	0.001
Mesopithecus pentelicus	Pik 1727	arboreal	0.647	0.353
Mesopithecus sp.	HD 1610	arboreal	0.732	0.268
Mesopithecus sp.	HD 916	arboreal	0.999	0.001
Mesopithecus sp.*	HD 1004	arboreal	0.999	4.0E-04
Paracolobus chemeroni	KNM-BC 3B	arboreal	0.977	0.023
*Rhinocolobus turkanensis**	KNM-ER 15420	arboreal	0.998	0.002
*Theropithecus brumpti**	KNM-WT 38738	arboreal	0.953	0.047
Theropithecus oswaldi	KNM-ER 18917	terrestrial	0.010	0.990
*Theropithecus oswaldi**	KNM-ER 5491	terrestrial	0.007	0.993

Table 3.8b. Fossil reconstructions based on the proximal humerus using two groups a-priori ("semi-terrestriralists" as unknown). Asterisk (*) denotes specimens that have missing data.

Specimen	Specimen #	Classification	PP Arboreal	PP Terrestrial
*Cercopithecoides kimeui**	KNM-ER 176G	arboreal	0.619	0.381
Mesopithecus pentelicus	Pik 298	arboreal	0.963	0.037
Mesopithecus sp.	HD 417	arboreal	0.995	0.005
Parapapio lothagamensis	KNM-LT 28769	arboreal	0.999	0.001
Theropithecus oswaldi	KNM-ER 567	arboreal	0.959	0.041
Theropithecus oswaldi	KNM-ER 13	arboreal	0.918	0.082
*Theropithecus oswaldi**	KNM-ER 601 C	terrestrial	0.179	0.821
Victoriapithecus macinnesi	KNM-MB 21809	arboreal	0.937	0.063
Victoriapithecus macinnesi	KNM-MB 2044	arboreal	1.000	0.000

Table 3.8c. Fossil reconstructions based on the distal humerus using two groups a-priori ("semi-terrestriralists" as unknown). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Cercopithecoies kimeui	AL577-1	arboreal	0.996	0.004
Dolichopithecus ruscinensis	Per010	arboreal	0.906	0.094
Dolichopithecus ruscinensis	Per011	terrestrial	0.177	0.823
Dolichopithecus ruscinensis	Per012	arboreal	0.990	0.010
Kuseracolobus hafu	ASI VP 2-59c	terrestrial	0.113	0.887
Mesopithecus pentelicus	Pik419	terrestrial	0.060	0.940
Mesopithecus pentelicus	Pik245	arboreal	0.980	0.020
*Mesopithecus pentelicus**	Pik356	arboreal	0.512	0.488
Mesopithecus sp.	HD 1625	arboreal	0.948	0.052
Mesopithecus sp.	HD 1612	arboreal	0.988	0.012
Mesopithecus sp.	HD 1611	arboreal	0.978	0.022
Microcolobus sp.	KNM-NA 47916	arboreal	0.963	0.037
*Paracolobus mutiwa**	KNM-WT 16827	arboreal	0.999	3.43E-05
Parapapio jonesi	AL363-12	arboreal	0.896	0.104
Parapapio lothagamensis	KNM-LT 23074	terrestrial	0.349	0.651
Parapresbytis eohanuman	PIN 3381-210	arboreal	0.995	0.005
Rhinocolobus turkanesis	AL300-1	arboreal	0.999	9.46E-06
Theropithecus brumpti	KNM-ER 3013	arboreal	0.948	0.052
Theropithecus oswaldi	KNM-ER 13B	arboreal	0.683	0.317
*Theropithecus oswaldi**	KNM-ER 3876	arboreal	0.992	0.008
Victoriapithecus macinnesi	KNM-MB 21207	arboreal	0.891	0.109
Victoriapithecus macinnesi	KNM-MB 21818	arboreal	0.769	0.231
Victoriapithecus macinnesi	KNM-MB 21822	arboreal	0.762	0.238
Victoriapithecus macinnesi	KNM-MB 19	terrestrial	0.218	0.782
Victoriapithecus macinnesi	KNM-MB 3	arboreal	0.999	0.001
*Victoriapithecus macinnesi**	KNM-MB 34712	arboreal	0.815	0.185

Table 3.8d. Fossil reconstructions based on the astragalus using two groups a-priori (“semi-terrestriralists” as unknown). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Dolichopithecus ruscinensis	Pp20a	arboreal	0.849	0.151
Dolichopithecus ruscinensis	Pp20b	arboreal	0.964	0.036
Mesopithecus pentelicus	Pik237	arboreal	0.561	0.439
Mesopithecus pentelicus	Pik368	arboreal	0.975	0.025
Mesopithecus pentelicus	Pik256	terrestrial	0.391	0.609
Mesopithecus pentelicus	Pik238	arboreal	0.760	0.240
Mesopithecus sp.	HD 1025	arboreal	0.600	0.400
Microcolobus sp.	KNM-NA 47915K	arboreal	0.947	0.053
Paracolobus chemeroni	KNM-BC 3 AQ	arboreal	0.897	0.103
Paracolobus mutiwa	KNM-WT 16827Q	arboreal	0.830	0.170
Parapapio lothamensis	KNM-LT 23081	arboreal	0.863	0.137
Theropithecus brumpti	KNM-WT 17544 D	arboreal	0.681	0.319
Theropithecus brumpti	L865-1t	terrestrial	0.061	0.939
Theropithecus oswaldi	KNM-ER 3876	arboreal	0.928	0.072
Theropithecus oswaldi	KNM-OG 1580	arboreal	0.850	0.150
Theropithecus oswaldi	KNM-OG 948	arboreal	0.901	0.099
*Theropithecus oswaldi**	KNM-OG 950	arboreal	0.991	0.009
*Theropithecus oswaldi**	KNM-OG 1188	arboreal	0.703	0.297
Victoriapithecus macinnesi	KNM-MB 34814	arboreal	0.960	0.040
Victoriapithecus macinnesi	KNM-MB 34810	arboreal	0.965	0.035
Victoriapithecus macinnesi	KNM-MB 34364	arboreal	0.765	0.235
Victoriapithecus macinnesi	KNM-MB 34812	arboreal	0.997	0.003
Victoriapithecus macinnesi	KNM-MB 34816	arboreal	0.542	0.458
Victoriapithecus macinnesi	KNM-MB 34809	arboreal	0.900	0.100
Victoriapithecus macinnesi	KNM-MB 12013	arboreal	0.982	0.018

Table 3.8e. Fossil reconstructions based on the calcaneus using two groups a-priori (“semi-terrestriralists” as unknown). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Mesopithecus pentelicus	Pik240	terrestrial	0.193	0.807
Mesopithecus pentelicus	Pik266	arboreal	0.996	0.004
Mesopithecus pentelicus	Pik1746	arboreal	0.934	0.066
Mesopithecus pentelicus	Pik239	arboreal	0.719	0.281
Mesopithecus sp.	HD 1569	arboreal	0.926	0.074
Mesopithecus sp.	HD 408	arboreal	0.994	0.006
Mesopithecus sp.	HD 1023	arboreal	0.976	0.024
Paracolobus chemeroni	KNM-BC 3 R	arboreal	0.822	0.178
Paracolobus mutiwa	KNM-WT 16827P	arboreal	0.705	0.295
Parapapio lothagamensis	KNM-LT 28575	arboreal	0.985	0.015
Parapapio lothagamensis	KNM-LT 24125	arboreal	0.989	0.011
Theropithecus brumpti	L865-1r	arboreal	0.512	0.488
Theropithecus oswaldi	KNM-OG 475	terrestrial	0.227	0.773
Theropithecus oswaldi	KNM-OG 1192	arboreal	0.975	0.025
Theropithecus oswaldi	KNM-OG 958	terrestrial	0.097	0.903
Theropithecus oswaldi	KNM-OG 484	arboreal	0.858	0.142
*Theropithecus oswaldi**	KNM-ER 3878	terrestrial	0.264	0.736
*Theropithecus oswaldi**	KNM-OG 1138	arboreal	0.983	0.017
*Theropithecus oswaldi**	KNM-OG 472	arboreal	0.893	0.107
Victoriapithecus macinnesi	KNM-MB 35573	arboreal	0.964	0.036
Victoriapithecus macinnesi	KNM-MB 34820	arboreal	0.970	0.030
Victoriapithecus macinnesi	KNM-MB 12006	arboreal	0.999	4.47E-04
*Victoriapithecus macinnesi**	KNM-MB 21211	arboreal	0.999	3.38E-04
*Victoriapithecus macinnesi**	KNM-MB 46664	arboreal	0.996	0.004
*Victoriapithecus macinnesi**	KNM-MB 34821	arboreal	0.839	0.161
*Victoriapithecus macinnesi**	KNM-MB 21208	arboreal	0.960	0.040
*Victoriapithecus macinnesi**	KNM-MB 21209	arboreal	0.969	0.031
*Victoriapithecus macinnesi**	KNM-MB 14375	terrestrial	0.184	0.816
*Victoriapithecus macinnesi**	KNM-MB 35571	arboreal	0.997	0.003

Table 3.8f. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using two groups a-priori ("semi-terrestriralists" as unknown). Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Paracolobus chemeroni	KNM-BC 3B	arboreal	0.979	0.021
Mesopithecus pentelicus	composite	arboreal	0.999	4.225E-04

Table 3.8g. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using two groups a-priori ("semi-terrestriralists" as unknown). Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Victoriapithecus macinnesi	composite	arboreal	0.999	4.75E-05
*Theropithecus oswaldi**	composite	terrestrial	0.019	0.981
Parapapio lothagamensis	composite	arboreal	0.999	5.09E+00
Mesopithecus sp.	composite	arboreal	0.998	0.002

Table 3.8h. Fossil reconstructions based on a combination of the distal humerus and astragalus using two groups a-priori ("semi-terrestriralists" as unknown)

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Microcolobus sp.	KNM-NA 47915/6	arboreal	0.994	0.006
Theropithecus brumpti	composite	arboreal	0.709	0.291
Dolichopithecus ruscinensis	composite	arboreal	0.929	0.071

Table 3.9a. Fossil reconstructions based on the humerus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
*Cercopithecoides meavae**	AL2-63/64	terrestrial	0.287	0.713
*Cercopithecoides williamsi**	KNM-ER 4420C	terrestrial	0.237	0.763
Mesopithecus pentelicus	Pik 355	arboreal	0.701	0.299
Mesopithecus pentelicus	Pik 244	arboreal	0.883	0.117
Mesopithecus pentelicus	Pik 1727	terrestrial	0.320	0.680
Mesopithecus sp.	HD 1610	terrestrial	0.145	0.855
Mesopithecus sp.	HD 916	arboreal	0.942	0.058
Mesopithecus sp.*	HD 1004	arboreal	0.873	0.127
Paracolobus chemeroni	KNM-BC 3B	terrestrial	0.425	0.575
*Rhinocolobus turkanensis**	KNM-ER 15420	arboreal	0.849	0.151
*Theropithecus brumpti**	KNM-WT 38738	terrestrial	0.410	0.590
Theropithecus oswaldi	KNM-ER 18917	terrestrial	0.032	0.968
*Theropithecus oswaldi**	KNM-ER 5491	terrestrial	0.030	0.970

Table 3.9b. Fossil reconstructions based on the proximal humerus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
*Cercopithecoides kimeui**	KNM-ER 176G	arboreal	0.531	0.469
Mesopithecus pentelicus	Pik 298	arboreal	0.702	0.298
Mesopithecus sp.	HD 417	arboreal	0.854	0.146
Parapapio lothagamensis	KNM-LT 28769	arboreal	0.966	0.034
Theropithecus oswaldi	KNM-ER 567	arboreal	0.689	0.311
Theropithecus oswaldi	KNM-ER 13	terrestrial	0.460	0.540
*Theropithecus oswaldi**	KNM-ER 601 C	terrestrial	0.121	0.879
Victoriapithecus macinnesi	KNM-MB 21809	arboreal	0.756	0.244
Victoriapithecus macinnesi	KNM-MB 2044	arboreal	0.959	0.041

Table 3.9c. Fossil reconstructions based on the distal humerus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP terrestrial**
Cercopithecoies kimeui	AL577-1	arboreal	0.671	0.329
Dolichopithecus ruscinensis	Per010	arboreal	0.593	0.407
Dolichopithecus ruscinensis	Per011	terrestrial	0.145	0.855
Dolichopithecus ruscinensis	Per012	arboreal	0.728	0.272
Kuseracolobus hafu	ASI VP 2-59c	terrestrial	0.137	0.863
Mesopithecus pentelicus	Pik419	terrestrial	0.047	0.953
Mesopithecus pentelicus	Pik245	arboreal	0.544	0.456
*Mesopithecus pentelicus**	Pik356	terrestrial	0.234	0.766
Mesopithecus sp.	HD 1625	terrestrial	0.432	0.568
Mesopithecus sp.	HD 1612	arboreal	0.935	0.065
Mesopithecus sp.	HD 1611	arboreal	0.781	0.219
Microcolobus sp.	KNM-NA 47916	arboreal	0.699	0.301
Parapapio jonesi	AL363-12	terrestrial	0.338	0.662
Parapapio lothagamensis	KNM-LT 23074	terrestrial	0.062	0.938
Parapresbytis eohanuman	PIN 3381-210	arboreal	0.717	0.283
Rhinocolobus turkanesis	AL300-1	arboreal	0.985	0.015
Theropithecus brumpti	KNM-ER 3013	arboreal	0.514	0.486
Theropithecus oswaldi	KNM-ER 13B	terrestrial	0.172	0.828
*Theropithecus oswaldi**	KNM-ER 3876	arboreal	0.552	0.448
Victoriapithecus macinnesi	KNM-MB 21207	terrestrial	0.271	0.729
Victoriapithecus macinnesi	KNM-MB 21818	terrestrial	0.349	0.651
Victoriapithecus macinnesi	KNM-MB 21822	terrestrial	0.170	0.830
Victoriapithecus macinnesi	KNM-MB 19	terrestrial	0.119	0.881
Victoriapithecus macinnesi	KNM-MB 3	arboreal	0.797	0.203
*Victoriapithecus macinnesi**	KNM-MB 34712	terrestrial	0.313	0.687

Table 3.9d. Fossil reconstructions based on the astragalus using two groups a-priori (“semi-terrestrialist” included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Dolichopithecus ruscinensis	Pp20a	arboreal	0.557	0.443
Dolichopithecus ruscinensis	Pp20b	arboreal	0.897	0.103
Mesopithecus pentelicus	Pik237	terrestrial	0.367	0.633
Mesopithecus pentelicus	Pik368	arboreal	0.502	0.498
Mesopithecus pentelicus	Pik256	terrestrial	0.209	0.791
Mesopithecus pentelicus	Pik238	terrestrial	0.304	0.696
Mesopithecus sp.	HD 1025	terrestrial	0.265	0.735
Microcolobus sp.	KNM-NA 47915K	arboreal	0.825	0.175
Paracolobus chemeroni	KNM-BC 3 AQ	arboreal	0.631	0.369
Parapapio lothamensis	KNM-LT 23081	terrestrial	0.240	0.760
Theropithecus brumpti	KNM-WT 17544 D	terrestrial	0.259	0.741
Theropithecus brumpti	L865-1t	terrestrial	0.011	0.989
Theropithecus oswaldi	KNM-ER 3876	terrestrial	0.391	0.609
Theropithecus oswaldi	KNM-OG 1580	arboreal	0.611	0.389
Theropithecus oswaldi	KNM-OG 948	arboreal	0.663	0.337
*Theropithecus oswaldi**	KNM-OG 950	arboreal	0.702	0.298
*Theropithecus oswaldi**	KNM-OG 1188	terrestrial	0.308	0.692
Victoriapithecus macinnesi	KNM-MB 34814	arboreal	0.609	0.391
Victoriapithecus macinnesi	KNM-MB 34810	arboreal	0.730	0.270
Victoriapithecus macinnesi	KNM-MB 34364	arboreal	0.526	0.474
Victoriapithecus macinnesi	KNM-MB 34812	arboreal	0.871	0.129
Victoriapithecus macinnesi	KNM-MB 34816	terrestrial	0.204	0.796
Victoriapithecus macinnesi	KNM-MB 34809	terrestrial	0.270	0.730
Victoriapithecus macinnesi	KNM-MB 12013	terrestrial	0.496	0.504

Table 3.9e. Fossil reconstructions based on the calcaneus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data. n/a refers to specimens that could not be run in this analysis due to missing data (see text for explanation).

Specimen	**Specimen #**	**Classification**	**PP Arboreal**	**PP terrestrial**
Mesopithecus pentelicus	Pik240	terrestrial	0.185	0.815
Mesopithecus pentelicus	Pik266	arboreal	0.792	0.208
Mesopithecus pentelicus	Pik1746	arboreal	0.551	0.449
Mesopithecus pentelicus	Pik239	terrestrial	0.461	0.539
Mesopithecus sp.	HD 1569	arboreal	0.541	0.459
Mesopithecus sp.	HD 408	arboreal	0.796	0.204
Mesopithecus sp.	HD 1023	arboreal	0.710	0.290
Paracolobus chemeroni	KNM-BC 3 R	arboreal	0.588	0.412
Parapapio lothagamensis	KNM-LT 28575	arboreal	0.718	0.282
Parapapio lothagamensis	KNM-LT 24125	arboreal	0.772	0.228
Theropithecus brumpti	L865-1r	terrestrial	0.361	0.639
Theropithecus oswaldi	KNM-OG 475	terrestrial	0.250	0.750
Theropithecus oswaldi	KNM-OG 1192	arboreal	0.654	0.346
Theropithecus oswaldi	KNM-OG 958	terrestrial	0.174	0.826
Theropithecus oswaldi	KNM-OG 484	terrestrial	0.396	0.604
*Theropithecus oswaldi**	KNM-ER 3878	terrestrial	0.148	0.852
*Theropithecus oswaldi**	KNM-OG 1138	arboreal	0.808	0.192
*Theropithecus oswaldi**	KNM-OG 472	arboreal	0.563	0.437
Victoriapithecus macinnesi	KNM-MB 35573	terrestrial	0.393	0.607
Victoriapithecus macinnesi	KNM-MB 34820	arboreal	0.618	0.382
Victoriapithecus macinnesi	KNM-MB 12006	arboreal	0.880	0.120
*Victoriapithecus macinnesi**	KNM-MB 21211	arboreal	0.885	1.15E-01
*Victoriapithecus macinnesi**	KNM-MB 46664	arboreal	0.614	0.386
*Victoriapithecus macinnesi**	KNM-MB 34821	terrestrial	0.287	0.713
*Victoriapithecus macinnesi**	KNM-MB 21208	n/a		
*Victoriapithecus macinnesi**	KNM-MB 21209	n/a		
*Victoriapithecus macinnesi**	KNM-MB 14375	n/a		
*Victoriapithecus macinnesi**	KNM-MB 35571	arboreal	0.756	0.244

Table 3.9g. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, distal femur, astragalus, and calcaneus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Paracolobus chemeroni	KNM-BC 3	arboreal	0.787	0.213
Mesopithecus pentelicus	composite	arboreal	0.754	0.246

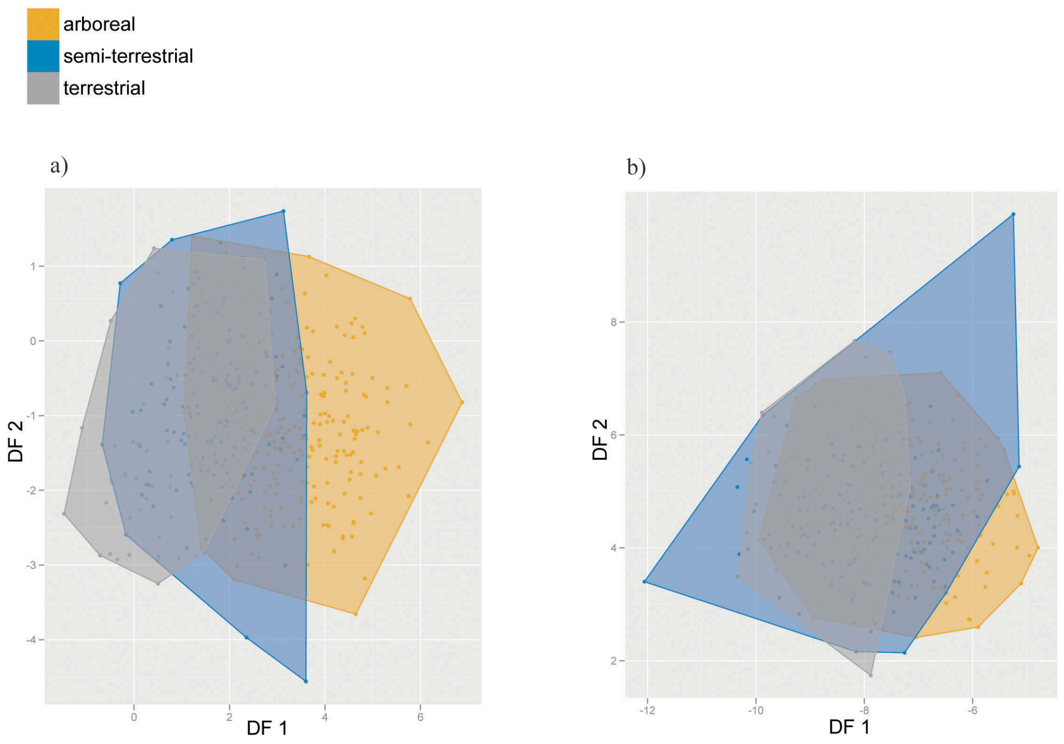
Table 3.9g. Fossil reconstructions based on a combination of the proximal humerus, distal humerus, astragalus, and calcaneus using two groups a-priori ("semi-terrestrialist" included in terrestrial group). Asterisk (*) denotes specimens that have missing data.

Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Victoriapithecus macinnesi	composite	arboreal	0.750	2.50E-01
*Theropithecus oswaldi**	composite	terrestrial	0.022	0.978
Parapapio lothagamensis	composite	arboreal	0.516	0.484
Mesopithecus sp.	composite	arboreal	0.612	0.388

Table 3.9h. Fossil reconstructions based on a combination of the distal humerus and astragalus using two groups a-priori ("semi-terrestrialist" included in terrestrial group)

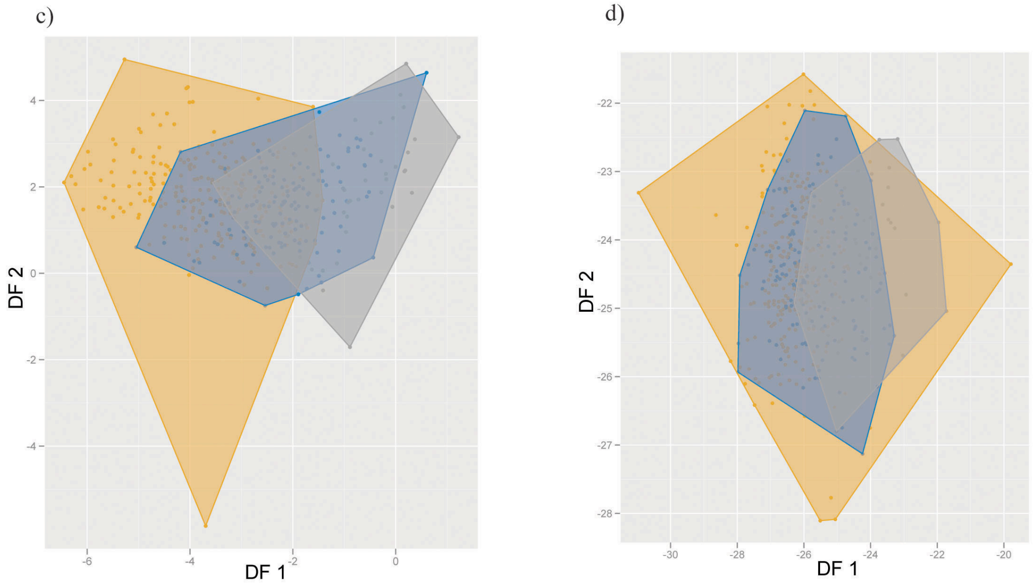
Species	**Specimen #**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Microcolobus sp.	KNM-NA 47915/6	arboreal	0.899	0.101
Theropithecus brumpti	composite	terrestrial	0.199	0.801
Dolichopithecus ruscinensis	composite	arboreal	0.698	0.302

Figure 3.1. Plots of discriminant function analyses using three groups a-priori. a) humerus, b) proximal humerus, c) distal humerus, d) femur, e) astragalus, f) calcaneus



Humerus

Proximal Humerus



Distal Humerus

Femur

Figure 3.1 continued.

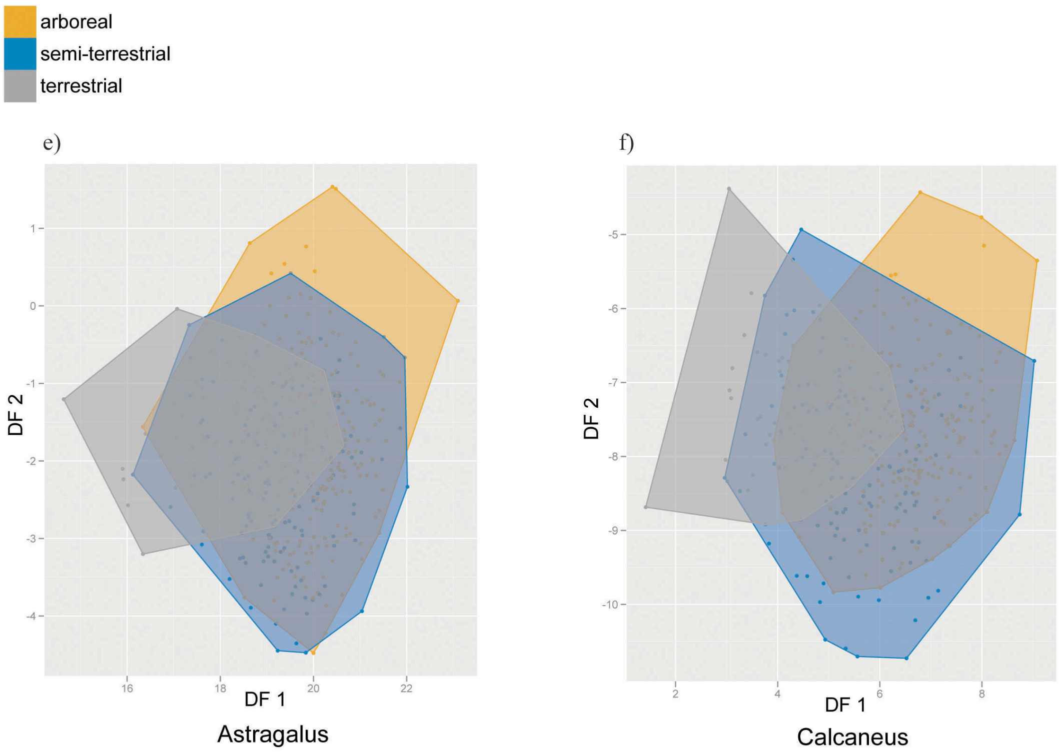
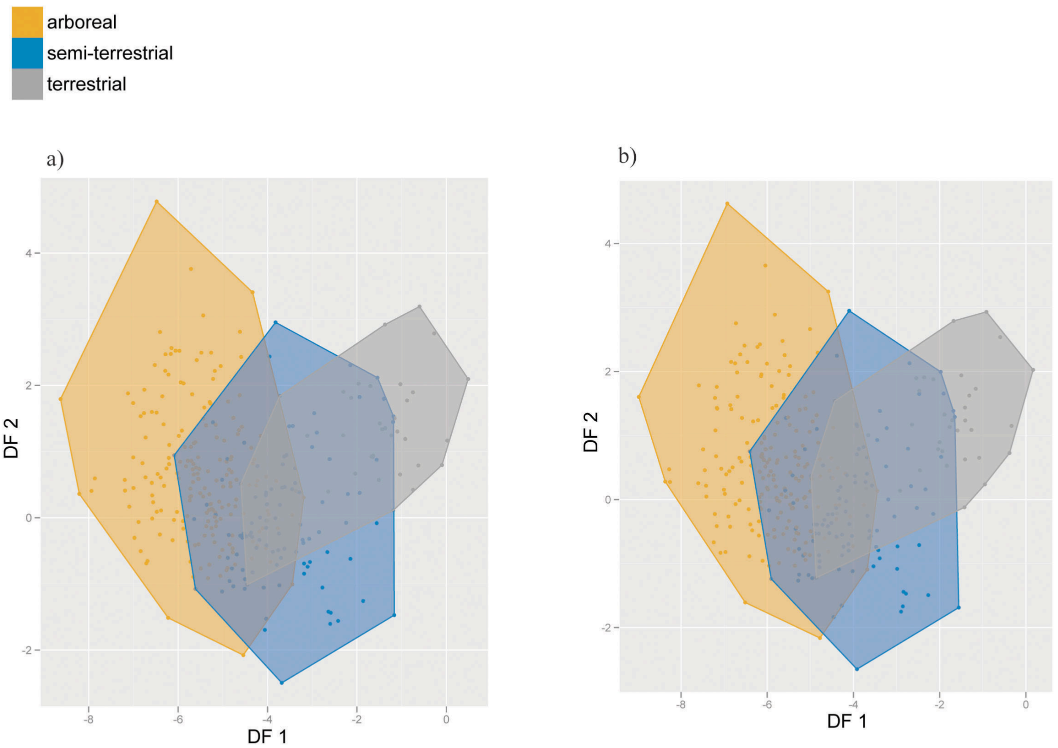
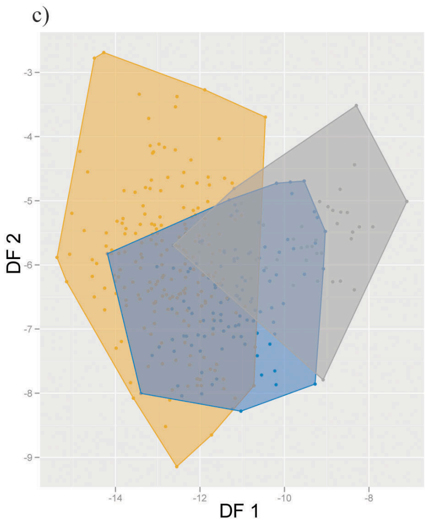


Figure 3.2. Plots of discriminant function analyses using three groups a-priori. a) all four elements combined, b) humerus, astragalus, and calcaneus, c) distal humerus and astragalus



Four Elements Combined

Humerus, Astragalus, Calcaneus



Distal Humerus and Astragalus

Figure 3.3. Plots of discriminant function analyses using two groups a-priori with "semi-terrestrial" individuals as unknown. a) humerus, b) proximal humerus, c) distal humerus, d) femur, e) astragalus, f) calcaneus

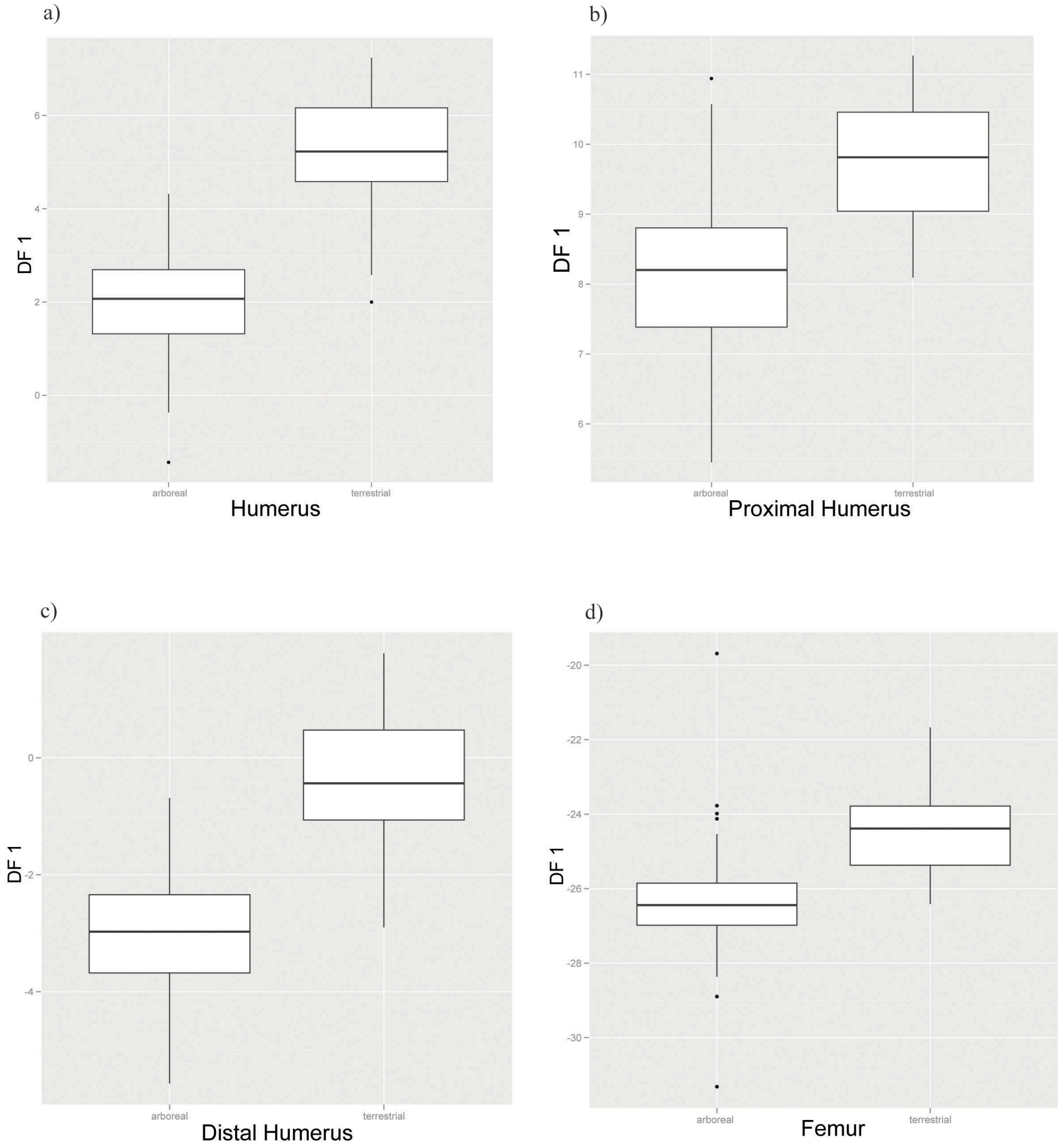


Figure 3.3 continued.

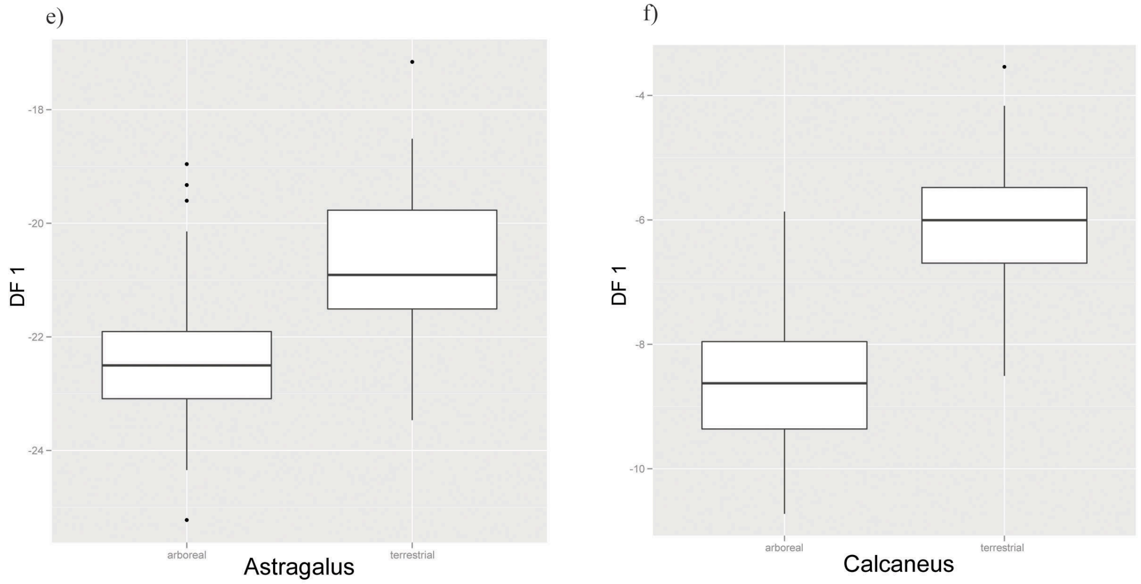


Figure 3.4. Plots of discriminant function analyses using two groups a-priori with "semi-terrestrial" individuals as unknown. a) all four elements combined, b) humerus, astragalus, and calcaneus, c) distal humerus and astragalus

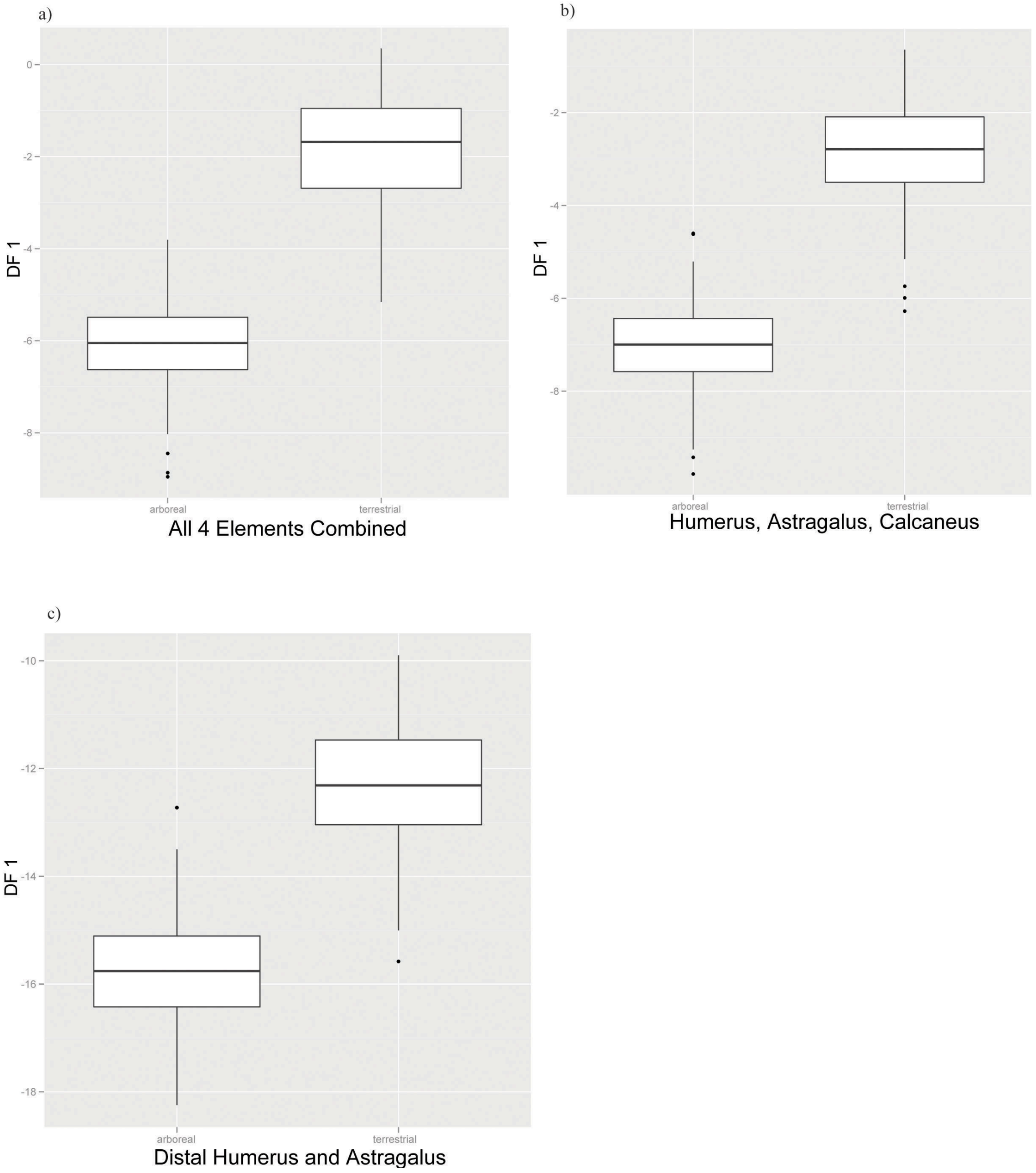


Figure 3.5. Plots of discriminant function analyses using two groups a-priori with "semi-terrestrial" individuals included in the terrestrial group. a) humerus, b) proximal humerus, c) distal humerus, d) femur, e) astragalus, f) calcaneus

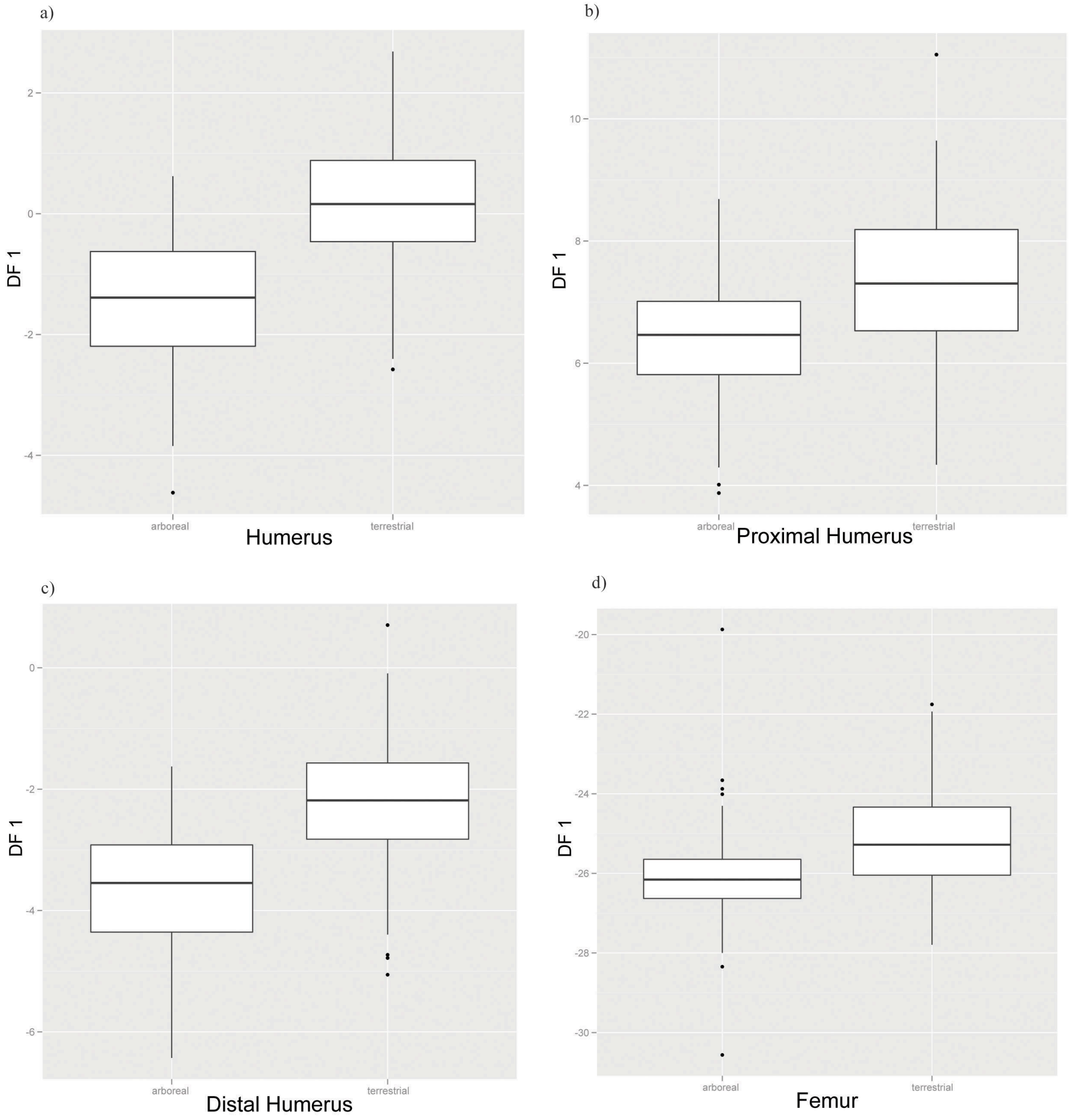


Figure 3.5 continued.

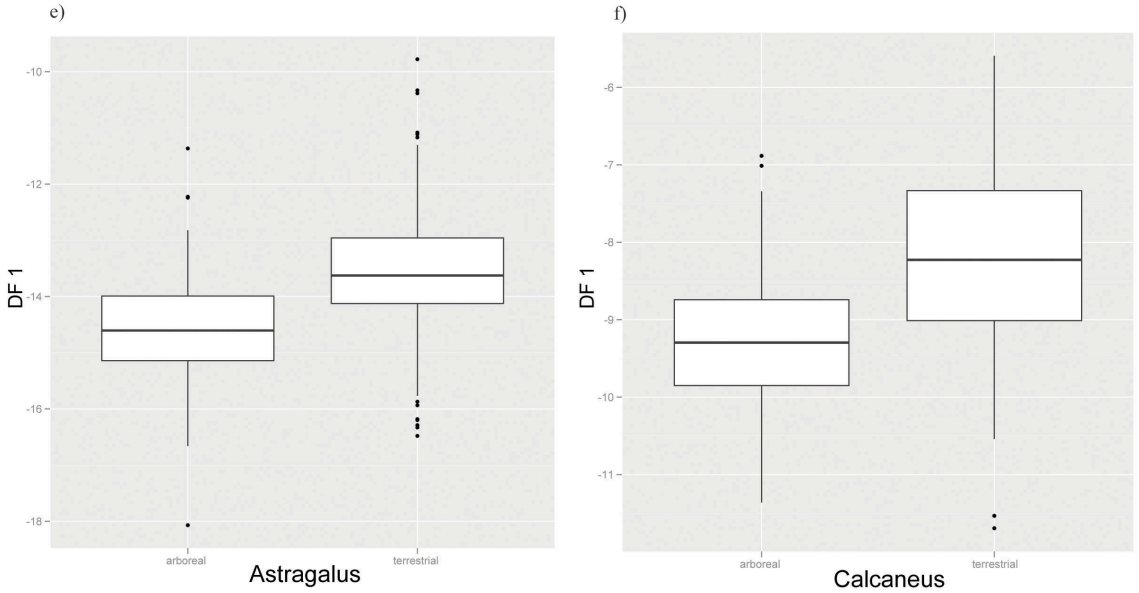
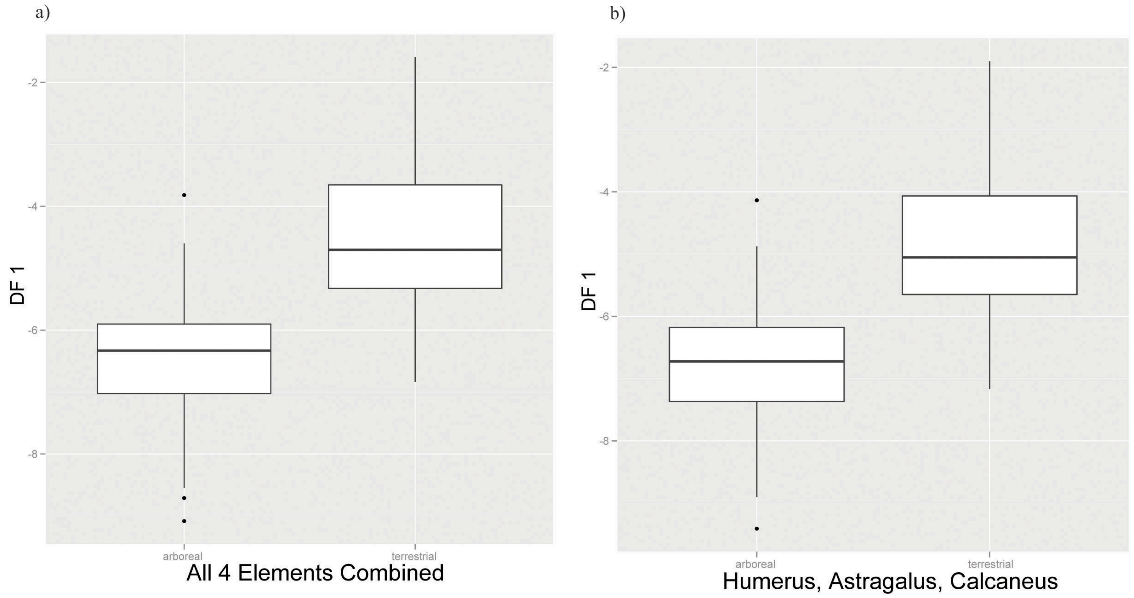


Figure 3.6. Plots of discriminant function analyses using two groups a-priori with “semi-terrestrial” individuals included in the terrestrial group. a) all four elements combined, b) humerus, astragalus, and calcaneus, c) distal humerus and astragalus



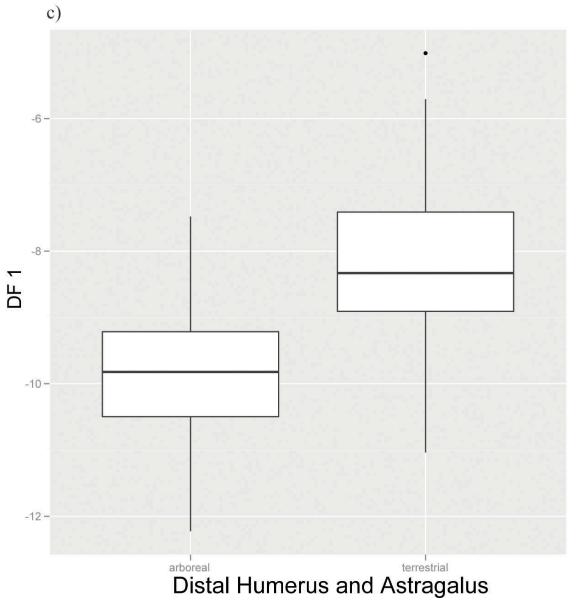


Figure 3.7. Posterior probabilities of extant species being assigned to the arboreal group using all four elements combined along a color gradient. 1.0 = 100% probability of being assigned to the arboreal group and 0.0 = 0% probability of being assigned to the arboreal group.

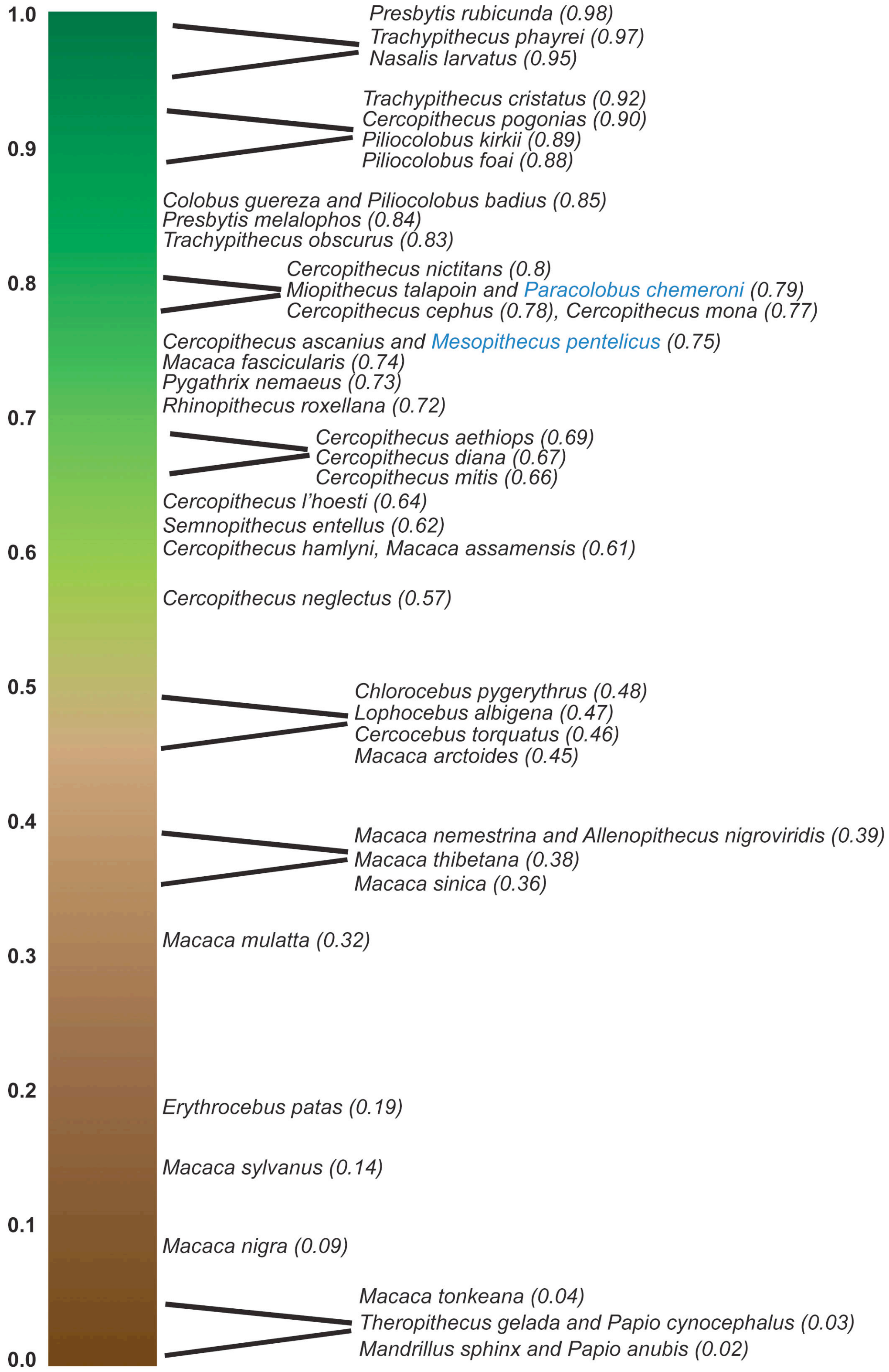


Figure 3.8. Posterior probabilities of extant species being assigned to the arboreal group using a combination of the humerus, astragalus, and calcaneus along a color gradient. 1.0 = 100% probability of being assigned to the arboreal group and 0.0 = 0% probability of being assigned to the arboreal group.

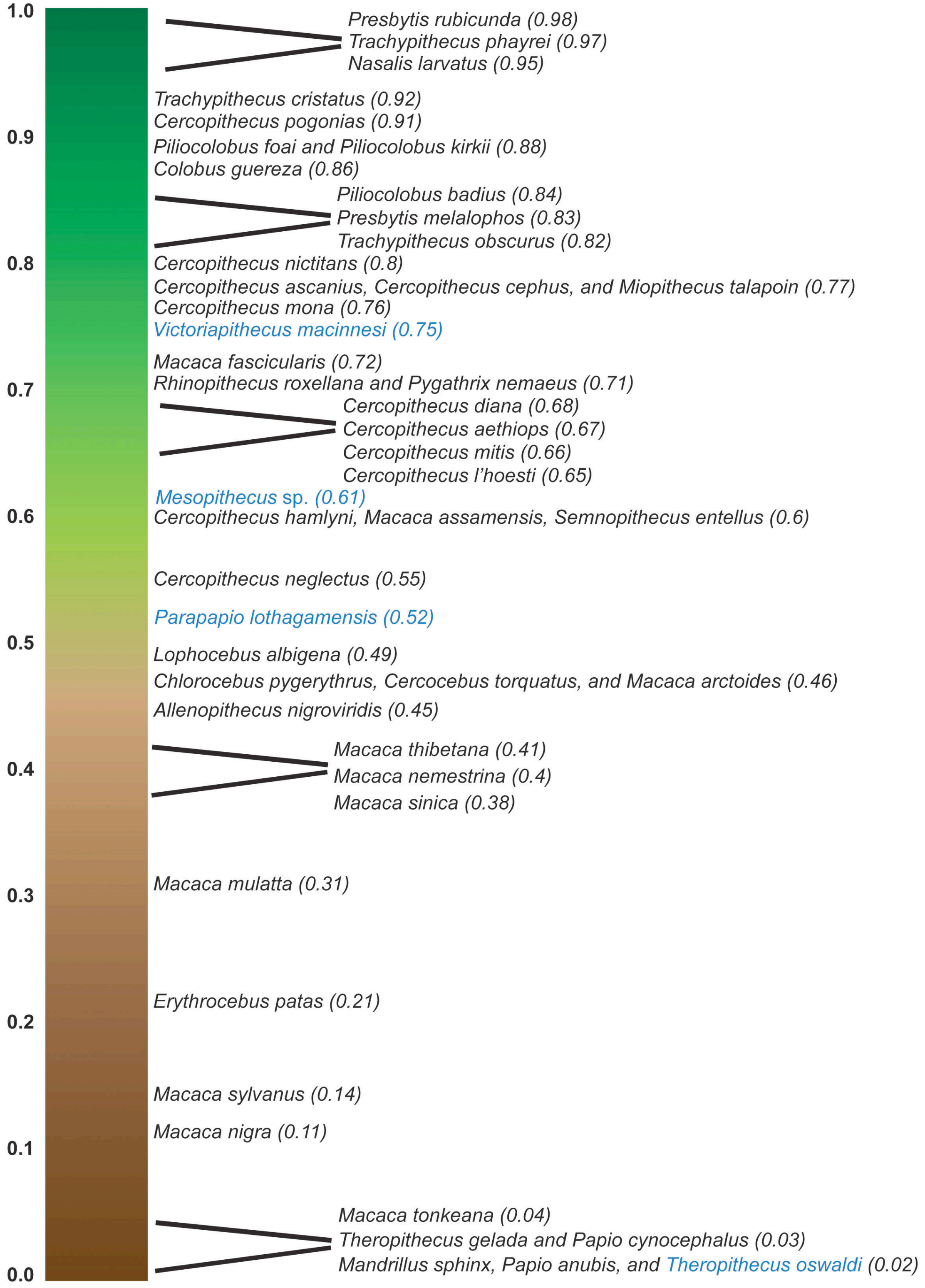


Figure 3.9. Posterior probabilities of extant species being assigned to the arboreal group using a combination of the distal humerus and astragalus along a color gradient. 1.0 = 100% probability of being assigned to the arboreal group and 0.0 = 0% probability of being assigned to the arboreal group.

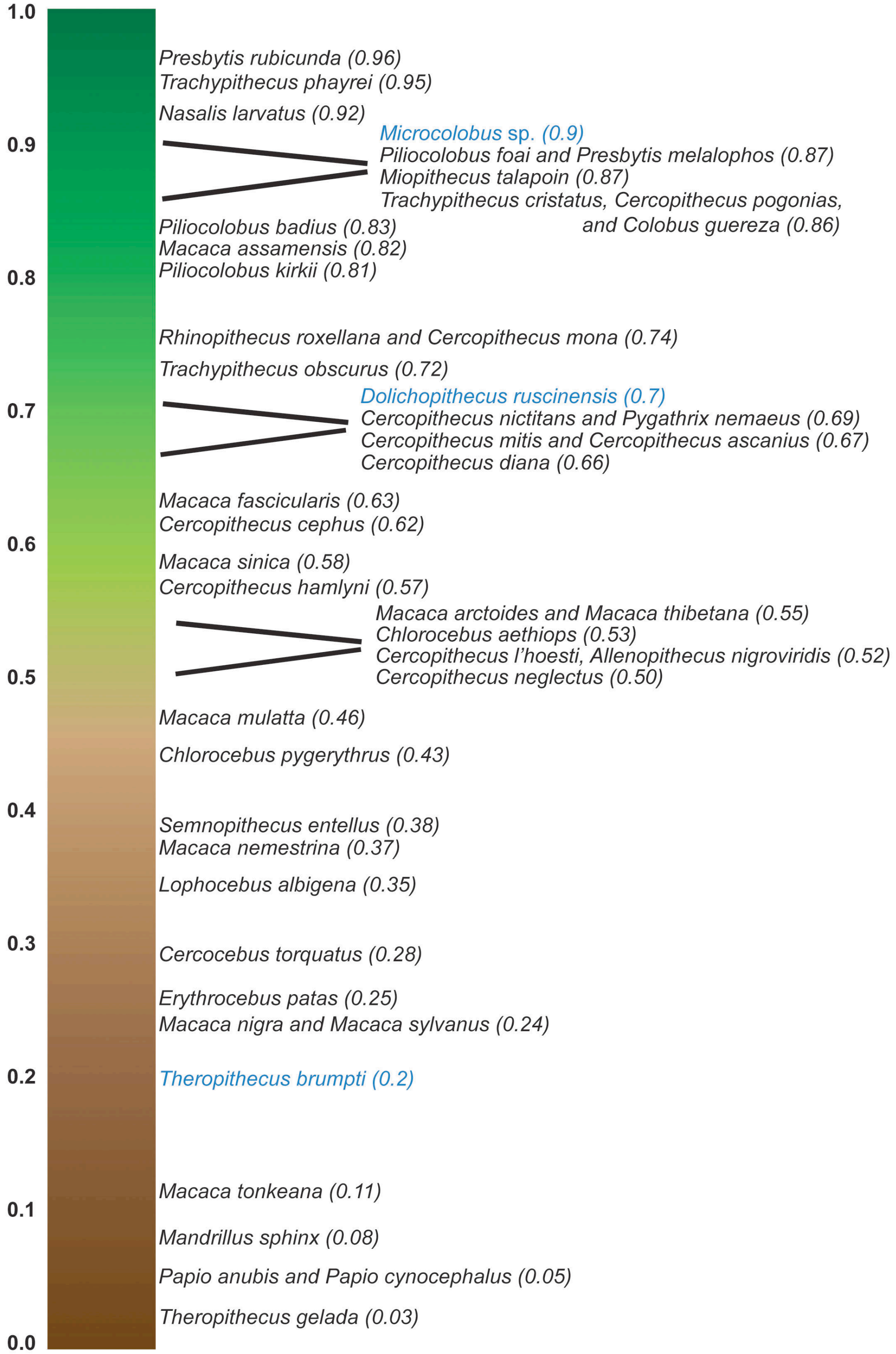


Figure 3.10. Distal humerus of extant cercopithecoids in distal view. Scale bar is 5 mm.

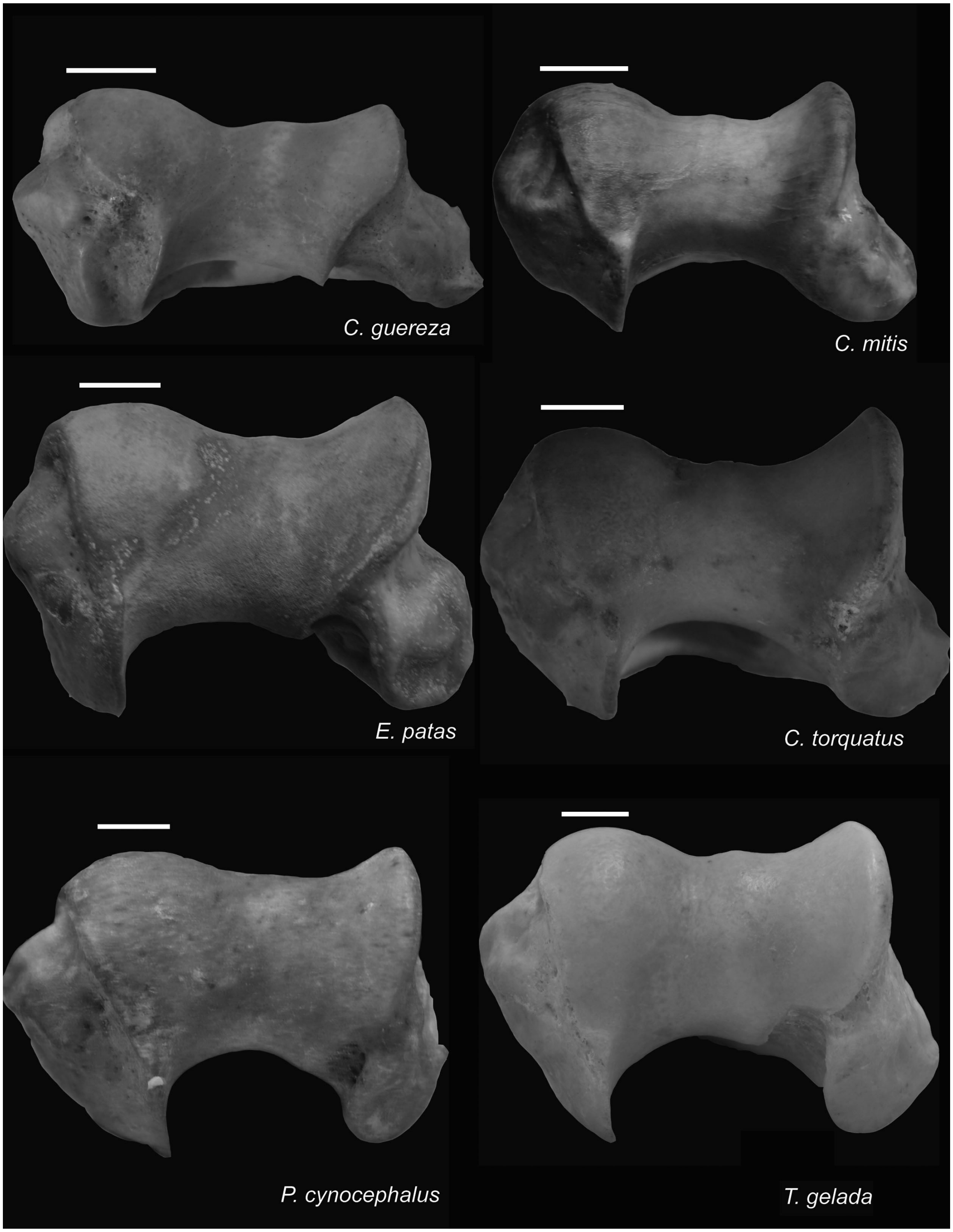


Figure 3.11. Proximal humerus of extant cercopithecoids in lateral view. Scale bar is 5 mm.

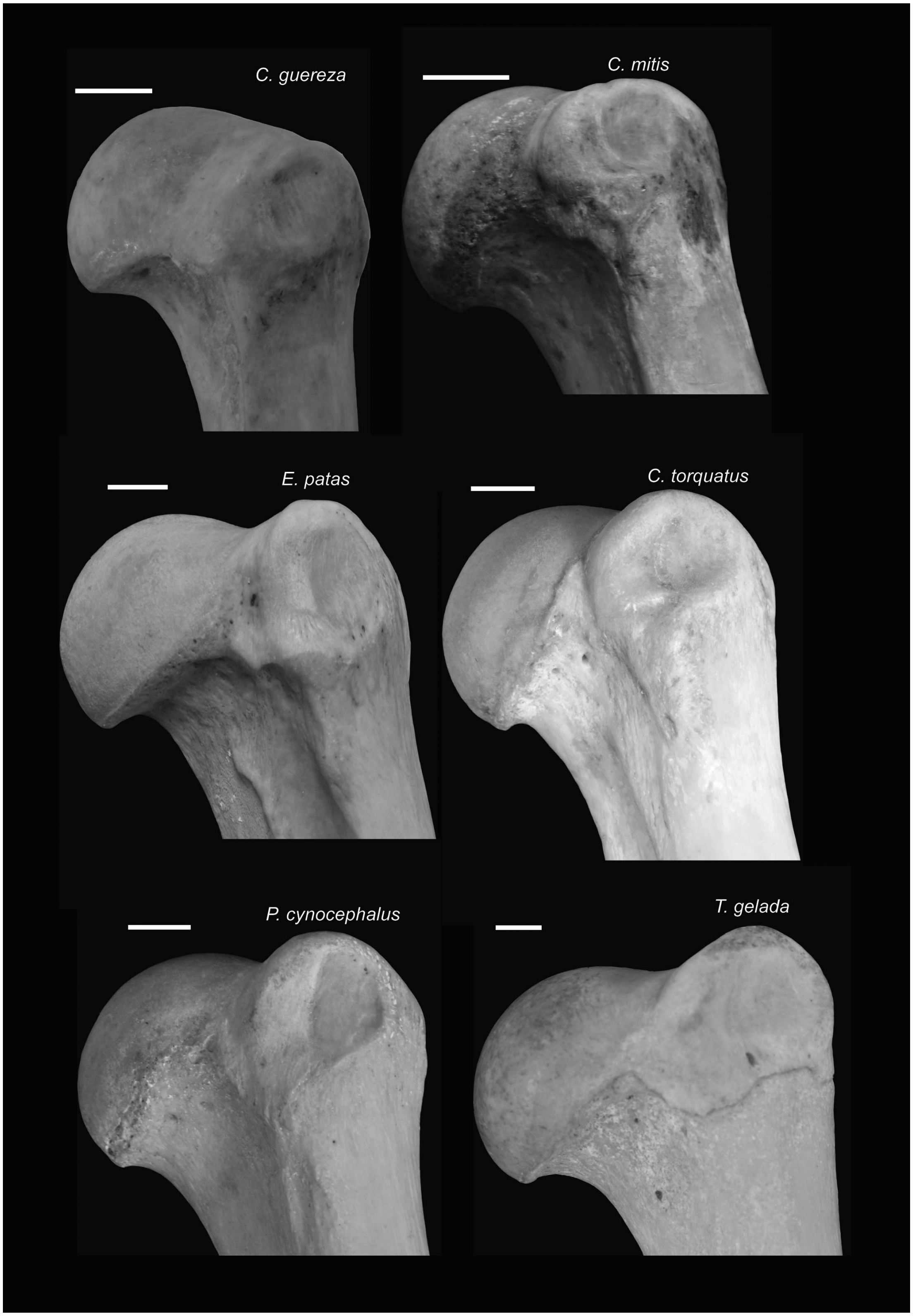


Figure 3.12. Humerus of *Victoriapithecus* in lateral and distal view. Scale bar is 5 mm.

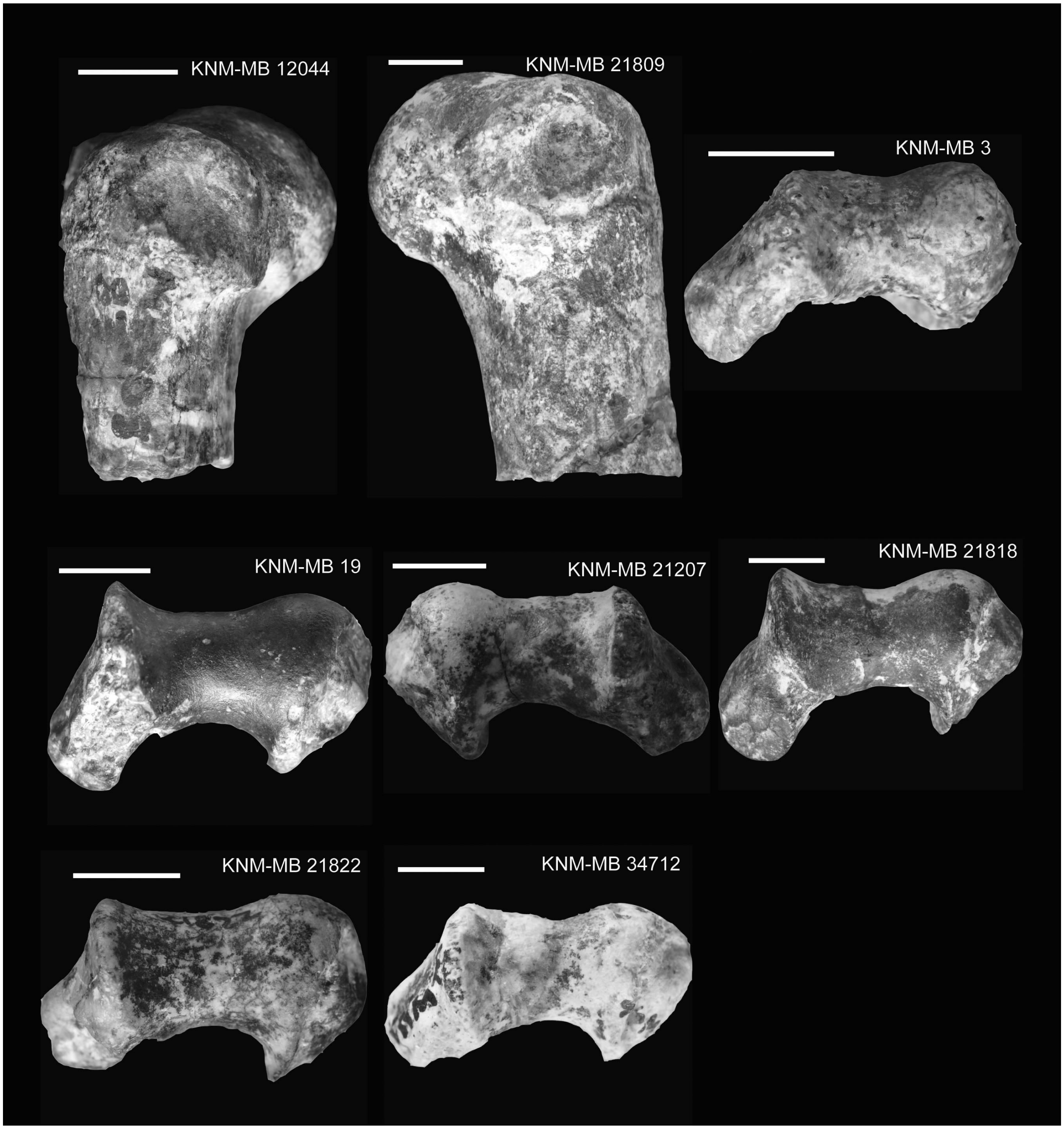


Figure 3.13. Humerus of *Microcolobus, Kuseracolobus,* and *Paracolobus* in distal view and lateral view. Scale bar is 5 mm.

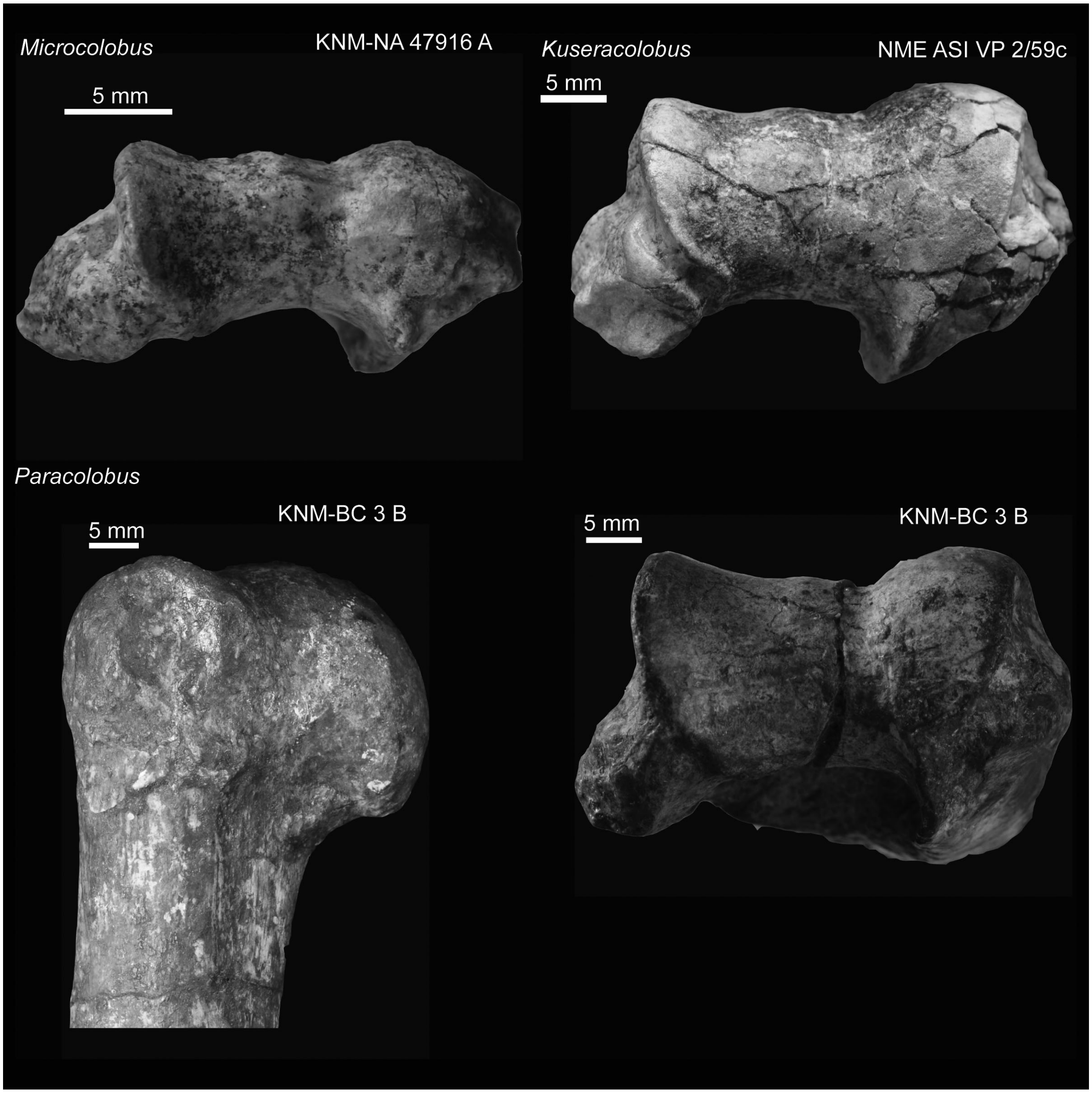


Figure 3.14. Humerus of *Rhinocolobus* in distal view and lateral view. Scale bar is 5 mm.

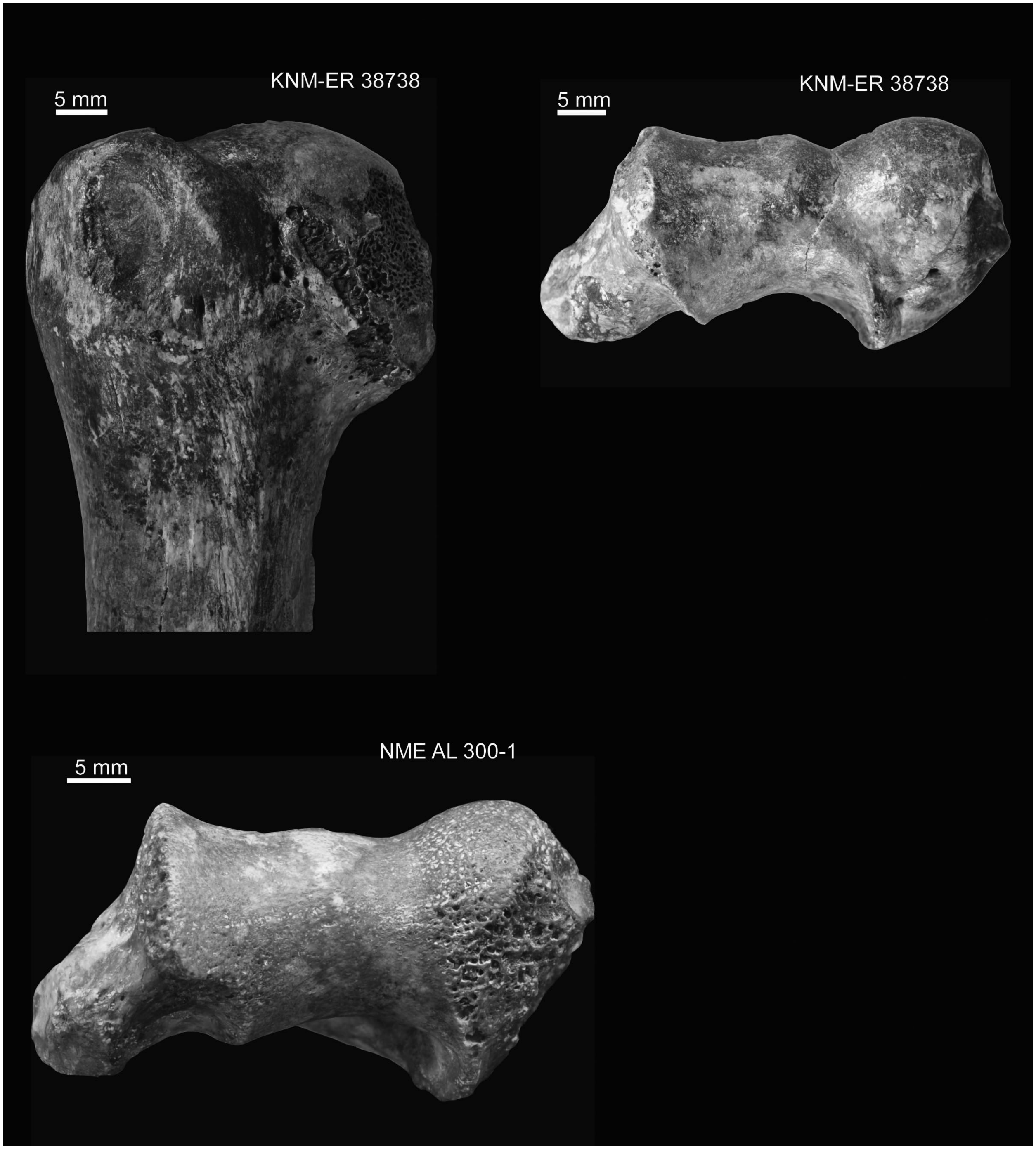


Figure 3.15. Humerus of *Cercopithecoides* in lateral and distal view. Scale bar is 5 mm.

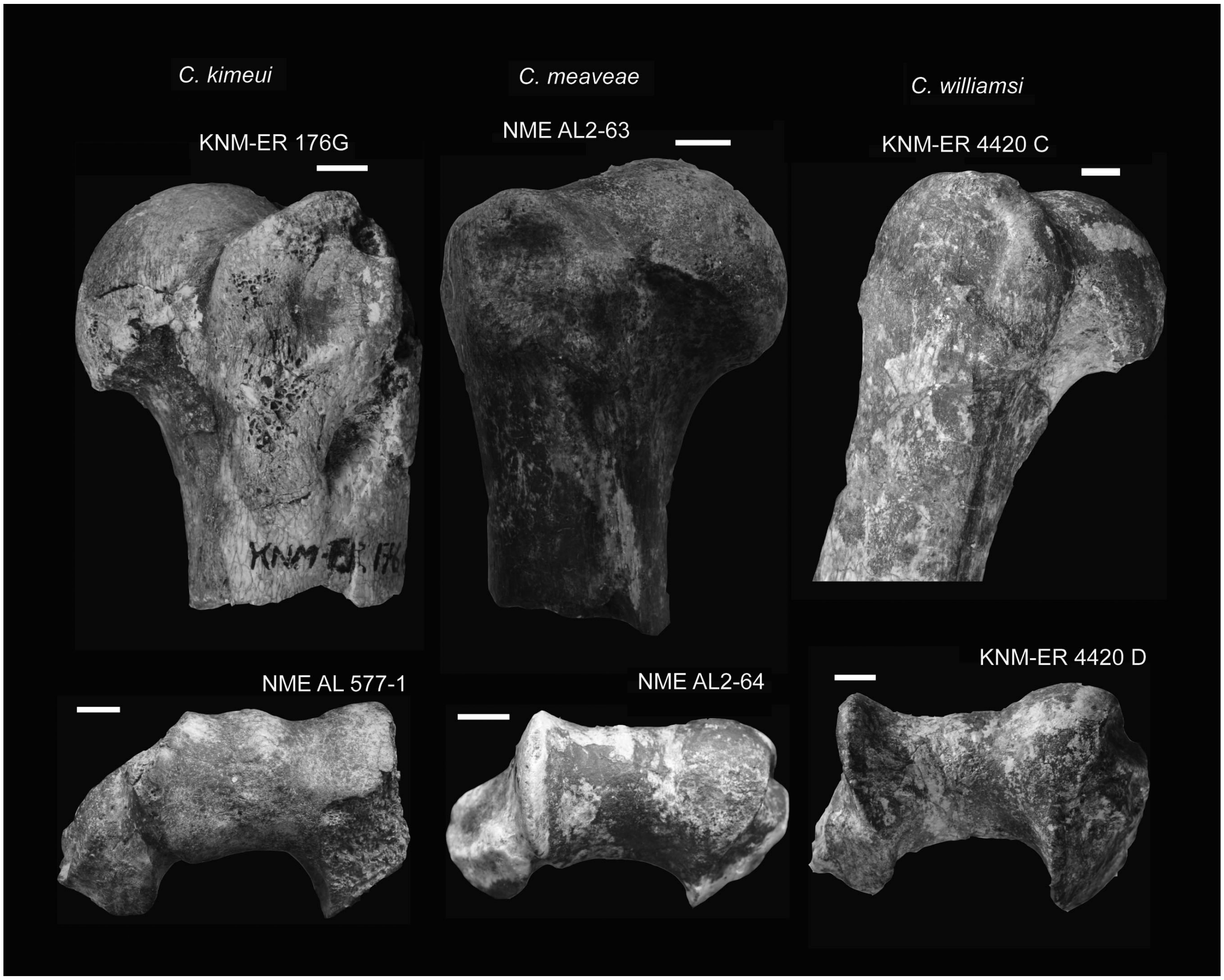


Figure 3.16. Humerus of *Parapapio jonesi* and *Parapapio lothagamensis* in lateral and distal view. Scale bar is 5 mm.

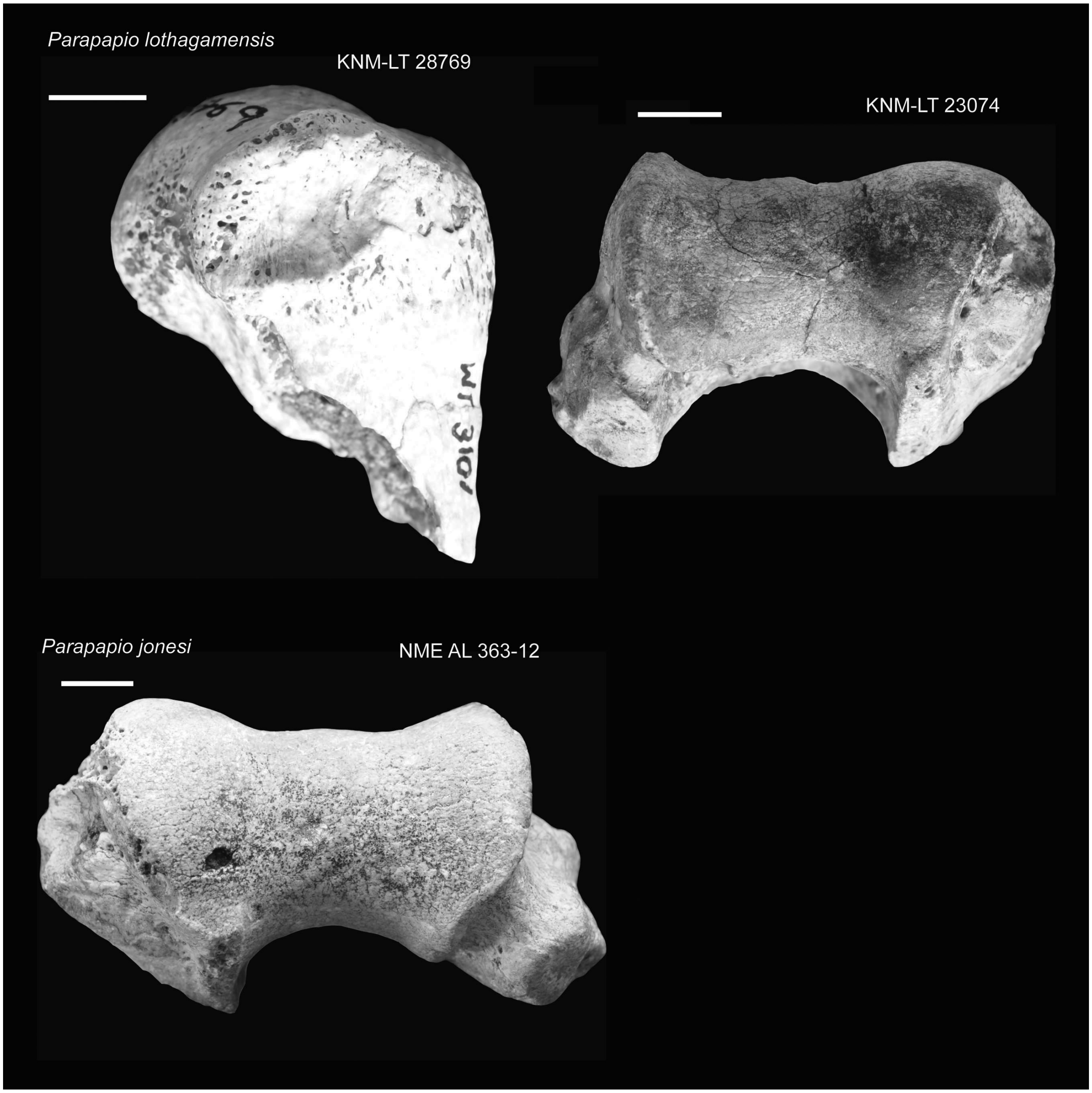


Figure 3.17. Humerus of *Theropitheus brumpti* in lateral and distal view. Scale bar is 5 mm.

Figure 3.18. Humerus of *Theropithecus oswaldi* in lateral and distal view. Scale bar is 5 mm.

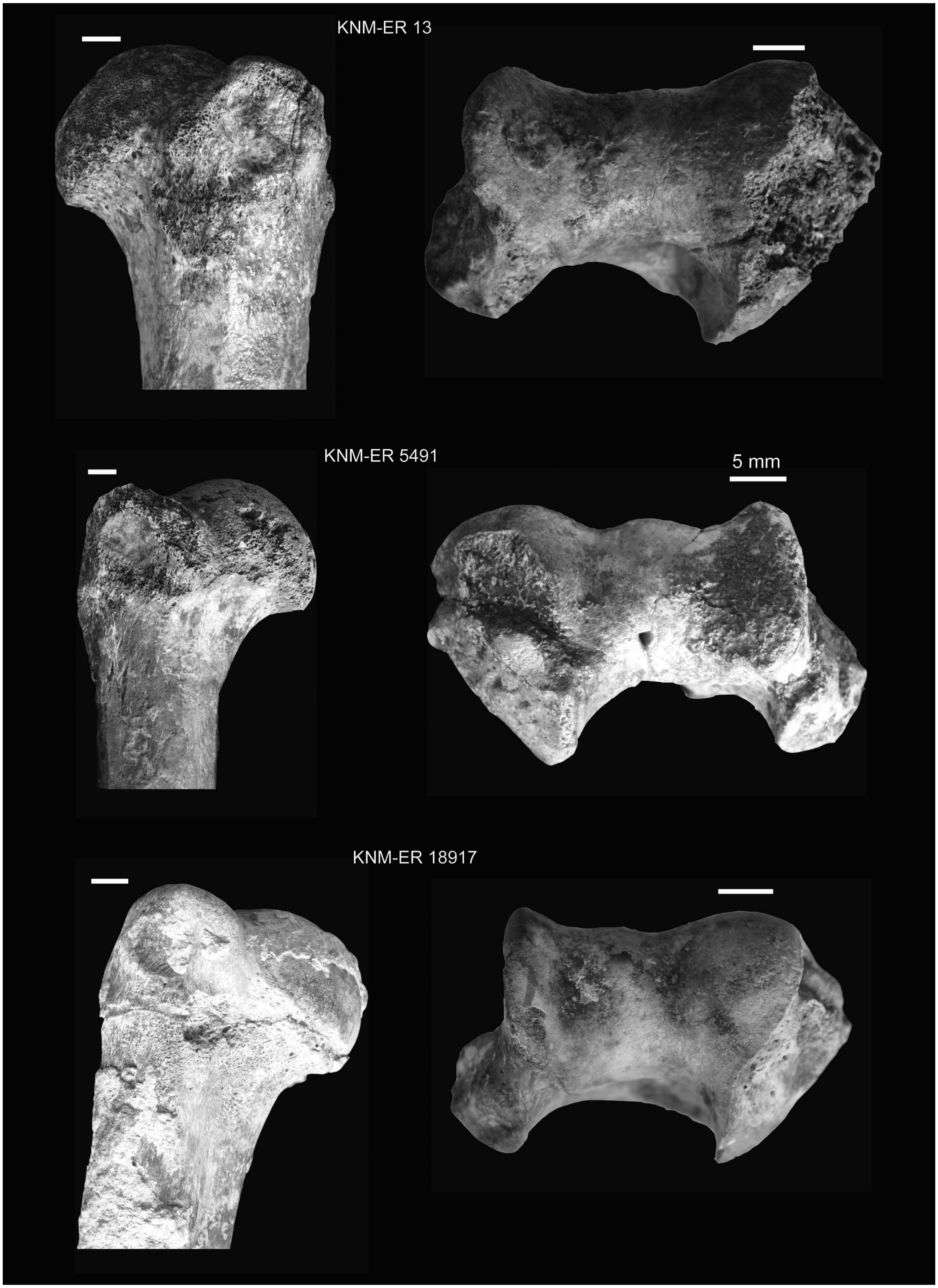
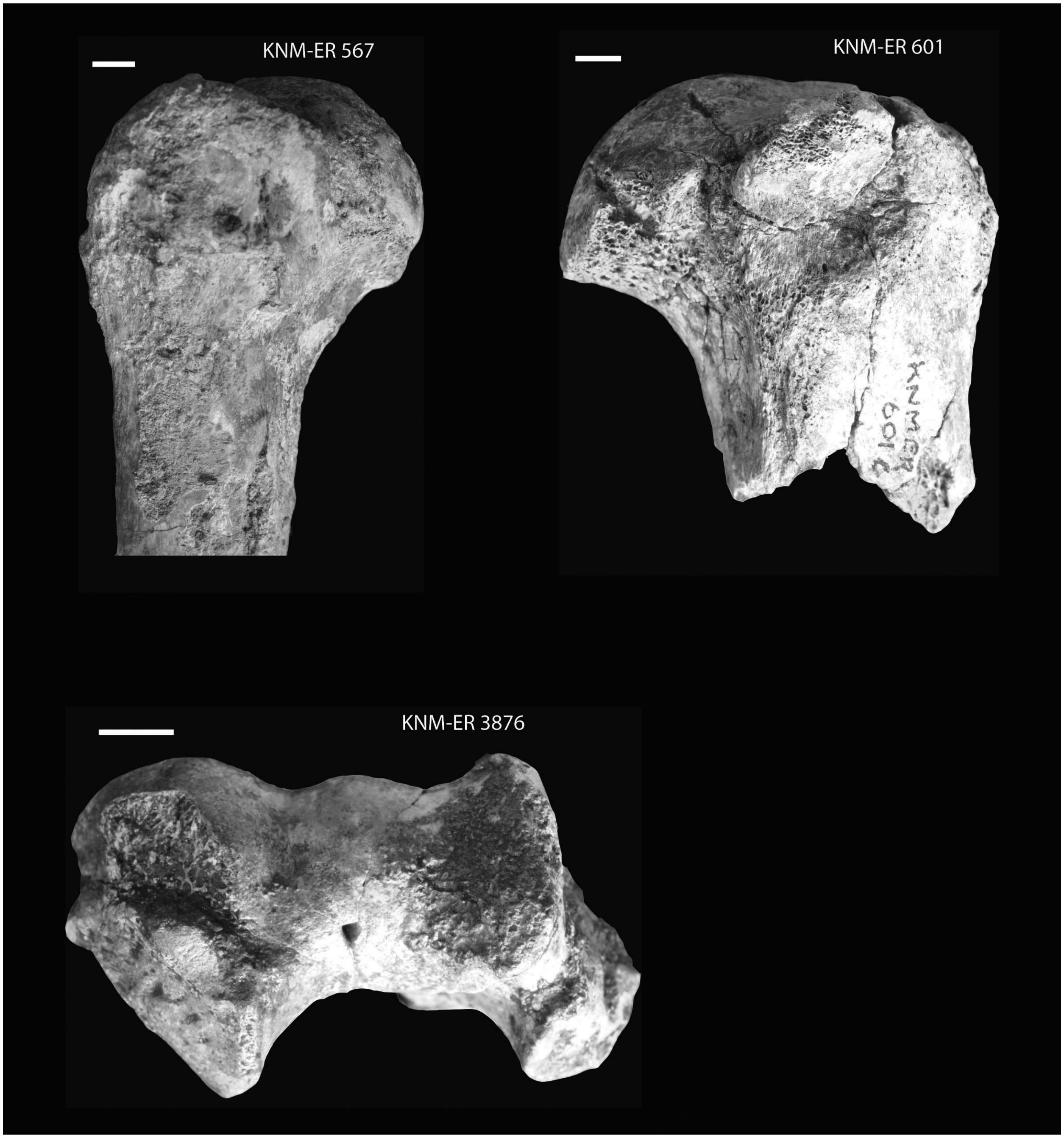


Figure 3.18 continued.



Chapter 4
Ancestral State Reconstructions of Locomotor Preference in Cercopithecoids with Implications for the Evolution of Terrestriality

4.1: Introduction

Previous work on cercopithecoid locomotor evolution has sought to determine the substrate preferences of the last common ancestor (LCA) of crown cercopithecoids and crown colobines through the study of fossil species that are considered to be closely related to the origin of the crown groups (Harrison 1989; Ciochon 1993; McCrossin et al. 1998; Hlusko 2007; Hlusko 2006; Nakatsukasa et al. 2010). Since the discovery of a fossil specimen that represents the LCA of the crown cercopithecoid or crown colobine group is highly unlikely – and impossible to confirm as such – the current hypotheses for the locomotor adaptations of these LCAs have been based largely on the fossil taxa *Victoriapithecus macinnesi* and *Microcolobus tugenensis*. Two hypotheses for the evolution of terrestriality in cercopithecoids are currently suggested: 1) the LCA of cercopithecoids was partly terrestrial, and dedicated arboreality evolved convergently multiple times during this group's evolution (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003) and 2) that the LCA of colobines was arboreal and that terrestriality evolved independently in this group during the Plio-Pleistocene (Hlusko 2007; Hlusko 2006; Gilbert et al. 2010; Nakatsukasa et al. 2010). These two hypotheses are not necessarily mutually exclusive but do contradict each other in some important ways.

First, Leakey et al. (2003) suggest that because the earliest colobines (at the time of their study), such as *Mesopithecus*, are considered to have adaptations for terrestrial behavior and that the LCA of cercopithecoids was mostly likely to have engaged in terrestrial behavior based on the morphology of *Victoriapithecus*, then arboreality evolved late in colobine evolution. Additionally, they suggest that arboreality likely evolved in parallel within Colobinae because the split of African and Asian colobines predates the first evidence of arboreality, which occurs in the late Pliocene with the fossils *Paracolobus* and *Rhinocolobus* (Leakey 1982). The more recent fossil discoveries of *Microcolobus* (Nakatsukasa et al. 2010), *Kuseracolobus* (Hlusko 2006), and some postcranial material attributed to Colobinae with genus and species indeterminate (Hlusko 2007; Gilbert et al. 2010), document adaptations for arboreality prior to the late Pliocene. These fossils provide evidence that the LCA of colobine was arboreal, and weaken the hypothesis that arboreality evolved in parallel in the group.

Second, the discovery of these early, and probably arboreal, colobines casts some doubt on the reconstruction of a terrestrial or even semi-terrestrial LCA for crown cercopithecoids. It is possible that the LCA of crown cercopithecoids was terrestrial and that arboreality re-evolved in stem colobines. However, another possible evolutionary scenario is that while the side-branch leading to *Victoriapithecus* evolved adaptations for terrestriality, the lineage that ultimately led to the LCA of crown cercopithecoids remained dedicated to an arboreal existence.

The previous chapter used fossil reconstruction methods to address these competing/alternative hypotheses of early cercopithecoid locomotor evolution. Based on fossil reconstructions of the humerus, astragalus, and calcaneus of *Victoriapithecus*, this species was likely to have been more adept in arboreal settings than has been previously suggested (McCrossin et al. 1998; Benefit 1999a). However, the reconstructions also suggested that *Victoriapithecus* exhibited a few adaptations for terrestrial behavior, most notably in the relatively dorsal orientation of the medial epicondyle. The previous chapter supported reconstructions of *Microcolobus* as having been primarily arboreal. The chapter concluded that while the LCA of crown cercopithecoids may have engaged in a modest amount of terrestrial behavior, the body plan of this ancestor was probably not sufficiently reorganized as to make a primarily arboreal lifestyle at the the crown colobine node unlikely.

This chapter seeks to further document changes in locomotor behavior over the course of cercopithecoid evolution using ancestral state reconstruction (ASR) methods. ASR methods employ an algorithm to estimate the most likely character state of an internal node based on data from terminal taxa, which can include both extant and fossil species, from a known phylogeny (for a review see Pagel 1999a). Previously, these methods would have been unsuitable for cercopithecoids because of the high degree of phylogenetic uncertainty in this group. Over the last decade, several molecular supermatrices examining primate diversification have presented a consistent picture of a monophyletic Colobinae and Cercopithecinae with well-resolved relationships among subclades (e.g., Fabre et al. 2009; Perelman et al. 2011; Springer et al. 2012).

Maximum square change parsimony was the earliest and most frequently used method for ASR, but more complex approaches using maximum likelihood and Bayesian inferences have been developed (Hansen and Martins 1996; Martins and Hansen 1997; Pagel 1997; Schluter et al. 1997; Pagel 1999b; Pagel 1999a; Nunn 2011). A maximum likelihood approach was used recently by Jones (2008) to determine the most likely locomotor mode of the LCA of atelines. In addition to estimating character states of internal nodes, mapping a morphological variable along a phylogeny makes it is possible to study to evolution of a trait through time and across different lineages, which has recently been applied to primates (Jones 2008; Boyer and Seiffert 2013; Boyer et al. 2013).

The goal of this chapter is to study the character evolution of morphological features shown in Chapter 2 to be associated with locomotor behavior using a Bayesian ASR method to both reconstruct the most likely locomotor mode of the LCA of crown cercopithecoids and other important crown groups within cercopithecoids. This chapter also examines the character state evolution of the morphological features under study to understand how these features have evolved in the cercopithecoid lineage. Finally, this chapter seeks to understand how different phylogenetic topologies effects ASR results, specifically examining the effect of branch length of nodal reconstructions.

4.2: Methods

4.2.1: Phylogenies

Six different phylogenies of anthropoids were used for the ASR analyses. Although additional outgroups, such as strepsirhines or tarsiers, could have been added to ASR analyses, such taxonomic sampling was outside the scope of this dissertation. The first two phylogenies included only extant taxa but differed in the divergence ages of major crown groups. The first phylogeny was downloaded from the 10K Trees website (version 3, Arnold et al. 2010) and is the same tree that was used to run phylogenetic analyses of variance in Chapter 1. The 10K phylogeny used four clade constraints and node ages were inferred using mean molecular branch lengths and six fossil calibration points (see Table 3 of 10KTrees Documentations). This tree provides origins of crown Cercopithecoidea at about 21.5 mya, crown Catarrhini at about 30 mya, and crown Anthropoidea dated at about 50 mya. These dates suggest much earlier divergences than what is expected based on the primate fossil record (for a review see Hartwig 2002). The oldest known stem catarrhine, *Catopithecus*, is dated to about 34 Ma (Seiffert 2006), which suggests a 16 Ma ghost lineage. A second phylogeny was modified from Springer et al. (2012) because the divergences recovered are more consistent with the fossil record (specifically the tree reconstructed using auto-correlated rates and hard-bounded constraints, see (Springer et al. 2012)supplementary information). This phylogeny used 14 calibration points that were determined based on the oldest crown fossil of each clade and other methods (see Text S3 of Springer et al. 2012). This tree estimates divergences for crown Cercopithecoidea at 13.9 mya, crown Catarrhini at 25.09 mya, and crown Anthropoidea at 39.95 mya.

Aside from the differences in divergence times, the topologies of these trees were largely consistent, with just five differences in the placement of tip taxa (Figure 4.1). First, in the 10K phylogeny, *Allenopithecus* and *Miopithecus* are consecutive sister taxa of other guenons, whereas in the Springer et al. phylogeny *Allenopithecus* and *Miopithecus* are sister-taxa, and together are the sister clade of other crown cercopithecins. Second, in the 10K phylogeny *Cercopithecus diana* is the sister taxon of *Cercopithecus neglectus*, but in the Springer et al. phylogeny *Cercopithecus diana* is the sister taxon of a clade that includes *C. nictitans*, *C. mitis*, *C. ascanius*, and *C. cephus*. Third, in the 10K phylogeny *Macaca assamensis* and *Macaca thibetana* are relatively distantly related among the macaques but these species are sister taxa in the Springer et al. phylogeny. Fourth, in the 10K phylogeny, *Papio* is the outgroup to *Theropithecus* and *Lophocebus*, but in the Springer et al. phylogeny *Theropithecus* is the outgroup to *Papio* and *Lophocebus*. Guevara and Steiper (in press) support the Springer et al. topology but they suggest that hybridization among these lineages early in their evolution make the resolution of this clade difficult. Finally, in the 10K tree, *Trachypithecus phayrei* is the sister taxon of *Trachypithecus cristatus* and *Trachypithecus obscurus* but the Springer et al. phylogeny has *Trachypithecus cristatus* as the sister taxon of the other *Trachypithecus* species. Given the overall similarity of the placement of tip taxa, it seems unlikely these inconsistencies would have a great effect on ancestral state reconstructions.

The remaining four phylogenies are modified versions of the phylogenies just discussed. Both phylogenies were modified to include a combination of two fossil species (*Victoriapithecus macinnesi* and *Parapapio lothagamensis*) and eight fossil species (*Apidium phiomense*, *Aegyptopithecus zeuxis*, *Proconsul africanus*, *Victoriapithecus macinnesi*, *Microcolobus* sp., *Parapapio lothagamensis*, *Theropithecus brumpti*, and *Theropithecus oswaldi*). Placement of fossil species in the phylogenies follows Boyer et al. (2013; 2013) in which lineages are placed 1 mya prior to the crown node. Although other methods for adding fossils to phylogenies are possible, (for midnode placement see Steiper and Seiffert 2012), the method chosen here provides a reasonable estimate for fossil branch lengths. Further, the effect of branch lengths on ASR will be tested in the study since the 10K phylogeny and the Springer et al. phylogeny differ in the timing of divergences of crown nodes. Therefore, this study will evaluate the relative importance of the length of fossil branches. Phylogenetic position of fossils is as follows: *Apidium* – stem anthropoid (for a review see Seiffert 2012), *Aegyptopithecus* – stem catarrhine (for a review see Seiffert, 2012), *Proconsul* – stem hominoid (Stevens et al. 2013), *Victoriapithecus* – stem cercopithecoid (Miller et al. 2009), *Microcolobus* – stem colobine (Rossie et al. 2013), *Parapapio* – stem papionin (Gilbert 2013), *Theropithecus oswaldi* and *Theropithecus brumpti* – sister to *Theropithecus gelada* (Gilbert 2013). The age of the locality from which the specific specimens included in the study came was used as the species age (Table

4.1). The branch length for each fossil was set so that the fossil lineage terminated at the species age.

Aegyptopithecus zeuxis could not be placed 1 Ma down from crown Catarrhini in the phylogeny modified from Springer et al. (2012) because crown Catarrhini is dated to 25.09 Ma and *Aegyptopithecus* is dated to 30.2 Ma. To solve this problem, the divergence between crown catarrhines and *Aegyptopithecus* was placed at 31.2 Ma and *Aegyptopithecus* was given a branch length of 1.0 Ma such that the lineage ends at 30.2 Ma (see Figure 4.2). *Theropithecus oswaldi* and *Theropithecus brumpti* also could not be placed 1 mya prior to the divergence of the *Theropithecus* lineage in the Springer et al. phylogeny. *Theropithecus* is estimated to have diverged at about 5.2 Ma in the 10K phylogeny and about 4.2 Ma in the Springer et al. phylogeny. Given that *Theropithecus brumpti* and *Theropithecus oswaldi* are dated to 3.3 and 2.2, respectively, the placement of these fossils 1 Ma prior to divergence of *Theropithecus* would place these fossils before the divergences of *Lophocebus* or *Lophocebus/Papio* from *Theropithecus* (topology differs between the two trees – see Figure 4.1). Therefore, a similar solution was used as in the case of *Aegyptopithecus*, except with 100 ky branch lengths. The divergence of *Theropithecus brumpti* and *Theropithecus gelada* was placed at 3.31 and the divergence of *Theropithecus oswaldi* was placed at 2.21. Each fossil was given a branch length of 100 ky (see Figure 4.2). The placement of *Theropithecus oswaldi* and *Theropithecus brumpti* in the 10K phylogeny was done in the same manner for consistency. A branch length of 100ky was chosen because the papionins have undergone rapid diversification since the Pliocene. All phylogenies used in the ASR analyses are listed in Appendix F.

Since changing branch length of a taxon changes its influence on nodal reconstructions, different protocols for placing fossil taxa in the phylogeny can be expected to change nodal reconstructions. Though the protocol used here for placement of fossil lineages is only one possible approach (see Steiper and Seiffert (2012) for another approach), the slight differences that result from such protocol differences is likely insignificant compared to the effect of uncertainty in divergence dates of major clades. The effect of uncertainty in branch lengths on nodal reconstructions will be tested in this chapter since branches lengths are longer in the 10K phylogenies and shorter in the Springer et al. phylogenies. Therefore, the results from this study will help resolve the relative importance of branch lengths in nodal reconstructions.

Several fossil crown colobines, including *Mesopithecus*, *Dolichopithecus, Paracolobus*, *Rhinocolobus*, *Cercopithecoides*, and *Kuseracolobus*, were not included in the ASR analyses. Currently the phylogenetic positions of these taxa are unknown with only *Mesopithecus* reported to have affinities with the Asian colobine group (Jablonski and Peng 1993; Jablonski 1998; Pan et al. 2004). Although multiple phylogenies with different topologies for the fossil colobines could have been created, I chose to exclude these fossils my ASR analyses because none of the hypotheses for the phylogenetic placement of these species have undergone a rigorous cladistic analyses. Without some degree of confidence in phylogenetic placement of these fossil taxa, their addition to the ASR analyses would result in a high degree of uncertainty in the nodal reconstructions. When the relationships between extant and fossil colobines are better resolved these species can be added to future ASR analyses to provide a better picture of the locomotor evolution within crown Colobinae.

4.2.2: Ancestral State Reconstruction Methods

ASR analyses were run in BayesTraits (Pagel 1999a), a package developed to study correlated trait evolution, associations between traits, and discrete and continuous character state evolution. BayesTraits uses a Markov chain Monte Carlo (MCMC) method to create posterior probability distributions that can be sampled to determine model fit. The main difference between Bayesian inference and Maximum Likelihood estimation is how model fit is determined. In classical probability statistics and Maximum Likelihood estimation, the observed data are considered to be random and the parameters that may explain the data are fixed. The goal is to determine how well the data fit the parameters and choose the model with highest likelihood. In Bayesian inference, because the data are *observed*, they are considered fixed, and the parameters are considered random. The best model under Bayesian is the one in which the parameters best fit the data (for a review see Lynch 2007). Additionally, while Maximum Likelihood provides a point estimate of likelihood (i.e., a single probability), Bayesian inference using MCMC provides a posterior probability distribution that models the uncertainty given the data and the parameters (Lynch 2007).

Four models of character evolution were evaluated to determine the best model of evolution for each variable under study, given a specified phylogeny. Model A is a random walk equivalent to Brownian motion, in which changes in the trait under study are directly proportional to phylogenetic distance from the root. Under random walk, more change will occur on longer branches than shorter branches and this change is not influenced by previous changes or changes along any other branches (Pagel 1997; Pagel 1999b; Nunn 2011). Model B is a directional model, which tests if a correlation between the trait under study and the distance between the root and different tips exists. Under the directional model, tips with a shorter distance from the root (extinct lineages in the case of this study) have consistently larger, or smaller, trait values than tips with a longer distance from the root (i.e., extant species). Essentially, trait values should consistently increase, or decrease, as distance from the root increases and larger changes in trait values should be seen in tip with the longest branch lengths (Pagel 1997; Pagel 1999b; Freckleton et al. 2002; Nunn 2011). Model B cannot be used on ultrametric trees (i.e., lineages of extant taxa are measured in absolute time and branches all end at the "top" of the phylogeny) because there needs to be variation in branch length to test for correlation. Therefore, Model B was used only for the phylogenies with added fossil taxa.

In addition, a tree transformation, lambda, was added to both Model A and Model B to determine if an additional parameter increased model fit. Lambda measures the covariation of the trait under study in relation to the shared evolutionary history of species along a phylogeny (Pagel 1997; Pagel 1999b; Freckleton et al. 2002; Nunn 2011). When lambda = 0, there is no correlation between phylogeny and the trait under study, and the phylogeny can be hypothetically thought of as a "star-phylogeny" in which all branches emanate from the root. When lambda = 1, the trait under study is directly correlated with phylogenetic relatedness among species. The value of lambda (varying from 0 to 1) can then be used to scale the variance-covariance matrix, which transforms branch lengths in the phylogeny such that they represent the amount of evolutionary change that has occurred (Pagel 1997; Pagel 1999b; Freckleton et al. 2002; Nunn 2011) This scaling occurs in the off-diagonals of the variance-covariance matrix, which represent the *expected* covariance between any two observations (e.g., species). The off-diagonals can be thought of as the shared evolutionary history of any two given species in the trait under study (Nunn 2011). If lambda = 1, then the *expected* covariance (off-diagonals) is consistent with a pure Brownian motion model and no scaling is needed. If lambda > 1, then the *expected* covariance is suggesting a greater amount of shared history between any pair of species than the observed relationship between the trait and relatedness of species. In this case, lambda is used to scale the off-diagonals to more accurately represent the amount of share evolutionary history between any pair of species (Nunn 2011).

When using extant-only phylogenies, variables were tested using Model A and Model A plus lambda. When using phylogenies with added taxa, variables were tested using Model A, Model A plus lambda, Model B, and Model B plus lambda. Bayes Factors tests were used to determine the best model with the fewest added parameters. To obtain models, each variable was run for a total of 10,000,000 iterations with a burn-in period of 50,000 iterations (i.e. the first 50,000 iterations were ignored). Following the burn-in period, iterations were sampled every 1000 to avoid autocorrelation. A Bayes Factor test was used (see BayesTraits Documentation) to determine which model (i.e. Model A, Model A plus lambda, Model B, or Model B plus lambda) best fit the data for each combination of variables and phylogenies.

Model A (i.e. random walk) was the best model for all variables across all phylogenies. Following model fit, 30 nodes were reconstructed along the phylogeny (Table 4.2, Figure 4.3) using a total run of 10,000,000 iterations with a burn-in period of 50,000 iterations and a sampling period of 1000 iterations. For each node reconstructed, the mean and 95% confidence intervals were calculated from the 9,950 estimates sampled during the analysis run.

Section 4.2.3: Variable Selection and Discriminant Function Analyses

The variables found to be associated with locomotor behavior in Chapter 1 were used in the ASR analyses. These include several variables from the humerus, distal humerus, astragalus, and calcaneus (Table 4.3). Following ASR analysis, each node was given a “phenotype” by combining each node’s reconstructions for all variables included. Nodal “phenotypes” where then entered into the DFAs from Chapter 2 as unknowns. These DFAs included 1) a three group *a priori* grouping with individuals assigned to the arboreal, semi-terrestrial, or terrestrial group, 2) a two group *a priori* grouping with “semi-terrestrialists” left as unknown, and 3) a two group *a priori* grouping with “semi-terrestrialists” included in the terrestrial group. Although several DFAs examining isolated elements were presented in the previous chapter, only DFAs using a combination of elements are used in this chapter - specifically, the DFA including the humerus, astragalus and calcaneus, and the DFA including the distal humerus and astragalus. Finally, character state changes in the variables with the highest loadings in the DFAs were examined. These variables include the humeral head index (HHI), height of greater tubercle (GTH), angle of the medial epicondyle (AME), overall length of the astragalus (AL), and ectal facet length (EL).

Section 4.2.4: Trait Evolution

Patterns of trait evolution were examined in the variables that had the highest loading on the DFAs, which include the humeral head index (HHI), height of the greater tubercle (GTH), angle of the medial epicondyle (AME), overall length of the astragalus (AL), and ectal facet length (EL). The reconstructed character states of seventeen nodes were plotted to investigate how morphological features changed through time along different lineages. The seventeen nodes include crown Anthropoidea, crown Platyrrhini, crown Catarrhini, crown Hominoidea, crown Cercopithecoidea, crown Colobinae, crown Colobini (referred to in the chapter as the African colobines), crown Presbytini (referred to in the chapter as the Asian colobines), crown

Cercopithecinae, crown Cercopithecini, Crown Papionini, crown Papionina, and crown *Macaca*. The remaining two nodes are Node 15, which includes the divergences of *Erythrcebus*, *Chlorocebus,* and *Allochrocebus lhoesti* (referred to in the chapter as the "terrestrial" guenons) and Node 16, the last common ancestor of the *Cercopithecus* genus (referred to in the chapter as the "arboreal" guenons). Although the character states of crown Platyrrhini and crown Hominoidea are presented, these data are only meant to provide a context for interpreting crown Catarrhini and crown Anthropoidea and are not meant to provide reconstructions of locomotor behavior for these groups.

4.3: Results from ASR using extant-only phylogenies

4.3.1: Results from DFAs using a combination of the humerus, astragalus, and calcaneus

The nodal reconstructions for the 10K phylogeny and the Springer et al. phylogenies are generally consistent across all analyses and are listed in Tables 4.4a-c. Crown Anthropoidea, crown Catarrhini, crown Cercopithecoidea, and crown Colobinae are classified as arboreal by all sets of analyses. Crown Cercopithecinae and Crown Cercopithecini are about equally likely to be classified as arboreal or semi-terrestrial in the DFA using three groups *a priori*. These nodes are classified as arboreal when using two groups *a priori* with "semi-terrestrialists" as unknown and are about equally likely to be placed either in the arboreal or in the terrestrial group when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

Crown Papionini, crown *Macaca*, and crown Papionina are classified as semi-terrestrial by the DFAs using three groups *a priori*. These nodes are classified as arboreal by the DFAs with two groups *a priori* with "semi-terrestrialists" as unknown, although crown Papionina is equally likely to be classified as arboreal or terrestrial using the Springer et al. phylogeny. These nodes are classified as terrestrial by the DFAs with two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

All nodes within crown Colobinae (Nodes 5-10) are reconstructed as arboreal by all analyses. Within crown Cercopithecini, Nodes 13 – 15 are about equally likely to be placed in either the arboreal or semi-terrestrial group using the DFAs with three groups *a priori*. These nodes include all guenons except *Allenopithecus* (Node 13), all guenons except *Allenopithecus* and *Miopithecus* (Node 14), and the "terrestrial" guenons (Node 15), which include *Chlorocebus*, *Erythrocebus*, and *Allochrocebus lhoesti*. Nodes 16 – 18, which include the divergences among the *Cercopithecus* genus, are more confidently placed in the arboreal group with posterior probabilities above 0.68. All nodes within crown Cercopithecini are placed in the arboreal group with high posterior probabilities when using the DFAs with two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 13 – 15 are about equally likely to be placed in either the arboreal or terrestrial group and Nodes 16 – 18 are classified as arboreal using the DFAs with two groups *a priori* and "semi-terrestrialists" included in the terrestrial group.

All nodes within crown Papionini (Nodes 21 – 28) are classified as semi-terrestrial by the DFAs using three groups *a priori*. In the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown, Nodes 21 and 22, which include the divergences of the Papionina are classified as terrestrial. All nodes with crown *Macaca* (Nodes 24 – 28) are classified as arboreal. All nodes within crown Papionini (Nodes 21 – 28) are classified as terrestrial when using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. But, Node 25 under the Springer et al. phylogeny and Node 28 under the 10K phylogeny are about equally likely to be classified as arboreal or terrestrial.

4.3.2: Results from DFAs using a combination of the distal humerus and astragalus

The nodal reconstructions for the 10K phylogeny and the Springer et al. phylogenies are generally consistent across all analyses are listed in Tables 4.5a-c. Crown Catarrhini, crown Cercopithecoidea, crown Colobinae, and crown Cercopithecini (guenons) are classified as arboreal by all analyses. However, crown Cercopithecini is placed in the arboreal group with a relatively low posterior probability (0.6 with the 10K phylogeny and 0.63 with the Springer et al. phylogeny). Crown Anthropoidea is classified as terrestrial by all but one analysis, which is an unexpected result. Crown Anthropoidea is classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group when using the Springer et al. phylogeny.

Crown Cercopithecinae is about equally likely to be classified as arboreal or semi-terrestrial by the DFAs using three groups *a priori*. This node is classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" treated as unknown. Crown Cercopithecinae is about equally like to be classified as aboreal or terrestrial by the DFA using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

Crown Papionini and crown Papionin are classified as semi-terrestrial by the DFAs using three groups *a priori*. The posterior probability for crown Papionini is low at about 0.59 for both the 10K or Springer et al. phylogenies but there is more confidence in the assigment of crown Papionina with a posterior probability of 0.67 and 0.7 for the 10K and Springer et al. phylogenies, respectively. Crown *Macaca* is equally likely to be placed in the arboreal or semi-terrestrial group. These nodes are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown, although crown Papionina is classified with relatively low posterior probability of 0.66 by the Springer et al. phylogeny. These nodes are classified as terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. However, the 10K phylogeny produces relatively low posterior probabilities for crown Papionini (0.67) and crown *Macaca* (0.61).

All nodes within crown Colobinae (Nodes 5 – 10) are classified as arboreal. Within crown Cercopithecini, Nodes 13 – 15 are about equally likely to be classified as arboreal or semi-terrestrial by the DFAs using three groups *a priori*. Nodes 16 – 18 are more confidently assigned to the arboreal group but the posterior probabilities are still relatively low (~ 0.65). These nodes are classified as arboreal with high posterior probabilities by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 13 – 15 are about equally likely to be placed in the arboreal or terrestrial group by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terretrial group. Nodes 16 – 18 are assigned to the arboreal group, but the posterior probabilities are relatively low (~ 0.65).

Within crown Papionina, Node 21 (divergence of *Cercocebus* and *Mandrillus*) is classified to the semi-terrestrial group by the DFAs using three groups *a priori*. Node 22 (divergence of *Theropithecus-Lophocebus-Papio*) is also classified to the semi-terrestrial but with a relatively low posterior probability of 0.62. Node 21 is equally likely to be classified as arboreal or terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Node 22 is classified as terrestrial with a high posterior probability. Both nodes are classified as terrestrial with high posterior probabilities by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

All nodes within crown *Macaca* (Nodes 24 – 28) are equally likely to be classified as arboreal or terrestrial by the DFAs using three groups *a priori*. These nodes are classified as arboreal with high posterior probabilites by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 24 – 28 are classified as terrestrial with low posterior probabilities or are equally likely to be classified as arboreal or terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" in the terrestrial group.

Overall, the results from the analyses using either three or two elements are consistent. The 10K phylogeny and the Springer et al. phylogeny are also consistent within each set of analyses. Crown Catarrhini, crown Cercopithecoidea, and crown Colobinae are consistently classified as arboreal. Crown Anthropoidea is classified as arboreal by the analyses using three elements, but as terrestrial when using only two elements. Crown Cercopithecinae and crown Cercopithecini are about equally likely to be classified as arboreal or semi-terrestrial. Finally, crown Papionini, crown Papionina, and crown *Macaca* are generally classified as semi-terrestrial.

4.4: Results from ASR using phylogenies that include fossil taxa

4.4.1: Results from DFAs using two fossil taxa and a combination of the humerus, astragalus, and calcaneus

The nodal reconstructions for the 10K phylogeny and the Springer et al. phylogenies with two added fossils are generally consistent in all three sets of analyses, and are listed in Tables 4.6a-c. Crown Anthropoidea, crown Catarrhini, crown Cercopithecoidea, and crown Colobinae are classified as arboreal in all sets of analyses.

Crown Cercopithecinae and crown Cercopithecini are about equally likely to be placed in the arboreal or terrestrial group by the DFAs using three groups *a priori*. These nodes are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. These nodes are equally likely to be placed in the arboreal or terrestrial groups by the DFA using to group *a priori* with "semi-terrestrialists" included in the terrestrial group.

Papionini, crown *Macaca,* and crown Papionina are classified as semi-terrestrial by the DFAs using three groups *a priori*. These nodes are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown and as terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

All nodes within crown Colobinae (Nodes 5 – 10) are classified as arboreal by all sets of analyses. Within crown Cercopithecini, Nodes 13 – 15 are equally likely to be classified to the arboreal or semi-terrestrial group by the DFAs using three groups *a priori*. Nodes 16 – 18 are assigned to the arboreal with posterior probabilities ranging from 0.63 to 0.76. All nodes with crown Cercopithecini are assigned to the arboreal group by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 13 – 15 are equally likely to be classified as arboreal or terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. Nodes 16 – 18 are classified as arboreal with posterior probabilities above 0.67.

All nodes with crown Papionini (Nodes 21 -28) are classified as semi-terrestrial by the DFAs using three groups *a priori*. All nodes within crown *Macaca* (Nodes 24 – 28) are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknowns. Node 21 (divergence of *Cercocebus* and *Mandrillus*) and Node 22 (divergences of *Theropithecus-Lophocebus-Papio)* are classified as terrestrial, but Node 21 has a relatively low posterior probability when using the 10K phylogeny of 0.64). Most nodes within crown Papionini (Nodes 21 – 28) are classified as terrestrial with posteriori probabilites above 0.66 by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. Nodes 24 and 25 have classified with posterior probabilites of 0.63 and 0.59 by the Springer et al. phylogeny and Node 28 is classified with a posterior probability of 0.59 by the 10K phylogeny. Finally, the reconstructions from the ASR analyses using either an extant-only phylogeny or a phylogeny with two fossil taxa added are consistent across all sets of analyses.

4.4.2: Results from DFAs using eight fossil taxa and a combination of the distal humerus and astragalus

The nodal reconstructions for the 10K phylogeny and the Springer et al. phylogeny are generally consistent in all three sets of analyses and are listed in Tables 4.7a-c. Crown Anthropoidea, crown Catarrhini, crown Cercopithecoidea, and crown Colobinae, are classified as arboreal in all sets of analyses. Crown Cercopithecinae is equally likely to be classified to either the arboreal or semi-terrestrial group by the DFA using the 10K phylogeny and three groups *a priori*. Crown Cercopithecinae is assigned to the semi-terrestrial group with a higher posterior probability of 0.69 by the Springer et al. phylogeny. This node is classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Crown Cercopithecinae is equally likely to be assigned to either the arboreal or semi-terrestrial group by the 10K phylogeny and the terrestrial group by the Springer et al. phylogeny (posterior probability of 0.73) using the DFAs with two groups *a priori* and "semi-terrestrialists" included in the terrestrial group.

Crown Cercopithecini are equally likely to be classified as arboreal or semi-terrestrial by the DFAs using three groups *a priori*. This node is classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown, but as terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

Crown Papionini and crown Papionini are classified as semi-terrestrial by the DFAs using three groups *a priori* with posterior probabilities above 0.67. Crown *Macaca* is also classified as semi-terrestrial but the posterior probabilities are relatively lower (0.6 for the 10K phylogeny and 0.65 for the Springer et al. phylogeny). These nodes are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. All three nodes are classified as terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group but crown *Macaca* is classified with a relatively low posterior probability of 0.64 when using the 10K phylogeny.

All nodes within crown Colobinae (Nodes 5 – 10) are classified as arboreal by all sets of analyses. Within crown Cercopithecini, Nodes 13 – 15 are about equally likely to be classified as arboreal or semi-terrestrial by the DFAs using three groups *a priori*. Nodes 16 – 18 are classified to the arboreal group with posterior probabilities above 0.61. All nodes with crown Cercopithecini (13 – 18) are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 13 – 15 are equally likely to be placed in the arboreal or terrestrial group by the DFAs using two groups *a priori* with "semi-terrestrialists" placed in the terrestrial group. Nodes 16 – 18 are classified as arboreal with posterior probabilities above 0.6.

Both nodes with crown Papionina are classified as semi-terrestrial by the DFAs using three groups *a priori*. Both these nodes are about equally likely to be placed in the arboreal or terrestrial group by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. These nodes are classified as terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group.

Most nodes within crown *Macaca* (Nodes 24 – 28) are about equally likely to be placed in either the arboreal or semi-terrestrial group by the DFAs with three groups *a priori*. Node 27 (including the divergences of *M. tonkeana, M. nigra,* and *M. nemestrina*) is placed in the semi-terrestrial group with posterior probabilities of 0.67 (10K phylogeny) and 0.64 (Springer et al. phylogeny). All nodes within crown *Macaca* are classified as arboreal by the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown. Nodes 24 – 26 and 28 are equally likely to be classified as either arboreal or terrestrial by the DFAs using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group. Node 27 is classified as terrestrial with posterior probabilities of 0.73 (10K phylogeny) and 0.69 (Springer et al. phylogeny).

Overall, the results from the ASR analyses are consistent when using either an extant-only phylogeny or a phylogeny with fossil taxa added. The most significant difference is that crown Anthropoidea is classified as terrestrial by almost all analyses using extant only phylogenies. However, crown Anthropoidea is consistently classified as arboreal in the phylogenies with added fossils. Additionally, in the DFAs using two groups *a priori* with "semi-terrestrialists" as unknown, Node 22 (the divergences of *Theropithecus, Papio,* and *Lophocebus*) is classified as terrestrial by the extant-only phylogenies and as arboreal on the phylogenies that include fossil taxa. This result is surprising given the addition of *Theropithecus oswaldi* and *Theropithecus brumpti* to the phylogeny. However, because *Theropithecus brumpti* is more arboreal than modern *Theropithecus* and possibly modern *Papio*, Node 22 may have been classified as arboreal because of the combined evidence from *Lophocebus* and *Theropithecus brumpti.*

Section 4.5: Character State Evolution Results

Humeral Head Index (HHI)

From the original state at crown Anthropoidea, HHI decreases (i.e. the humeral head becomes increasing globular) at crown Platyrrhini (Figure 4.4) and increases (i.e., the humeral head becomes increasingly elliptical) at crown Catarrhini. In the extant only phylogenies, HHI retains a similar value at crown Hominoidea but slightly increases in phylgoenies with added fossil taxa. HHI increases at crown Cercopithecoidea from the crown catarrhine condition in all phylogenies. In the extant only phylogenies, HHI increases slightly at crown Colobinae but this increase in greater in the phylogenies with added fossil taxa. In all phylogenies, HHI increases at crown Cercopithecinae from its state at crown Cercopithecoidea. From crown Colobinae, HHI decreases at the Asian colobines and increases at the African colobines. HHI increases at crown Cercopithecini from crown Cercopithecinae and HHI continues to increase to the "terrestrial" guenons. In the extant only phylogenies, HHI decreases along the stem lineage of the "arboreal guenons" from its state at crown Cercopithecini. However, in the phylogenies with added fossil taxa "arboreal guenons" retain a similar state to that of crown Cercopitheicni. Crown Papionini has a small increase from the condition at crown Cercopithecinae. HHI continues to increase along the *Macaca* stem lineage. In the extant only phylogenies, HHI decreases at crown Papionina, but in the phylogenies with added fossils crown Papionina retains a similar state to crown Papionini. HHI increases from crown Papionina to the divergence between *Cercocebus* and *Mandrillus*, but decreases at the node representing the divergences of *Theropithecus*, *Lophocebus*, and *Papio*.

Height of the Greater Tubercle (GTH)

GTH increases (i.e., increasing height of the greater tubercle relative to the humeral head) from crown Anthropoidea to crown Platyrrhini and crown Catarrhini (Figure 4.5). GTH continues to independently increase from crown Catarrhini along the hominoid and cercopithecoid stem lineages. There is little change in GTH at crown Colobinae and both the African and Asian colobines have similar GTH values to crown Colobinae. In the extant only phylogenies, GTH increases from crown Cercopithecoidea to crown Cercopithecinae. However, in the phylogenies with added fossil taxa, GTH slightly decreases at crown Cercopithecinae from its state at crown Cercopithecoidea. In the extant only phylogenies, GTH decreases in crown Cercopithecini and the “arboreal” guenons retain a similar GTH value while “terrestrial” guenons have an increase in GTH. In the phylogenies with added fossils, GTH increases at crown Cercopithecini with increases continuing along the “arboreal” and “terrestrial” guenon lineages, although the increase is greater in the “terrestrial guenons.” GTH increases from crown Cercopithecinae to crown Papionini. In the extant only phylogenies, GTH decreases at crown *Macaca* and increases at crown Papionina. In the phylogenies with added fossils, GTH increases in both the *Macaca* and Papionini lineages. In the extant only phylogenies, GTH retains a similar value at the divergence of *Cercocebus* and *Mandrillus*, but increases in the phylogenies with added fossils. All phylogenies show increases in GTH at the node representing the divergences of *Theropithecus, Lophocebus*, and *Papio*.

Angle of the Medial Epicondyle (AME)

When comparing AME among the different phylogenies, differences in trait evolution exist for the earliest divergences. In the extant-only phylogenies and the phylogenies with two fossils added, AME decreases (i.e. epicondyle is more medially oriented) from crown Anthropoidea to crown Platyrrhini and crown Catarrhini, but the decrease is larger at crown Platyrrhini (Figure 4.6). AME decreases from crown Catarrhini to crown Hominoidea, but AME increases (i.e. epicondyle is more dorsally oriented) at crown Cercopithecoidea. In the phylogenies that include eight fossils, crown Platyrrhini retains the same value as crown Anthropoidea, but AME decreases at crown Catarrhini. AME increases independently in crown Hominoidea and crown Cercopithecoidea, although this increase is much larger for the latter group (Figure 4.6). It is interesting to note that although AME increases at the crown Cercopithecoid node from the trait value at crown Catarrhini, the crown Cercopithecoid node is still consistently classified as arboreal. This finding is consistent with those from Chapters 2 and 3, which document that a more dorsally directed medial epicondyle does not necessarily correlate with a high degree of terrestriality. It is possible that stem cercopithecoids were engaging in relatively more terrestrial behavior than stem catarrhines and therefore evolved a more dorsally directed medial epicondyle. However, as was seen in *Semnopithecus entellus* in Chapter 2 and

Victoriapithecus in Chapter 3, a relatively dorsally oriented medial epicondyle can be present in an generally arboreal species that engages in limited terrestrial behavior.

Patterns of trait evolution subsequent to crown Cercopithecoidea are similar across all phylogenies. AME decreases at crown Colobinae but this decrease is larger in the extant-only phylogenies. Asian colobines retain the same state as crown Colobinae but AME decreases in African colobines. AME increases at crown Cercopithecinae from its state at crown Cercopithecoidea. AME decreases slightly at crown Cercopithecini with "arboreal" guenons exhibiting a decrease in AME and "terrestrial" guenons exhibiting an increase in AME. AME increases from crown Cercopithecinae to crown Papionini and crown *Macaca* either retains a similar value (extant-only phylogenies) or shows decrease in AME (phylogenies with added fossils). AME increases from crown Papionini to crown Papionina but these increases are larger in the extant-only phylogenies. AME continues to increase at the *Cercocebus* and *Mandrillus* divergence in the extant only phylogenies but this divergence retains a similar state to crown Papionina in the phylogenies with added fossils. Increases in AME are seen at the node including the divergences of *Theropithecus*, *Lophocebus*, and *Papio*, in the extant only phylogenies and the phylogenies including two fossil taxa. However, AME decreases at this divergence in the phylogenies with 7 fossils added.

Length of the Astragalus (AL)

When comparing AL among the different phylogenies, differences in trait evolution exist for the earliest divergences. In the extant-only phylogenies and the phylogenies with two added fossils, crown Anthropoidea has a very low value for AL (i.e. a relatively short astragalus), and AL increases at both crown Platyrrhini and crown Catarrhini, although this increase is much larger for the platyrrhines (Figure 4.7). AL increases (extant only phylogeny) or decreases (phylogeny with two added fossils) from crown Catarrhini to crown Hominoidea. AL increases from crown Catarrhini to crown Cercopithecoidea. AL increases slightly from crown Cercopithecoidea to crown Cercopithecinae and crown Colobinae with both nodes having similar values. In the phylogenies with eight fossils added, crown Anthropoidea has a high value for AL (i.e., a relatively long astragalus) and AL increases at crown Platyrrhini. AL decreases at crown Catarrhini and continues to decrease at crown Hominoidea and crown Cercopithecoidea, but the decrease is much greater for the cercopithecoids (Figure 4.7). AL decreases at crown Colobinae and crown Cercopithecinae, but the decrease is slightly larger for the cercopithecines.

Changes in AL subsequent to the divergences of crown Cercopithecinae and crown Colobinae are similar across all phylogenies. From crown Colobinae, AL increases slightly at the African Colobines and decreases slightly for the Asian colobines. AL increases from crown Cercopithecinae to crown Cercopithecini and the "arboreal" guenons retain a similar value. AL increases the "terrestrial" guenons, which is an unexpected result given that a relatively shorter astragalus is associated with increasing terrestriality. Chapter 3 documented that *Erythrocebus patas* was assigned to the terrestrial group when using the humerus but to the arboreal group when using the astragalus. As was shown in the previous chapter, different regions of the postcranium are adapted for different functional demands (see also, Sargis et al. 2008) and it is possible that a relatively long astragalus may help "terrestrial" guenons maintain behavioral flexibity. AL decreases from crown Cercopithecinae to crown Papionini and crown *Macaca* retains a similar AL value. AL decreases slightly from crown Papionini to crown Papionina. The node including the divergences of *Theropithecus*, *Lophocebus*, and *Papio* retain a similar value but AL decreases at the divergence of *Cercocebus* and *Mandrillus*.

Length of the Ectal Facet (EL)

When comparing changes in EL differences exist among the earliest divergences. In the extant only phylogenies and the phylogenies with two added fossils, EL increases (i.e. the ectal facet becomes more tightly curved) from crown Anthropoidea to crown Platyrrhini and crown Catarrhini, but this increase is greater in the platyrrhines (Figure 4.8). EL increases from crown Catarrhini to crown Hominoidea, but decreases in Cercopithecoidea. In the phylogenies with eight fossils included, crown Anthropoidea has the highest EL value and EL decreases at both crown Playrrhini and crown Catarrhini. EL decreases from crown Catarrhini in both crown Hominoidea and crown Cercopithecoidea, but this decrease is larger for cercopithecoids.

EL slightly decreases at crown Colobinae from crown Cercopithecoidea in the extant only phylogenies, but increases in the phylogenies with added fossils, especially the when eight fossils are added. In the extant only phylogenies, EL increases in the African colobines and decreases in the Asian colobines. In the phylogenies with two added fossils, Asian colobines retain a similar state as crown Colobinae, but EL has a small increase at the African colobines. In the phylogenies with eight fossils added, African colobines retain a similar state to crown Colobinae, and EL decreases in the Asian colobine lineage. EL decreases from crown Cercopithecoidea to crown Cercopithecinae. In the extant-only phylogenies EL decreases slightly at crown Cercopithecini, but in the phylogenies with added fossil taxa crown Cercopithecini retains a similar value as crown Cercopithecinae. EL increases from crown Cercopithecini to the "arboreal" guenons and decreases at the "terrestrial" guenons. EL decreases from crown Cercopithecinae to crown Papionini, with a subsequent increase in EL in crown *Macaca* and a decrease along the Papionina stem lineage. EL decreases at the divergence between *Cercocebus* and *Mandrillus*. In the extant-only phylogenies and the phylogenies with two added fossils, the node including the divergence between *Theropithecus*, *Lophocebus*, and *Papio* retains a similar value to crown Papioninia. EL has a large decrease at this node relative to crown Papionina in the phylogeny with eight added fossils.

Section 4.6: Confidence Intervals of ASR analyses

The previous discussion of classifications for ancestral nodes and character trait evolution is based on the mean value for each node estimated by the ASR analyses. However, previous work has documented that the confidence intervals (CIs) surrounding the means from ASR analyses are generally so wide that they often exceed the variation exhibited by the tip data (Schluter et al. 1997; Garland et al. 1999; Oakley and Cunningham 2000; Polly 2001; Webster and Purvis 2002). Wide CIs are problematic because the node of interest can often be classified into more than one *a-priori* group, making the utility of ASR method problematic.

The CIs for the means reconstructed in the ASR analyses presented here are also wide and most nodes have overlapping CIs. Additionally most nodes have CI ranges that overlap the arboreal and terrestrial morphospaces (Figure 4.9 – 4.13). However, node reconstructions across different phylogenies provide consistent CI patterns (Figures 4.9-4.13), which at least suggests that the trends in characters state changes are the same across different analyses.

Figures 4.9 – 4.13 show the CI ranges for crown Anthropoidea (Node 1), crown Catarrhini (Node 2), crown Cercopithecoidea (Node 3), crown Colobinae (Node 4), the African colobines (Node 5), the Asian colobines, (Node 6), crown Cercopithecinae (Node 11), crown Cercopithecini (Node 12), the "terrestrial" guenons (Node 15), the "arboreal" guenons (Node16), crown Papionini (Node 19), crown Papionina (Node 20), the divergence of *Cercocebus* and *Mandrillus* (Node 21), the divergences of *Theropithecus, Lophocebus*, and *Papio* (Node 22), and crown *Macaca* (Node 23) for the humeral head index (HHI), height of the greater tubercle (GTH), angle of the medial epicondyle (AME), overall length of the astragalus (AL), and ectal facet length (EL). The 95% CIs for arboreal cercopithecoids and terrestrial cercopithecoids (including both terrestrial and semi-terrestrial species) are also plotted. In some plot the CIs for crown Anthropoidea and crown Catarrhini do not overlap with the 95% CIs for arboreal or terrestrial cercopithecoids. This result is because the reconstructions are based on an anthropoid sample, which particularly affect the estimation of the crown Anthropoid and crown Catarrhine nodes.

Although Figures 4.9 – 4.13 show that the CIs for these nodes overlap substaintially and mostly overlap with both CIs for both arboreal and terrestrial cercopithecoids, the trends discussed in the above section on character state evolution generally hold for the CI ranges as well. The CI for crown Cercopithecoidea (Node 3) is generally similar to that of crown Colobinae (Node 4) and crown Cercopithecinae (Node 11). However, the CIs for crown Colobinae shift to values indicating increasing arboreality relative to crown Cercopithecoidea in AME (Figure 4.11), AL (Figure 4.12b), and EL (Figure 4.13b). The CIs for crown Cercopithecinae shift to values indicating increasingly terrestriality relative to crown Cercopithecoidea in HHI (Figure 4.9), AME (Figure 4.11), AL (Figure 4.12b), and EL (Figure 4.13). The CI for crown Cercopithecinae overlap exclusively with the CI range of terrestrial cercopithecoids in AME (Figure 4.11b).

The CI ranges for crown Colobinae, the African colobines, and the Asian colobines (Nodes 4 – 6) are generally similar to each other and in some cases these nodes overlap exclusivlely with the CI range for arboreal cercopithecoids in AME (Figure 4.11) EL (Figure 4.13). The CIs for the "terrestrial" guenons (Node 15) is generally shifted towatds values indicating increasing terrestriality relative to crown Cercopithecini (Node 12) and the "arboreal" guenons (Node 16). The CI for the "terrestrial" guenons (Node) overlaps exclusively with the CI range for terrestrial cercopithecoids in AME (Figure 4.11). Nodes 19 – 20 (nodes within crown Papionini) are generally shifted in their range towards values indicating increaasing terrestriality and in some cases the CIs of these nodes overlap exclusively with the CI range for terrestrial cercopithecoids (see Figures 4.10 – 13).

Section 4.7: Discussion

Overall ASR analyses produced similar character states and group classifications for reconstructed nodes across all phylogenies. These results suggest that trees with differing branch lengths but similar topologies of tip taxa provide consistent nodal reconstructions. The largest differences are present between extant-only phylogenies and the phylogeny including eight fossils. The results from the phylogeny with two added fossils often resembled the results from extant-only phylogenies more than those of the phylogeny with eight added fossils. In these comparisons, the deeper nodes differ the most with crown Anthropoidea most strongly affected in these comparisons. The character states reconstructed at crown Anthropoidea for angle of the medial epicondyle (AME), overall length of the astragalus (AL), and ectal facet length (EL) using extant-only phylogenies and the phylogeny with two added fossils were more similar to character states of nodes internal to crown Cercopithecoidea than the character states of the crown catarrhine or crown platyrrhine nodes (Figures 4.6-4.8), suggesting a more cercopithecoid-like ancestral anthropoid. However, when fossil taxa were added, especially early primates like *Aegyptopithecus* and *Apidium*, the character states of crown Anthropoidea reflect expectations given the fossil record (Figures 4.6-4.8), and are more similar to the character states of the crown catarrhine and crown platyrrhine nodes.

The especially low value of crown Anthropoidea for AL (i.e. a relatively short astragalus) and the relatively high value for AME (i.e. a more dorsally directed medial epicondyle) are the reason that crown Anthropoidea is assinged to the terrestrial groups in the DFAs using extant-only phylogenies and a combination of the distal humerus, and astragalus. Since ancestral state reconstruction methods are based on a weighted mean (Nunn 2011), the character states of crown Anthropoidea can be considered roughly as an average of all taxa included in the analysis. Since the majority of taxa in the sample are cercopithecoids, it is not surprising that character states at the crown Anthropoid node would be drawn towards the range of Cercopithecoids. This finding demonstrates the importance of adding fossil taxa to ASR analyses (see also, Hansen and Martins 1996; Finarelli and Flynn 2006; Boyer and Seiffert 2013).

The results also show that ASR analyses produce wide CIs that often exceed the range of tip variation, overlap substantially between reconstructed nodes, and also overlap with more than one *a priori* locomotor group, which is consistent with previous studies (Schluter et al. 1997; Garland et al. 1999; Oakley and Cunningham 2000; Polly 2001; Webster and Purvis 2002). Wide CIs weaken the results from DFAs and patterns of trait evolution based on mean values, because when considering the values encompassed in the 95% confidence interval most reconstructed nodes could be classified into any of the *a priori* locomotor groups. Although the wide CIs are problematic in creating definitive locomotor reconstructions of ancestral nodes, results from ASR analyses can still be used to produce hypotheses about patterns of evolution. The results from this study showed that while CIs are wide, the CIs for each variable are consistent across multiple phylogenies and shift in the ranges of the CIs can be compared across multiple nodes (Figure 4.9 – 4.13) to examine trait evolution in the same way as comparing shifts in mean values across nodes (Figures 4.4 – 4.8).

Generally, the DFAs classified ASR reconstructions of crown Anthropoidea, crown Catarrhini, crown Cercopithecoidea, and crown Colobinae, as arboreal. These reconstructions do not support the hypothesis that early cercopithecoids were semi-terrestrial. However, these findings do support previous assertions that colobines evolved from an arboreal ancestor (Hlusko 2006; Hlusko 2007; Gilbert et al. 2010; Nakatsukasa et al. 2010). Figures 4.4 – 4.8 show that the character states for crown Cercopithecoidea and subsequent divergences are shifted in the morphospace from that of other earlier crown groups, suggesting that although these nodes are all classified as "arboreal," the postcranial morphology reflecting this locomotor adaptation is different among the major groups of anthropoids. Generally, crown Colobinae retains a similar state to that of crown Cercopithecoidea with slight changes occurring in the African and Asian colobine lineages. This pattern can also be seen in Figure 4.9, which shows that posterior probability of being assigned to the arboreal group in the DFA using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group (Figure 4.14 uses posterior probabilities from the analysis run using the Springer et al phylogeny).

Crown Cercopithecinae and crown Cercopithecini are inconsistently classified as arboreal, semi-terrestrial, and terrestrial depending on which DFA is used (i.e. these inconsistencies are not related to the choice of phylogeny). Additionally, the nodes representing divergences within crown Cercopithecini are also classified inconsistently as arboreal, semi-terrestrial, and terrestrial. These nodes include the divergence of *Miopithecus* (Node 13), the divergence of the genus *Cercopithecus* from other guenon genera (Node 14), and the node representing the divergences of *Erythrocebus*, *Chlorocebus*, and *Allochrocebus* (Node 15, i.e., the "terrestrial" guenons). The nodes including the divergences among the *Cercopithecus* species (Nodes 16 – 18) are most consistently assigned to the arboreal group although with relatively low posterior probabilities in the range of 0.6 – 0.7. These results suggest uncertainty in reconstruction of the locomotor behavior of crown Cercopithecini. If the LCA of guenons engaged in terrestrial behavior, then Nodes 13, 14, and 15 would likely have retained this locomotor behavior and arboreality would have evolved secondarily in the stem lineage of *Cercopithecus* (i.e., Node 16). It should be noted that if a different topology of guenons were used in which the "terrestrial" guenons do not form a clade (i.e., Guschanski et al. 2013), then the results for the crown Cercopithecini node and for the cercopithecin nodes may differ from what is presented here. It is likely that these nodes would all be reconstructed as arboreal with terrestriality evolved independently along the *Allochrocebus*, *Chlorocebus*, and *Erythrocebus* lineages.

Classification of crown Papionini, crown *Macaca*, crown Papionina, and many of the more recent nodes (i.e., Nodes 21 – 22 and 24 – 28) also exhibit similar inconsistencies. These inconsistencies are related to *a priori* groupings of the DFAs. In DFA using three groups *a priori*, nodes can be assigned to the arboreal, terrestrial, or semi-terrestrial group. In the DFA using two groups *a priori* with "semi-terrestrialists" left as unknown, nodes are "forced" into either the arboreal or terrestrial group. Given that the terrestrial group is made up of the most committed terrestrial primates, it is not surprising that these nodes would be classified as arboreal in this DFA. With no "intermediate" morphospace, these nodes are more similar to the arboreal group mean than the terrestrial group mean. However, in the DFA using 2 groups *a priori* with "semi-terrestrialists" included in the terrestrial group, a great deal of morphological variation exists in the terrestrial group. Given that any cercopithecoid that engages in a moderate amount of terrestrial behavior is included in the terrestrial group, it is again not surprising that these would be classified as terrestrial by this DFA. Unfortunately, the substantial overlap of "semi-terrestrial" cercopithecoids with primarily and terrestrial cercopithecoids, leads to poor resolution of locomotor behavior in reconstructed nodes. Given the reconstructions, it is likely the LCAs of crown Cercopithecinae, crown Cercopithecini, crown Papionini, crown *Macaca*, and crown Papionina, engaged in terrestrial behavior but may also have been adept at arboreal locomotion. Despite the limiations of ASR methods, the reconstruction of a "semi-terrestrial" crown cercopithecine node, with arboreality secondarily evolving in guenons, macaques, and papioninans is consistent with the hypotheses of put forward by Benenfit and Leakey (Benefit 1999b; Benefit 1999a; Benefit 2000; Leakey et al. 2003), although these authors suggest a much earlier acquisition of terrestriality and convergent evolution of arboreality in African and Asian colobines, which is not supported by this study.

Studying the character state evolution of traits with high loadings in the DFAs may provide more information about locomotor evolution in cercopithecoids than simply classifying the reconstructions. Generally, Figures 4.4 – 4.8 show that although crown Cercopithecinae is shifted from the condition at the crown Cercopithecoidea node, crown Colobinae retains a similar character state to crown Cercopithecoidea. The only trait that does not follow this pattern is overall length of the astragalus, which shows similar shifts in crown Cercopithecinae and crown Colobinae. These results suggest that the LCA of crown colobines probably retained a similar morphology to the LCA of crown cercopithecoids. However, the LCA of crown cercopithecines appears to have acquired morphological features associated with increasing amounts of terrestriality.

Some authors have suggested that *Mesopithecus* has affinities to Asian colobines (Jablonski and Peng 1993; Jablonski 1998; Pan et al. 2004). This work has further suggested that *Mesopithecus* may be more closely related to the odd-nose monkey group than the langur group (Jablonski and Peng 1993; Jablonski 1998; Pan et al. 2004). According to Springer et al. (2012) the crown African colobines are dated to 7.95 Ma and the crown Asian colobines are dated to 7.86 Ma. The earliest evidence for *Mesopithecus* is from the late Miocene (Szalay and Langdon 1986; Jablonski 2002) and therefore *Mesopithecus* (or a close ancestor of *Mesopithecus*) could be along the stem lineage of Asian colobines. The patterns of character evolution among the colobines show support for *Mesopithecus* or a *Mesopithecus* ancestor as being more closely related to the Asian colobines. In the humeral head index (Figure 4.4), angle of the medial epicondyle (Figure 4.6), overall length of the astragalus (Figure 4.7), and ectal facet length (Figure 4.8), the character state of the LCA of Asian colobines is shifted towards a condition that would be expected given an increase in terrestriality, while the character state of the LCA of African colobines is shifted towards an increase in arboreality. Although these shifts are modest and the LCA of Asian colobines does not approach the degree of terrestriality seen in some guenons or papionins, this pattern supports a scenario in which a stem Asian colobine (i.e., *Mesopithecus*) engaged in relatively more terrestrial behavior than exhibited by most extant Asian colobines. In addition to *Mesopithecus*, other fossil crown colobines were not included in the ASR analyses due the high degree of phylogenetic uncertainty. Better resolution of the phylogenetic relationships between extant and fossil colobines will allow for future ASR analyses that examine the evolution of terrestriality in the colobines.

Generally, crown cercopithecin nodes have reconstructions that are intermediate between those of the “arboreal” and “terrestrial” guenons. This result is likely due to the weight averaging of ASR methods as discussed previously. Because crown Cercopithecini includes both arboreal species and species that engage in terrestrial behavior and no known extinct stem or crown guenons exist in the fossil record, it is difficult to determine the most likely character state of this node. Additionally, the differences between the “arboreal” and “terrestrial” guenons may be largely driven by *Erythrocebus patas*. Chapter 2 shows that while the morphology of *E. patas* is more similar to that of the most committed terrestrial cercopithecoids, the other “terrestrial” guenons are more similar to other guenons (Gebo and Sargis 1994). Therefore, many of the adaptations for terrestriality seen in *Erythrocebus* may have evolved solely along this species’ lineage (Sargis et al. 2008).

The character states at Crown Papionini show a shift in morphology towards adaptations to increasing terrestriality from the character state at crown Cercopithecinae. The shift towards increasing terrestriality continues at crown Papionina and further continues at the divergences of *Cercocebus-Mandrillus* and *Theropithecus-Lophocebus-Papio*. Crown *Macaca* generally exhibits retention of the character state at crown Papionini or a slight shift towards increasing arboreality. The only exception to these patterns is in the humeral head index, where crown *Macaca* shows a large shift towards increasing terrestriality and the divergence of *Theropithecus-Lophocebus-Papio* shows a large shift towards increasing arboreality (Figure 4.4).

Section 4.8: Conclusions

The results from this chapter document the complexity of locomotor evolution in cercopithecoids. Several locomotor transitions occurred during the evolution of this clade with independent acquisitions of both arboreal and terrestrial behavior being possible. This chapter supports the hypothesis that the LCA of crown Colobinae was arboreal and that African and Asian colobines did not evolve arboreality in parallel (Hlusko 2006; Hlusko 2007; Gilbert et al. 2010; Nakatsukasa et al. 2010). The results from this study show the LCA of crown Cercopithecoidea probably engaged in more arboreal behavior than previously thought (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a), with this node bring consistently classified as arboreal and exhibiting character states that are more consistent with arboreal behavior relative to those of crown cercopithecines, which is well-represented by species that engage in terrestrial behavior. Additionally, crown Colobinae often retains a similar character state as crown Cercopithecoidea and considering that the stem lineage of colobines included primarily arboreal species (i.e., *Microcolobus)*, it seems likely that the LCA of crown Cercopithecoidea was also arboreal. The results from this chapter illustrate the importance of adding fossil taxa to ASR analyses and although some analyses included a few early anthropoids, the addition of more stem catarrhines, stem cercopithecoids, and stem hominoids as well as crown cercopithecoids, would provide more information for the character state of crown Cercopithecoidea.

As mentioned previously, the locomotor mode of the LCA of crown Cercopithecinae is difficult to reconstruct given the lack of fossil evidence around this divergence and the low posterior probabilities for group assignment by the DFAs. Thus, multiple evolutionary scenarios are possible for these nodes. One possibility is that the LCA of crown Cercopithecinae was "semi-terrestrial" and that subsequent lineages have become increasingly more dedicated to arboreal or terrestrialiy. However, a future reconstruction of a more arboreal LCA of crown cercopithecines would support the independent acquisition of terrestrial behavior within guenons and papionins. Better resolution of the character state of crown Cercopithecinae would also help resolve the reconstruction of the LCA of crown Papionini and crown Cercopithecini. Both these nodes and the subsequent divergences are inconsistently classified in the DFAs. These results may suggest that, like crown Cercopithecinae, the LCA of crown guenons and papionins was "semi-terrestrial," with some species retaining this "semi-terrestrial" lifestyle and other becoming more committed to an arboreal or terrestrial lifestyle. Future discoveries that produce fossils near the LCA of guenons or papionins will help to resolve this issue. In addition to more fossil material, better data on the locomotor habits of *Allenopithecus* and *Miopithecus* would help to resolve the most likely locomotor mode of crown Cercopithecinae and crown Cercopithecini.

In this chapter, crown Colobinae and all subsequent nodes were consistently classified as arboreal with high posterior probabilities. However, certain colobine lineages have also acquired terrestrial behavior, including the *Mesopithecus* lineage, the *Cercopithecoides* lineage, and *Semnopithecus.* Better resolution of the phylogenetic placement of fossil crown colobines would give a unique perspective of the evolution of terrestriality in colobines.

Although the conclusions of this study are limited, new hypotheses have been generated. First, I hypothesize that the LCA of crown Cercopithecoidea was probably considerably more arboreal than previously thought. Second, and in support of previous research, the LCA of crown Colobinae was primarily arboreal, having retained this condition from the cercopithecoid LCA.

Third, “semi-terrestriality” may have evolved along the stem lineage of cercopithecines. Fourth, upon resolution of the phylogenetic placement of *Mesopithecus*, it is possible that Asian colobines shared a close common ancestor with a species that engaged in a moderate amount of terrestrial behavior. And finally, if the LCA of crown cercopithecines are ancestrally “semi-terrestrial,” then highly arboreal guenons and macaques have evolved that lifestyle secondarily. The discovery of more fossil material, the addition of more morphological features from other regions of the postcranium to ASR analyses, and a better understanding the phylogenetic relationships between fossil and extant taxa will ultimately lead to a more complete picture of the locomotor evolution of cercopithecoids.

Table 4.1. Localities and ages for fossil specimens included in ASR analyses.

Taxon	**Locality**	**Date (Mya)**	**Reference**
Apidium	Fayum (Egypt)	30.2	Seiffert 2006
Aegyptopithecus zeuxis	Fayum (Egypt)	30.2	Seiffert 2006
Proconsul africanus	Rusinga Island (Kenya)	17	Peppe et al., 2009
Victoriapithecus macinnesi	Maboko Island (Kenya)	14.7	Feibel and Brown, 1991
Microcolobus sp.	Nakali Formation (Kenya)	9.8	Nakatsukasa et al., 2010; Kunimatsu et al., 2007
Parapapio lothagamensis	Lothagam (Kenya)	6.54	McDougall and Feibel, 1999
Theropithecus brumpti	East Turkana, West Turkana, Tugen Hills (Kenya), Omo Shungura (Ethiopia)	3.3	Reviewed in Guthrie, 2011
Theropithecus oswladi	Olorgesailie, East Turkana (Kenya)	2.0	Reviewed in Guthrie 2011 and Jablonski and Leakey, 2008

Table 4.2. Nodes reconstructed in ASR analyses according to 10K phylogeny. Asterisk indicates (*) differences in Springer phylogeny (see text and Figure 4.1)

Node #	Crown Group or Species Inlcuded in the Divergence
1	Crown Anthropoidea
2	Crown Catarhini
3	Crown Cercopithecoidea
4	Crown Colobinae
5	Crown African colobines
6	Crown Asian colobines
7	Divergence of *Presbytis rubicunda* and *P. melalophos*
8	Common node of odd-nosed monkeys and langurs
9	Common node of *Nasalis, Pygathrix, Rhinopithecus*
10*	Common node of the langurs
11	Crown Cercopithecinea
12	Crown Cercopithecini
13*	Node following divergence of *Allenopithecus*
14*	Node following divergence of *Miopithecus*
15	Common node of *Allochrocebus lhoesti, Erythrocebus patas, Chlorocebus aethiops, Chlorocebus pygerthryus*
16	Last common ancestor of the *Cercopithecus* genus
17*	Common node of *C. mona, C. pogonias, C. diana, C. neglectus, C. hamlyni*
18*	Common node of *C. mitis, C. nictitans, C. ascanius, C. cephus*
19	Crown Papionini
20	Common node for all non-macaque papionins
21	Divergence of *Cercocebus* and *Mandrillus*
22*	Common node of *Lophocebus, Theropithecus, Papio*
23	Crown *Macaca*
24	Node following divergence of *M. sylvanus*
25*	Common node *M. thibetana, M. fascicularis, M. mulatta*
26*	Common node of *M. arctoides, M. assamensis, M sinica, M. tonkeana, M nigra, M nemestrina*
27	Common node of *M. tonkeana, M nigra, M nemestrina*
28	Common node of *M. arctoides, M. assamensis, M sinica*
29	Crown Hominoidea
30	Crown Platyrrhini

Table 4.3. Variables included in the ASR analyses

Humerus	**Distal humerus**	**Astragalus**	**Calcaneus**
Humeral head index (HHI)	Height of the olecranon fossa (PDOF)	Overall length of the astragalus (AL)	Overall length of the calcaneus (CL)
Width of the greater tubercle (MGT)	Height of the capitulum (PDC)	Ectal facet length (EL)	Legnth of the distal segment of the calcaneus (PDA)
Height of the greater tubercle (GTH)	Angle of the medial epicondye (AME)	Width of the astragalar head (WTH)	Legnth of the calcaneal tuber (CTL)
Width of the lesser tubercle (MLT)		Angle of the astragalar head (ATH)	Width of the sustenaculum (MLS)
Height of capitulum (PDC)		Trochlear Wedging Index (WED)	Height of the cuboid facet (HCF)
Angle of the medial epicondyle (AME)			

Table 4.4a. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of three elements and using three groups *a priori*

Node	**Classification - 10K Tree**	**PP Arb**	**PP Semi**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Semi**	**PP Ter**
Node.01	arboreal	0.891	0.106	2.624E-03	arboreal	0.709	0.269	2.201E-02
Node.02	arboreal	0.973	0.026	1.734E-04	arboreal	0.973	0.027	2.709E-04
Node.03	arboreal	0.878	0.121	6.969E-04	arboreal	0.844	0.155	9.952E-04
Node.04	arboreal	0.941	0.059	1.311E-04	arboreal	0.937	0.062	1.495E-04
Node.05	arboreal	0.943	0.057	1.333E-04	arboreal	0.941	0.059	1.476E-04
Node.06	arboreal	0.953	0.047	7.249E-05	arboreal	0.956	0.044	6.585E-05
Node.07	arboreal	0.979	0.021	5.208E-06	arboreal	0.984	0.016	2.260E-06
Node.08	arboreal	0.953	0.047	7.458E-05	arboreal	0.956	0.044	6.833E-05
Node.09	arboreal	0.970	0.030	4.932E-05	arboreal	0.971	0.029	4.563E-05
Node.10	arboreal	0.941	0.059	1.013E-04	arboreal	0.925	0.075	1.424E-04
Node.11	semi-terrestrial	0.482	0.511	7.417E-03	semi-terrestrial	0.447	0.545	7.917E-03
Node.12	arboreal	0.573	0.425	1.969E-03	arboreal	0.598	0.400	1.379E-03
Node.13	arboreal	0.580	0.418	1.817E-03	arboreal	0.573	0.425	1.796E-03
Node.14	arboreal	0.552	0.446	1.843E-03	arboreal	0.568	0.431	1.776E-03
Node.15	semi-terrestrial	0.452	0.546	2.490E-03	semi-terrestrial	0.416	0.581	2.760E-03
Node.16	arboreal	0.676	0.322	1.087E-03	arboreal	0.646	0.353	1.299E-03
Node.17	arboreal	0.686	0.313	1.067E-03	arboreal	0.646	0.353	1.299E-03
Node.18	arboreal	0.727	0.272	7.682E-04	arboreal	0.750	0.249	6.205E-04
Node.19	semi-terrestrial	0.274	0.696	2.953E-02	semi-terrestrial	0.198	0.757	4.509E-02
Node.20	semi-terrestrial	0.169	0.759	7.187E-02	semi-terrestrial	0.115	0.776	1.091E-01
Node.21	semi-terrestrial	0.052	0.739	2.087E-01	semi-terrestrial	0.061	0.752	1.870E-01
Node.22	semi-terrestrial	0.045	0.573	3.825E-01	semi-terrestrial	0.042	0.586	3.720E-01
Node.23	semi-terrestrial	0.232	0.739	2.943E-02	semi-terrestrial	0.193	0.774	3.268E-02
Node.24	semi-terrestrial	0.276	0.704	1.948E-02	semi-terrestrial	0.313	0.674	1.293E-02
Node.25	semi-terrestrial	0.288	0.694	1.821E-02	semi-terrestrial	0.362	0.629	9.341E-03
Node.26	semi-terrestrial	0.270	0.712	1.861E-02	semi-terrestrial	0.232	0.747	2.163E-02
Node.27	semi-terrestrial	0.274	0.696	2.953E-02	semi-terrestrial	0.188	0.786	2.555E-02
Node.28	semi-terrestrial	0.333	0.654	1.286E-02	semi-terrestrial	0.317	0.670	1.295E-02
Node.29	arboreal	0.998	1.531E-03	5.029E-06	arboreal	0.998	2.393E-03	1.110E-05
Node.30	arboreal	1.000	1.257E-04	5.012E-09	arboreal	1.000	2.457E-04	2.061E-08

Table 4.4b. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of three elements and using two groups *a priori* with “semi-terrestrialists” as unknown

Node	Classification - 10K Tree	PP Arb	PP Ter	Classification - Springer	PP Arb	PP Ter
Node.01	arboreal	1.000	4.833E-04	arboreal	0.998	1.619E-03
Node.02	arboreal	1.000	9.771E-05	arboreal	1.000	1.043E-04
Node.03	arboreal	1.000	4.940E-04	arboreal	0.999	6.834E-04
Node.04	arboreal	1.000	9.651E-05	arboreal	1.000	1.103E-04
Node.05	arboreal	1.000	1.044E-04	arboreal	1.000	1.158E-04
Node.06	arboreal	1.000	5.237E-05	arboreal	1.000	4.750E-05
Node.07	arboreal	1.000	3.646E-06	arboreal	1.000	1.565E-06
Node.08	arboreal	1.000	5.378E-05	arboreal	1.000	4.921E-05
Node.09	arboreal	1.000	3.629E-05	arboreal	1.000	3.361E-05
Node.10	arboreal	1.000	7.251E-05	arboreal	1.000	1.013E-04
Node.11	arboreal	0.990	9.623E-03	arboreal	0.989	1.058E-02
Node.12	arboreal	0.998	1.530E-03	arboreal	0.999	9.268E-04
Node.13	arboreal	0.999	1.338E-03	arboreal	0.999	1.335E-03
Node.14	arboreal	0.999	1.395E-03	arboreal	0.999	1.323E-03
Node.15	arboreal	0.998	2.205E-03	arboreal	0.997	2.610E-03
Node.16	arboreal	0.999	6.983E-04	arboreal	0.999	8.798E-04
Node.17	arboreal	0.999	6.882E-04	arboreal	0.999	8.798E-04
Node.18	arboreal	1.000	4.494E-04	arboreal	1.000	3.399E-04
Node.19	arboreal	0.920	7.975E-02	arboreal	0.840	1.602E-01
Node.20	arboreal	0.710	0.290	arboreal	0.506	0.494461676
Node.21	terrestrial	0.146	0.854	terrestrial	0.197	0.802904983
Node.22	terrestrial	0.085	0.915	terrestrial	0.082	0.917762797
Node.23	arboreal	0.909	9.070E-02	arboreal	0.885	1.146E-01
Node.24	arboreal	0.953	4.738E-02	arboreal	0.976	2.433E-02
Node.25	arboreal	0.958	4.223E-02	arboreal	0.986	1.437E-02
Node.26	arboreal	0.955	4.500E-02	arboreal	0.940	5.959E-02
Node.27	arboreal	0.920	7.975E-02	arboreal	0.914	8.567E-02
Node.28	arboreal	0.977	2.323E-02	arboreal	0.976	2.414E-02
Node.29	arboreal	1.000	4.971E-06	arboreal	1.000	8.355E-06
Node.30	arboreal	1.000	2.291E-10	arboreal	1.000	8.002E-10

Table 4.4c. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of three elements and using two groups *a priori* with “semi-terrestrialists” included in the terrestrial group

Node	Classification - 10K Tree	PP Arb	PP Ter	Classification - Springer	PP Arb	PP Ter
Node.01	arboreal	0.727	0.273	arboreal	0.610	0.390

Node.02	arboreal	0.880	0.120	arboreal	0.881	0.119
Node.03	arboreal	0.758	0.242	arboreal	0.730	0.270
Node.04	arboreal	0.866	0.134	arboreal	0.863	0.137
Node.05	arboreal	0.879	0.121	arboreal	0.878	0.122
Node.06	arboreal	0.884	0.116	arboreal	0.886	0.114
Node.07	arboreal	0.933	0.067	arboreal	0.944	0.056
Node.08	arboreal	0.884	0.116	arboreal	0.885	0.115
Node.09	arboreal	0.893	0.107	arboreal	0.895	0.105
Node.10	arboreal	0.878	0.122	arboreal	0.868	0.132
Node.11	terrestrial	0.436	0.564	terrestrial	0.426	0.574
Node.12	arboreal	0.541	0.459	arboreal	0.574	0.426
Node.13	arboreal	0.555	0.445	arboreal	0.564	0.436
Node.14	arboreal	0.575	0.425	arboreal	0.583	0.417
Node.15	arboreal	0.516	0.484	terrestrial	0.494	0.506
Node.16	arboreal	0.689	0.311	arboreal	0.661	0.339
Node.17	arboreal	0.704	0.296	arboreal	0.661	0.339
Node.18	arboreal	0.722	0.278	arboreal	0.740	0.260
Node.19	terrestrial	0.274	0.726	terrestrial	0.218	0.782
Node.20	terrestrial	0.179	0.821	terrestrial	0.137	0.863
Node.21	terrestrial	0.075	0.925	terrestrial	0.085	0.915
Node.22	terrestrial	0.068	0.932	terrestrial	0.067	0.933
Node.23	terrestrial	0.282	0.718	terrestrial	0.248	0.752
Node.24	terrestrial	0.327	0.673	terrestrial	0.378	0.622
Node.25	terrestrial	0.337	0.663	terrestrial	0.409	0.591
Node.26	terrestrial	0.325	0.675	terrestrial	0.284	0.716
Node.27	terrestrial	0.274	0.726	terrestrial	0.222	0.778
Node.28	terrestrial	0.426	0.574	terrestrial	0.393	0.607
Node.29	arboreal	0.974	0.026	arboreal	0.967	0.033
Node.30	arboreal	0.999	0.001	arboreal	0.998	0.002

Table 4.5a. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of two elements and using three groups *a priori*

Node	**Classification - 10K Tree**	**PP Arb**	**PP Semi**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Semi**	**PP Ter**
Node.01	terrestrial	0.030	0.079	0.892	terrestrial	0.077	0.118	0.805
Node.02	arboreal	0.887	0.103	1.007E-02	arboreal	0.921	0.072	7.027E-03
Node.03	arboreal	0.810	0.185	4.997E-03	arboreal	0.807	0.189	4.323E-03

Node.04	arboreal	0.902	0.097	8.364E-04	arboreal	0.910	0.090	7.104E-04
Node.05	arboreal	0.932	0.068	5.021E-04	arboreal	0.938	0.062	4.349E-04
Node.06	arboreal	0.900	0.099	6.433E-04	arboreal	0.903	0.096	5.708E-04
Node.07	arboreal	0.928	0.072	1.170E-04	arboreal	0.936	0.064	6.798E-05
Node.08	arboreal	0.897	0.102	6.783E-04	arboreal	0.901	0.098	6.000E-04
Node.09	arboreal	0.919	0.081	4.594E-04	arboreal	0.921	0.078	4.195E-04
Node.10	arboreal	0.875	0.124	9.513E-04	arboreal	0.846	0.153	1.371E-03
Node.11	arboreal	0.527	0.457	1.623E-02	arboreal	0.510	0.474	1.581E-02
Node.12	arboreal	0.603	0.391	5.896E-03	arboreal	0.627	0.369	4.246E-03
Node.13	arboreal	0.610	0.384	5.624E-03	arboreal	0.606	0.389	5.250E-03
Node.14	arboreal	0.585	0.409	5.947E-03	arboreal	0.599	0.396	5.325E-03
Node.15	arboreal	0.520	0.472	8.062E-03	arboreal	0.498	0.493	8.625E-03
Node.16	arboreal	0.652	0.344	3.901E-03	arboreal	0.642	0.353	4.074E-03
Node.17	arboreal	0.664	0.333	3.603E-03	arboreal	0.642	0.353	4.074E-03
Node.18	arboreal	0.673	0.324	3.404E-03	arboreal	0.678	0.318	3.067E-03
Node.19	semi-terrestrial	0.369	0.590	0.041	semi-terrestrial	0.300	0.644	5.605E-02
Node.20	semi-terrestrial	0.254	0.667	0.079	semi-terrestrial	0.196	0.697	0.107
Node.21	semi-terrestrial	0.115	0.723	0.162	semi-terrestrial	0.127	0.720	0.153
Node.22	semi-terrestrial	0.084	0.617	0.300	semi-terrestrial	0.082	0.624	0.294
Node.23	semi-terrestrial	0.403	0.563	3.458E-02	semi-terrestrial	0.355	0.603	4.157E-02
Node.24	semi-terrestrial	0.456	0.521	2.329E-02	semi-terrestrial	0.483	0.501	1.632E-02
Node.25	semi-terrestrial	0.466	0.512	2.179E-02	arboreal	0.500	0.487	1.302E-02
Node.26	semi-terrestrial	0.449	0.527	2.320E-02	semi-terrestrial	0.392	0.578	3.044E-02
Node.27	semi-terrestrial	0.369	0.590	4.106E-02	semi-terrestrial	0.328	0.628	4.411E-02
Node.28	arboreal	0.539	0.448	1.300E-02	arboreal	0.501	0.483	1.516E-02
Node.29	arboreal	0.993	0.007	1.756E-04	arboreal	0.991	0.009	2.549E-04
Node.30	arboreal	0.998	0.002	7.860E-07	arboreal	0.997	0.003	2.060E-06

Table 4.5b. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of two elements and using two groups *a priori* with "semi-terrestrialists" as unknown

Node	**Classification - 10K Tree**	**PP Arb**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Ter**
Node.01	terrestrial	0.015	0.985	terrestrial	0.070	0.930
Node.02	arboreal	0.983	0.017	arboreal	0.990	0.010
Node.03	arboreal	0.994	6.371E-03	arboreal	0.995	5.082E-03
Node.04	arboreal	0.999	9.545E-04	arboreal	0.999	7.844E-04
Node.05	arboreal	0.999	5.527E-04	arboreal	1.000	4.656E-04
Node.06	arboreal	0.999	7.398E-04	arboreal	0.999	6.525E-04
Node.07	arboreal	1.000	1.286E-04	arboreal	1.000	7.355E-05
Node.08	arboreal	0.999	7.839E-04	arboreal	0.999	6.893E-04
Node.09	arboreal	0.999	5.302E-04	arboreal	1.000	4.829E-04
Node.10	arboreal	0.999	1.123E-03	arboreal	0.998	1.663E-03
Node.11	arboreal	0.976	0.024	arboreal	0.977	0.023
Node.12	arboreal	0.994	6.084E-03	arboreal	0.996	3.894E-03
Node.13	arboreal	0.994	5.627E-03	arboreal	0.995	5.211E-03
Node.14	arboreal	0.994	6.276E-03	arboreal	0.995	5.394E-03
Node.15	arboreal	0.991	9.408E-03	arboreal	0.990	0.010
Node.16	arboreal	0.996	3.809E-03	arboreal	0.996	3.928E-03
Node.17	arboreal	0.997	3.427E-03	arboreal	0.996	3.928E-03
Node.18	arboreal	0.997	3.379E-03	arboreal	0.997	3.025E-03
Node.19	arboreal	0.915	0.085	arboreal	0.864	0.136
Node.20	arboreal	0.778	0.222	arboreal	0.660	0.340
Node.21	terrestrial	0.403	0.597	terrestrial	0.447	0.553
Node.22	terrestrial	0.198	0.802	terrestrial	0.200	0.800
Node.23	arboreal	0.941	0.059	arboreal	0.921	0.079
Node.24	arboreal	0.967	0.033	arboreal	0.980	0.020
Node.25	arboreal	0.970	0.030	arboreal	0.985	0.015
Node.26	arboreal	0.968	0.032	arboreal	0.951	0.049
Node.27	arboreal	0.915	0.085	arboreal	0.915	0.085
Node.28	arboreal	0.986	0.014	arboreal	0.982	0.018
Node.29	arboreal	1.000	3.513E-04	arboreal	1.000	4.667E-04
Node.30	arboreal	1.000	2.525E-07	arboreal	1.000	6.864E-07

Table 4.5c. Nodal reconstructions for the extant-only 10K phylogeny and modified Springer phylogeny with a combination of two elements and using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group

Node	**Classification - 10K Tree**	**PP Arb**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Ter**
Node.01	terrestrial	0.280	0.720	arboreal	0.610	0.390
Node.02	arboreal	0.845	0.155	arboreal	0.881	0.119
Node.03	arboreal	0.745	0.255	arboreal	0.730	0.270
Node.04	arboreal	0.849	0.151	arboreal	0.863	0.137
Node.05	arboreal	0.884	0.116	arboreal	0.878	0.122
Node.06	arboreal	0.850	0.150	arboreal	0.886	0.114
Node.07	arboreal	0.899	0.101	arboreal	0.944	0.056
Node.08	arboreal	0.846	0.154	arboreal	0.885	0.115
Node.09	arboreal	0.862	0.138	arboreal	0.895	0.105
Node.10	arboreal	0.827	0.173	arboreal	0.868	0.132
Node.11	terrestrial	0.473	0.527	terrestrial	0.426	0.574
Node.12	arboreal	0.552	0.448	arboreal	0.574	0.426
Node.13	arboreal	0.566	0.434	arboreal	0.564	0.436
Node.14	arboreal	0.563	0.437	arboreal	0.583	0.417
Node.15	arboreal	0.511	0.489	terrestrial	0.494	0.506
Node.16	arboreal	0.638	0.362	arboreal	0.661	0.339
Node.17	arboreal	0.653	0.347	arboreal	0.661	0.339
Node.18	arboreal	0.656	0.344	arboreal	0.740	0.260
Node.19	terrestrial	0.333	0.667	terrestrial	0.218	0.782
Node.20	terrestrial	0.231	0.769	terrestrial	0.137	0.863
Node.21	terrestrial	0.106	0.894	terrestrial	0.085	0.915
Node.22	terrestrial	0.095	0.905	terrestrial	0.067	0.933
Node.23	terrestrial	0.387	0.613	terrestrial	0.248	0.752
Node.24	terrestrial	0.455	0.545	terrestrial	0.378	0.622
Node.25	terrestrial	0.464	0.536	terrestrial	0.409	0.591
Node.26	terrestrial	0.459	0.541	terrestrial	0.284	0.716
Node.27	terrestrial	0.333	0.667	terrestrial	0.222	0.778
Node.28	arboreal	0.573	0.427	terrestrial	0.393	0.607
Node.29	arboreal	0.984	0.016	arboreal	0.967	0.033
Node.30	arboreal	0.997	0.003	arboreal	0.998	0.002

Table 4.6a. Nodal reconstructions for the fossil-added 10K phylogeny and modified Springer phylogeny with a combination of three elements and using three groups *a priori*

Node	Classification - 10K Tree	PP Arb	PP Semi	PP Ter	Classification - Springer	PP Arb	PP Semi	PP Ter
Node.01	arboreal	0.910	0.087	3.189E-03	arboreal	0.646	0.343	1.101E-02
Node.02	arboreal	0.970	0.030	1.720E-04	arboreal	0.972	0.028	1.991E-04
Node.03	arboreal	0.851	0.148	5.624E-04	arboreal	0.860	0.139	9.790E-04
Node.04	arboreal	0.940	0.060	1.258E-04	arboreal	0.944	0.056	1.458E-04
Node.05	arboreal	0.946	0.054	1.163E-04	arboreal	0.948	0.052	1.241E-04
Node.06	arboreal	0.954	0.046	7.401E-05	arboreal	0.960	0.040	7.513E-05
Node.07	arboreal	0.984	0.016	6.126E-06	arboreal	0.989	0.011	3.173E-06
Node.08	arboreal	0.954	0.046	7.776E-05	arboreal	0.959	0.041	7.909E-05
Node.09	arboreal	0.969	0.031	5.724E-05	arboreal	0.971	0.029	6.160E-05
Node.10	arboreal	0.941	0.059	1.044E-04	arboreal	0.930	0.070	1.551E-04
Node.11	semi-terrestrial	0.432	0.565	3.579E-03	semi-terrestrial	0.385	0.612	3.071E-03
Node.12	arboreal	0.554	0.445	1.397E-03	arboreal	0.582	0.417	1.220E-03
Node.13	arboreal	0.568	0.431	1.326E-03	arboreal	0.550	0.449	1.294E-03
Node.14	arboreal	0.547	0.451	1.537E-03	arboreal	0.549	0.449	1.371E-03
Node.15	semi-terrestrial	0.447	0.550	2.196E-03	semi-terrestrial	0.407	0.590	2.499E-03
Node.16	arboreal	0.678	0.321	9.384E-04	arboreal	0.633	0.365	1.086E-03
Node.17	arboreal	0.686	0.313	9.218E-04	arboreal	0.634	0.365	1.093E-03
Node.18	arboreal	0.736	0.264	6.695E-04	arboreal	0.755	0.244	5.785E-04
Node.19	semi-terrestrial	0.239	0.748	1.364E-02	semi-terrestrial	0.162	0.823	1.477E-02
Node.20	semi-terrestrial	0.154	0.810	3.597E-02	semi-terrestrial	0.102	0.850	4.818E-02
Node.21	semi-terrestrial	0.055	0.852	0.093	semi-terrestrial	0.056	0.791	0.152814012
Node.22	semi-terrestrial	0.044	0.628	0.328	semi-terrestrial	0.041	0.646	0.313552336
Node.23	semi-terrestrial	0.215	0.762	2.301E-02	semi-terrestrial	0.176	0.799	2.508E-02
Node.24	semi-terrestrial	0.268	0.715	1.741E-02	semi-terrestrial	0.304	0.682	1.342E-02
Node.25	semi-terrestrial	0.282	0.701	1.632E-02	semi-terrestrial	0.361	0.629	9.828E-03
Node.26	semi-terrestrial	0.261	0.721	1.746E-02	semi-terrestrial	0.218	0.764	1.786E-02
Node.27	semi-terrestrial	0.239	0.748	1.364E-02	semi-terrestrial	0.179	0.789	3.165E-02
Node.28	semi-terrestrial	0.322	0.666	1.243E-02	semi-terrestrial	0.304	0.685	1.139E-02
Node.29	arboreal	0.998	0.002	5.11E-06	arboreal	0.998	0.002	9.03E-06
Node.30	arboreal	1.000	0.000	4.70E-09	arboreal	1.000	0.000	1.16E-08

Table 4.6b. Nodal reconstructions for the fossil added 10K phylogeny and modified Springer phylogeny with a combination of three elements and using two groups *a priori* with "semi-terrestrialists" as unknown

Node	Classification - 10K Tree	PP Arb	PP Ter	Classification - Springer	PP Arb	PP Ter
Node.01	arboreal	1.000	2.011E-04	arboreal	1.000	4.849E-04

Node.02	arboreal	1.000	5.429E-05	arboreal	1.000	4.870E-05
Node.03	arboreal	1.000	2.310E-04	arboreal	1.000	3.978E-04
Node.04	arboreal	1.000	7.489E-05	arboreal	1.000	9.052E-05
Node.05	arboreal	1.000	7.682E-05	arboreal	1.000	8.466E-05
Node.06	arboreal	1.000	4.731E-05	arboreal	1.000	5.197E-05
Node.07	arboreal	1.000	3.580E-06	arboreal	1.000	1.910E-06
Node.08	arboreal	1.000	5.109E-05	arboreal	1.000	5.565E-05
Node.09	arboreal	1.000	4.097E-05	arboreal	1.000	4.677E-05
Node.10	arboreal	1.000	7.047E-05	arboreal	1.000	1.152E-04
Node.11	arboreal	0.997	2.854E-03	arboreal	0.998	2.032E-03
Node.12	arboreal	0.999	8.563E-04	arboreal	0.999	6.898E-04
Node.13	arboreal	0.999	7.932E-04	arboreal	0.999	7.446E-04
Node.14	arboreal	0.999	1.045E-03	arboreal	0.999	8.507E-04
Node.15	arboreal	0.998	1.845E-03	arboreal	0.998	2.242E-03
Node.16	arboreal	0.999	5.677E-04	arboreal	0.999	6.597E-04
Node.17	arboreal	0.999	5.650E-04	arboreal	0.999	6.657E-04
Node.18	arboreal	1.000	3.743E-04	arboreal	1.000	3.082E-04
Node.19	arboreal	0.975	0.025	arboreal	0.968	0.032
Node.20	arboreal	0.875	0.125	arboreal	0.785	0.215
Node.21	terrestrial	0.361	0.639	terrestrial	0.240	0.760
Node.22	terrestrial	0.110	0.890	terrestrial	0.114	0.886
Node.23	arboreal	0.936	0.064	arboreal	0.921	0.079
Node.24	arboreal	0.960	0.040	arboreal	0.975	0.025
Node.25	arboreal	0.965	0.035	arboreal	0.985	0.015
Node.26	arboreal	0.960	0.040	arboreal	0.955	0.045
Node.27	arboreal	0.975	0.025	arboreal	0.890	0.110
Node.28	arboreal	0.978	0.022	arboreal	0.980	0.020
Node.29	arboreal	1.000	4.136E-06	arboreal	1.000	5.670E-06
Node.30	arboreal	1.000	1.803E-10	arboreal	1.000	3.397E-10

Table 4.6c. Nodal reconstructions for the fossil added 10K phylogeny and modified Springer phylogeny with a combination of three elements and using two groups *a priori* with "semi-terrestrialists" included in the terrestrial group

Node	**Classification**	**PP Arboreal**	**PP Terrestrial**	**Classification**	**PP Arboreal**	**PP Terrestrial**
Node.01	arboreal	0.858	0.142	arboreal	0.521	0.479
Node.02	arboreal	0.903	0.097	arboreal	0.868	0.132
Node.03	arboreal	0.779	0.221	arboreal	0.738	0.262

Node.04	arboreal	0.879	0.121	arboreal	0.875	0.125
Node.05	arboreal	0.893	0.107	arboreal	0.892	0.108
Node.06	arboreal	0.896	0.104	arboreal	0.896	0.104
Node.07	arboreal	0.957	0.043	arboreal	0.967	0.033
Node.08	arboreal	0.894	0.106	arboreal	0.894	0.106
Node.09	arboreal	0.897	0.103	arboreal	0.896	0.104
Node.10	arboreal	0.886	0.114	arboreal	0.874	0.126
Node.11	terrestrial	0.466	0.534	terrestrial	0.472	0.528
Node.12	arboreal	0.558	0.442	arboreal	0.590	0.410
Node.13	arboreal	0.574	0.426	arboreal	0.584	0.416
Node.14	arboreal	0.587	0.413	arboreal	0.597	0.403
Node.15	arboreal	0.524	0.476	terrestrial	0.499	0.501
Node.16	arboreal	0.698	0.302	arboreal	0.670	0.330
Node.17	arboreal	0.710	0.290	arboreal	0.670	0.330
Node.18	arboreal	0.736	0.264	arboreal	0.752	0.248
Node.19	terrestrial	0.293	0.707	terrestrial	0.251	0.749
Node.20	terrestrial	0.192	0.808	terrestrial	0.154	0.846
Node.21	terrestrial	0.080	0.920	terrestrial	0.089	0.911
Node.22	terrestrial	0.068	0.932	terrestrial	0.068	0.932
Node.23	terrestrial	0.279	0.721	terrestrial	0.249	0.751
Node.24	terrestrial	0.324	0.676	terrestrial	0.375	0.625
Node.25	terrestrial	0.337	0.663	terrestrial	0.411	0.589
Node.26	terrestrial	0.319	0.681	terrestrial	0.284	0.716
Node.27	terrestrial	0.293	0.707	terrestrial	0.216	0.784
Node.28	terrestrial	0.412	0.588	terrestrial	0.391	0.609
Node.29	arboreal	0.976	0.024	arboreal	0.966	0.034
Node.30	arboreal	0.999	0.001	arboreal	0.998	0.002

Table 4.7a. Nodal reconstructions for the fossil added 10K phylogeny and modified Springer phylogeny with a combination of two elements and using three groups *a priori*

Node	Classification - 10K Tree	PP Arb	PP Semi	PP Ter	Classification - Springer	PP Arb	PP Semi	PP Ter
Node.01	arboreal	0.999	5.367E-04	3.417E-08	arboreal	1.000	4.777E-04	2.654E-08
Node.02	arboreal	1.000	2.124E-04	7.585E-09	arboreal	0.999	9.972E-04	1.802E-07
Node.03	arboreal	0.905	0.094	4.039E-04	arboreal	0.633	0.362	5.234E-03
Node.04	arboreal	0.915	0.084	5.612E-04	arboreal	0.877	0.121	1.482E-03
Node.05	arboreal	0.937	0.062	3.926E-04	arboreal	0.925	0.074	6.612E-04
Node.06	arboreal	0.916	0.084	4.641E-04	arboreal	0.902	0.097	6.811E-04
Node.07	arboreal	0.958	0.042	6.372E-05	arboreal	0.965	0.035	3.604E-05
Node.08	arboreal	0.912	0.088	5.074E-04	arboreal	0.902	0.098	6.889E-04
Node.09	arboreal	0.928	0.072	3.936E-04	arboreal	0.922	0.077	4.736E-04
Node.10	arboreal	0.891	0.108	7.199E-04	arboreal	0.854	0.145	1.304E-03
Node.11	semi-terrestrial	0.457	0.530	1.213E-02	semi-terrestrial	0.286	0.691	0.022
Node.12	arboreal	0.569	0.426	5.056E-03	arboreal	0.556	0.439	0.005
Node.13	arboreal	0.580	0.415	4.890E-03	arboreal	0.525	0.469	0.006
Node.14	arboreal	0.569	0.426	5.420E-03	arboreal	0.537	0.457	0.006
Node.15	arboreal	0.506	0.487	7.583E-03	semi-terrestrial	0.462	0.530	0.009
Node.16	arboreal	0.648	0.349	3.678E-03	arboreal	0.607	0.388	0.004
Node.17	arboreal	0.659	0.337	3.397E-03	arboreal	0.607	0.388	0.004
Node.18	arboreal	0.674	0.323	3.289E-03	arboreal	0.671	0.326	0.003
Node.19	semi-terrestrial	0.300	0.666	3.358E-02	semi-terrestrial	0.177	0.765	0.058
Node.20	semi-terrestrial	0.233	0.710	5.704E-02	semi-terrestrial	0.155	0.762	0.082
Node.21	semi-terrestrial	0.106	0.740	0.154	semi-terrestrial	0.110	0.755	0.135
Node.22	semi-terrestrial	0.156	0.711	0.133	semi-terrestrial	0.172	0.728	0.100
Node.23	semi-terrestrial	0.372	0.596	3.141E-02	semi-terrestrial	0.312	0.647	0.041
Node.24	semi-terrestrial	0.440	0.538	2.209E-02	semi-terrestrial	0.473	0.511	0.016
Node.25	semi-terrestrial	0.456	0.524	2.039E-02	arboreal	0.496	0.491	0.013
Node.26	semi-terrestrial	0.436	0.542	2.242E-02	semi-terrestrial	0.370	0.600	0.030
Node.27	semi-terrestrial	0.300	0.666	3.358E-02	semi-terrestrial	0.314	0.640	0.046
Node.28	arboreal	0.525	0.463	1.213E-02	semi-terrestrial	0.491	0.494	0.014
Node.29	arboreal	0.999	1.253E-03	1.508E-06	arboreal	0.998	1.601E-03	2.301E-06
Node.30	arboreal	1.000	4.848E-04	2.888E-08	arboreal	1.000	4.484E-04	2.628E-08

Table 4.7b. Nodal reconstructions for the fossil added 10K phylogeny and modified Springer phylogeny with a combination of two elements and using two groups *a priori* with “semi-terrestrialists” as unknown

Node	**Classification - 10K Tree**	**PP Arb**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Ter**
Node.01	arboreal	1.000	7.731E-09	arboreal	1.000	6.019E-09
Node.02	arboreal	1.000	2.599E-09	arboreal	1.000	7.129E-08
Node.03	arboreal	1.000	2.518E-04	arboreal	0.995	4.538E-03
Node.04	arboreal	0.999	5.323E-04	arboreal	0.998	1.571E-03
Node.05	arboreal	1.000	3.833E-04	arboreal	0.999	6.867E-04
Node.06	arboreal	1.000	4.681E-04	arboreal	0.999	7.405E-04
Node.07	arboreal	1.000	5.802E-05	arboreal	1.000	3.210E-05
Node.08	arboreal	0.999	5.262E-04	arboreal	0.999	7.577E-04
Node.09	arboreal	1.000	4.288E-04	arboreal	0.999	5.340E-04
Node.10	arboreal	0.999	7.753E-04	arboreal	0.998	1.526E-03
Node.11	arboreal	0.984	1.580E-02	arboreal	0.957	0.043
Node.12	arboreal	0.995	4.851E-03	arboreal	0.996	0.004
Node.13	arboreal	0.995	4.586E-03	arboreal	0.994	0.006
Node.14	arboreal	0.994	5.509E-03	arboreal	0.994	0.006
Node.15	arboreal	0.991	8.677E-03	arboreal	0.989	0.011
Node.16	arboreal	0.996	3.516E-03	arboreal	0.996	0.004
Node.17	arboreal	0.997	3.182E-03	arboreal	0.996	0.004
Node.18	arboreal	0.997	3.204E-03	arboreal	0.997	0.003
Node.19	arboreal	0.928	7.163E-02	arboreal	0.816	0.184
Node.20	arboreal	0.838	0.162	arboreal	0.698	0.302
Node.21	terrestrial	0.402	0.598	terrestrial	0.458	0.542
Node.22	arboreal	0.528	0.472	arboreal	0.627	0.373
Node.23	arboreal	0.946	5.423E-02	arboreal	0.918	0.082
Node.24	arboreal	0.969	3.078E-02	arboreal	0.981	0.019
Node.25	arboreal	0.973	2.737E-02	arboreal	0.985	0.015
Node.26	arboreal	0.969	3.102E-02	arboreal	0.950	0.050
Node.27	arboreal	0.928	7.163E-02	arboreal	0.909	0.091
Node.28	arboreal	0.987	1.281E-02	arboreal	0.983	0.017
Node.29	arboreal	1.000	9.187E-07	arboreal	1.000	1.472E-06
Node.30	arboreal	1.000	6.527E-09	arboreal	1.000	6.027E-09

Table 4.7c. Nodal reconstructions for the fossil added 10K phylogeny and modified Springer phylogeny with a combination of two elements and using two groups *a priori* with “semi-terrestrialists” included in the terrestrial group

Node	**Classification - 10K Tree**	**PP Arb**	**PP Ter**	**Classification - Springer**	**PP Arb**	**PP Ter**
Node.01	arboreal	0.999	0.001	arboreal	0.999	0.001
Node.02	arboreal	1.000	2.543E-04	arboreal	0.999	0.001
Node.03	arboreal	0.899	0.101	arboreal	0.657	0.343
Node.04	arboreal	0.900	0.100	arboreal	0.881	0.119
Node.05	arboreal	0.911	0.089	arboreal	0.904	0.096
Node.06	arboreal	0.892	0.108	arboreal	0.881	0.119
Node.07	arboreal	0.948	0.052	arboreal	0.958	0.042
Node.08	arboreal	0.885	0.115	arboreal	0.877	0.123
Node.09	arboreal	0.888	0.112	arboreal	0.884	0.116
Node.10	arboreal	0.864	0.136	arboreal	0.828	0.172
Node.11	terrestrial	0.423	0.577	terrestrial	0.269	0.731
Node.12	arboreal	0.529	0.471	arboreal	0.518	0.482
Node.13	arboreal	0.545	0.455	terrestrial	0.495	0.505
Node.14	arboreal	0.553	0.447	arboreal	0.519	0.481
Node.15	arboreal	0.502	0.498	terrestrial	0.461	0.539
Node.16	arboreal	0.636	0.364	arboreal	0.596	0.404
Node.17	arboreal	0.651	0.349	arboreal	0.596	0.404
Node.18	arboreal	0.655	0.345	arboreal	0.654	0.346
Node.19	terrestrial	0.273	0.727	terrestrial	0.162	0.838
Node.20	terrestrial	0.208	0.792	terrestrial	0.140	0.860
Node.21	terrestrial	0.094	0.906	terrestrial	0.098	0.902
Node.22	terrestrial	0.143	0.857	terrestrial	0.154	0.846
Node.23	terrestrial	0.359	0.641	terrestrial	0.303	0.697
Node.24	terrestrial	0.440	0.560	terrestrial	0.484	0.516
Node.25	terrestrial	0.454	0.546	arboreal	0.501	0.499
Node.26	terrestrial	0.445	0.555	terrestrial	0.371	0.629
Node.27	terrestrial	0.273	0.727	terrestrial	0.314	0.686
Node.28	arboreal	0.555	0.445	arboreal	0.508	0.492
Node.29	arboreal	0.998	0.002	arboreal	0.997	0.003
Node.30	arboreal	0.999	0.001	arboreal	0.999	0.001

Figure 4.1. Differences in topology between a) the 10K phylogeny and b) the modified Springer et al. (2012) phylogeny.

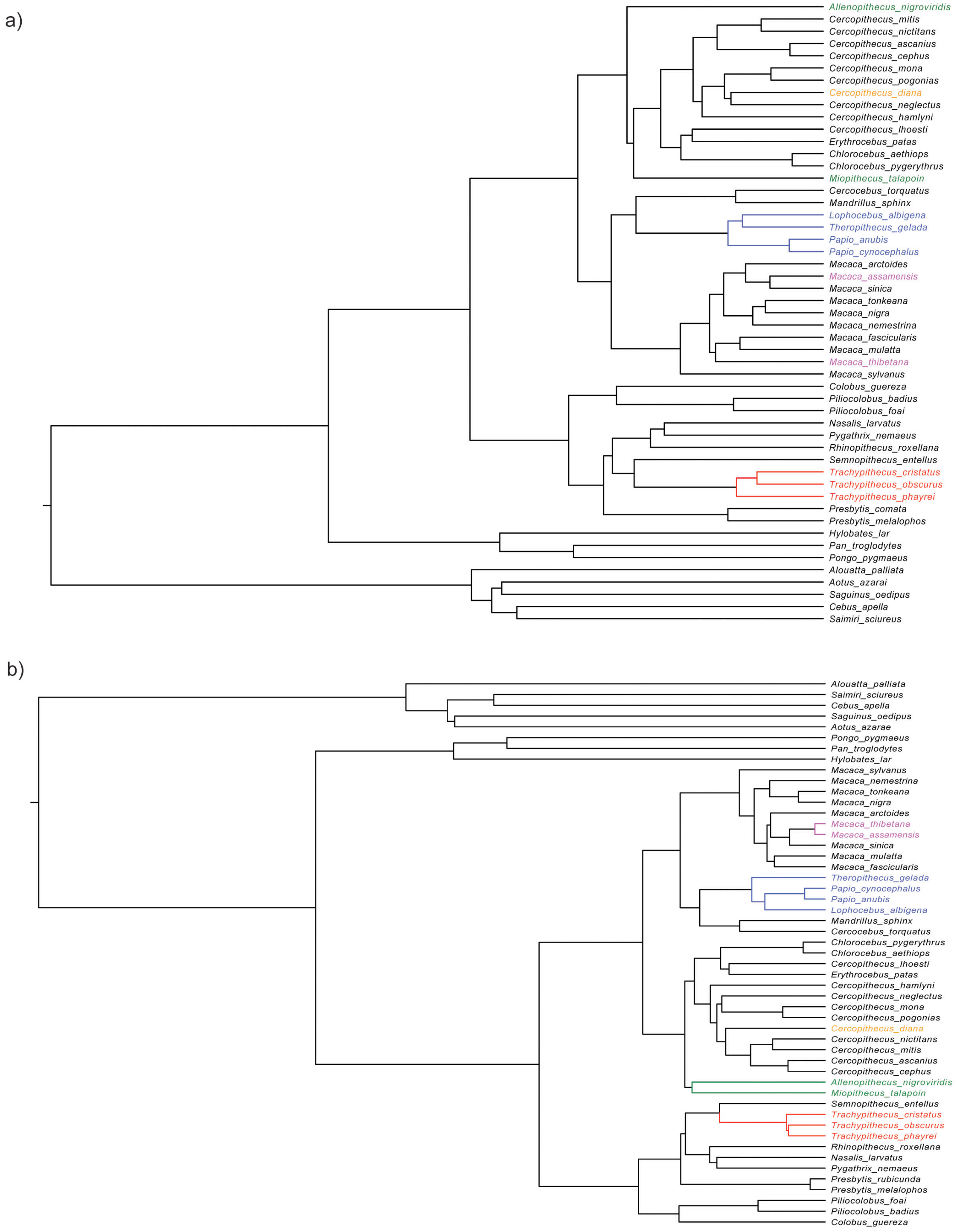
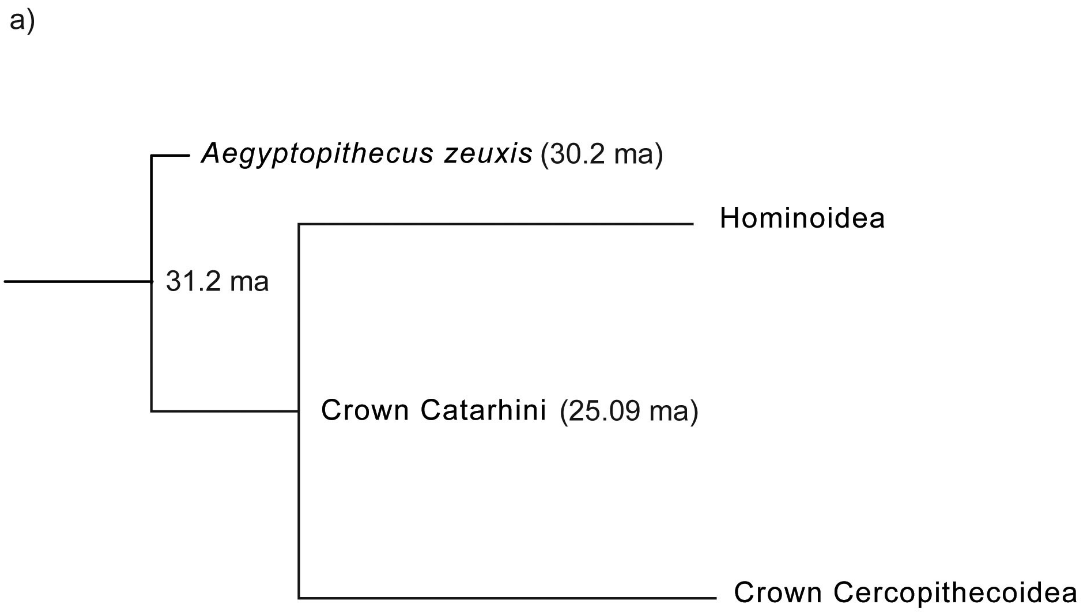


Figure 4.2. Schematic of divergences for a) *Aegyptopithecus* and b) *Theropithecus oswaldi* and *Theropithecus brumpti* on the modified Springer et al. (2012) phylogeny.



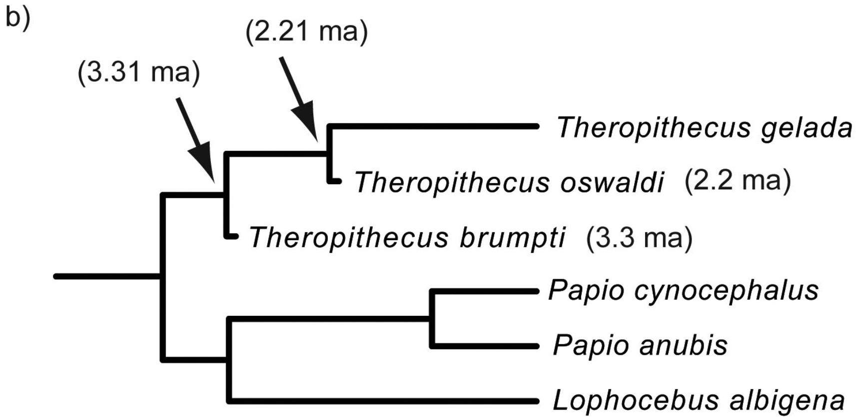


Figure 4.3. Nodes reconstructed in ASR analysis (10K tree phylogeny is presented although the nodes are the same along the modified Springer et al. 2012 phylogeny)

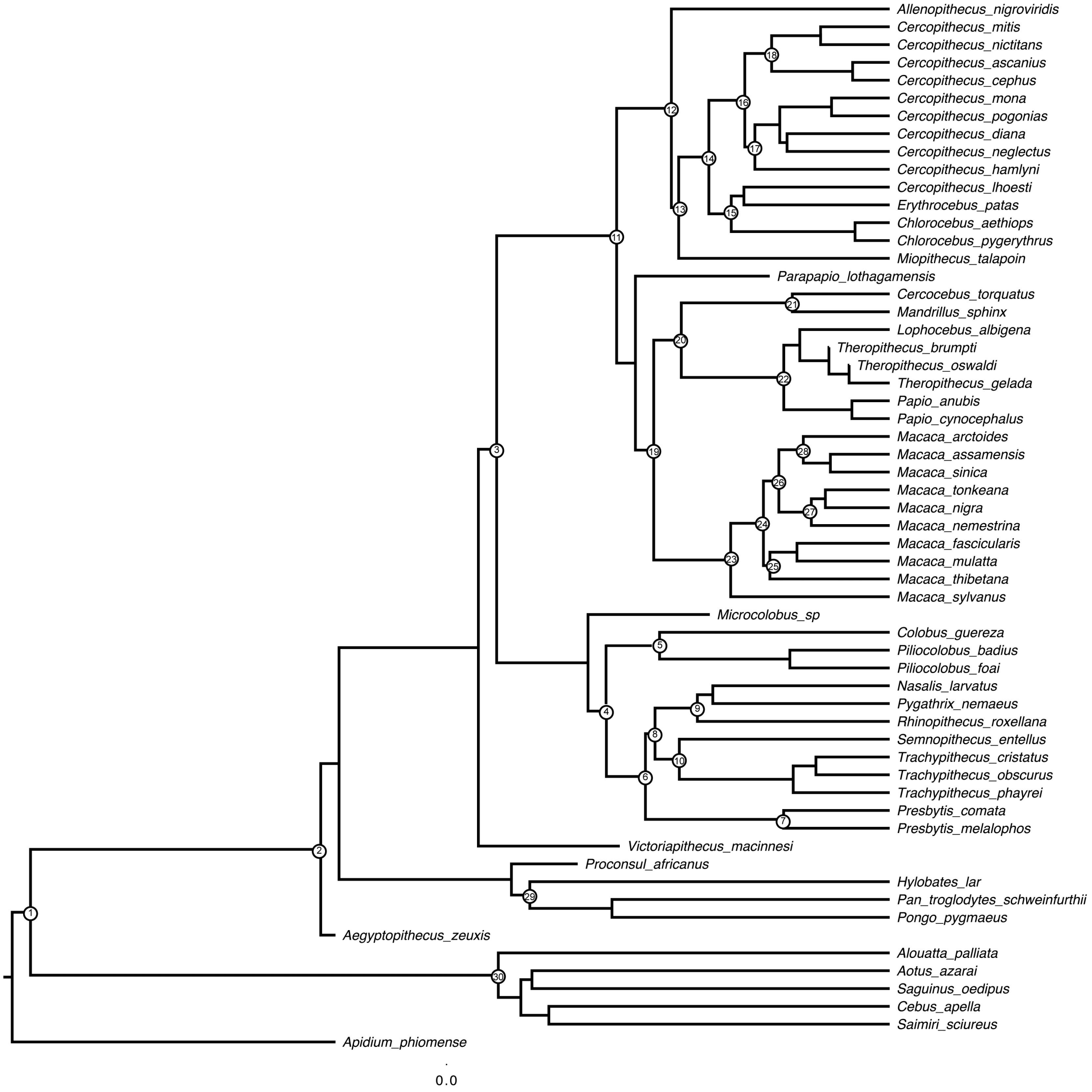


Figure 4.4. Character trait evolution for the humeral head index (HHI) along a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 2 added fossils (y-axis is in log10 scale)

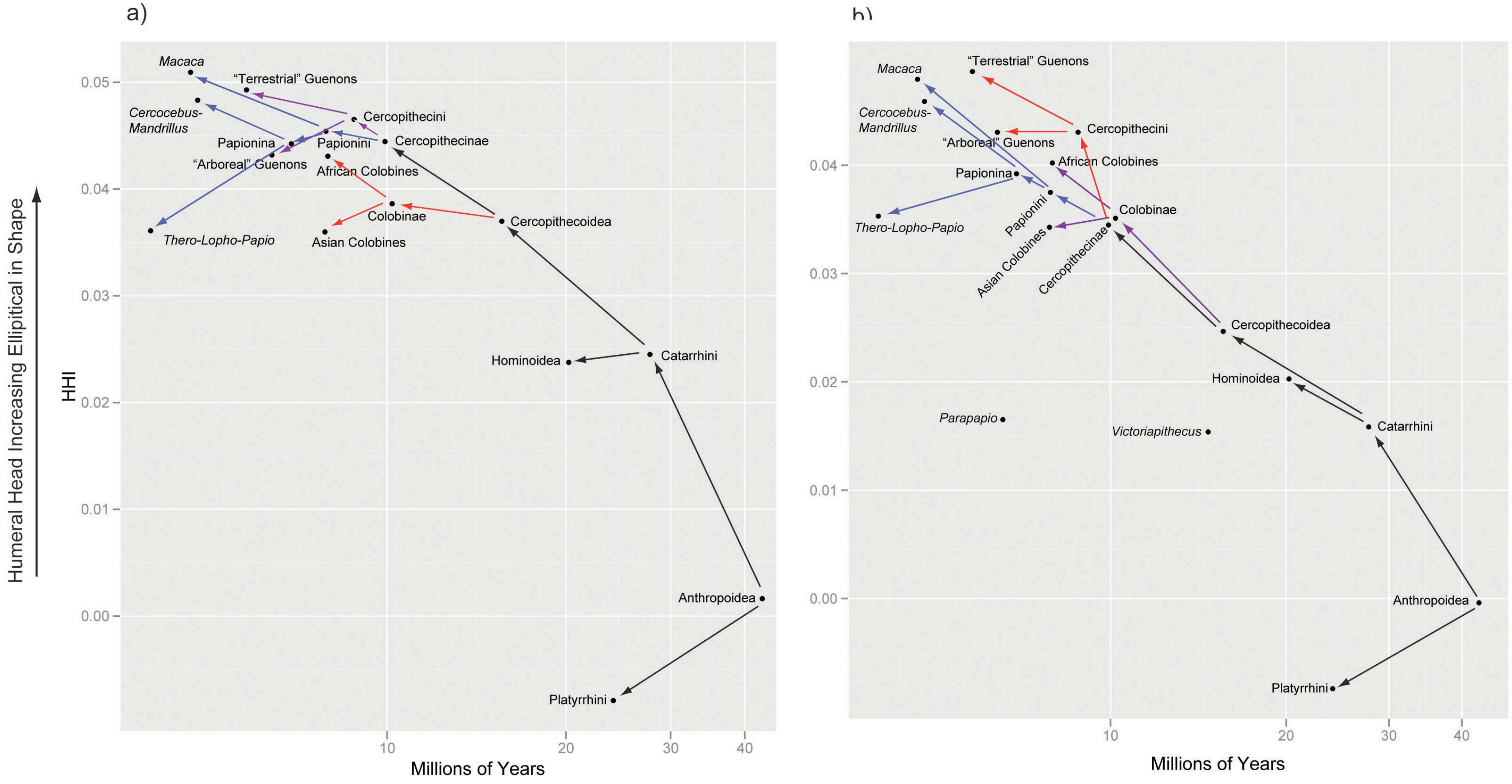


Figure 4.5. Character trait evolution for the height of the greater tubercle (GTH) along a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 2 added fossils (y-axis is in log10 scale)

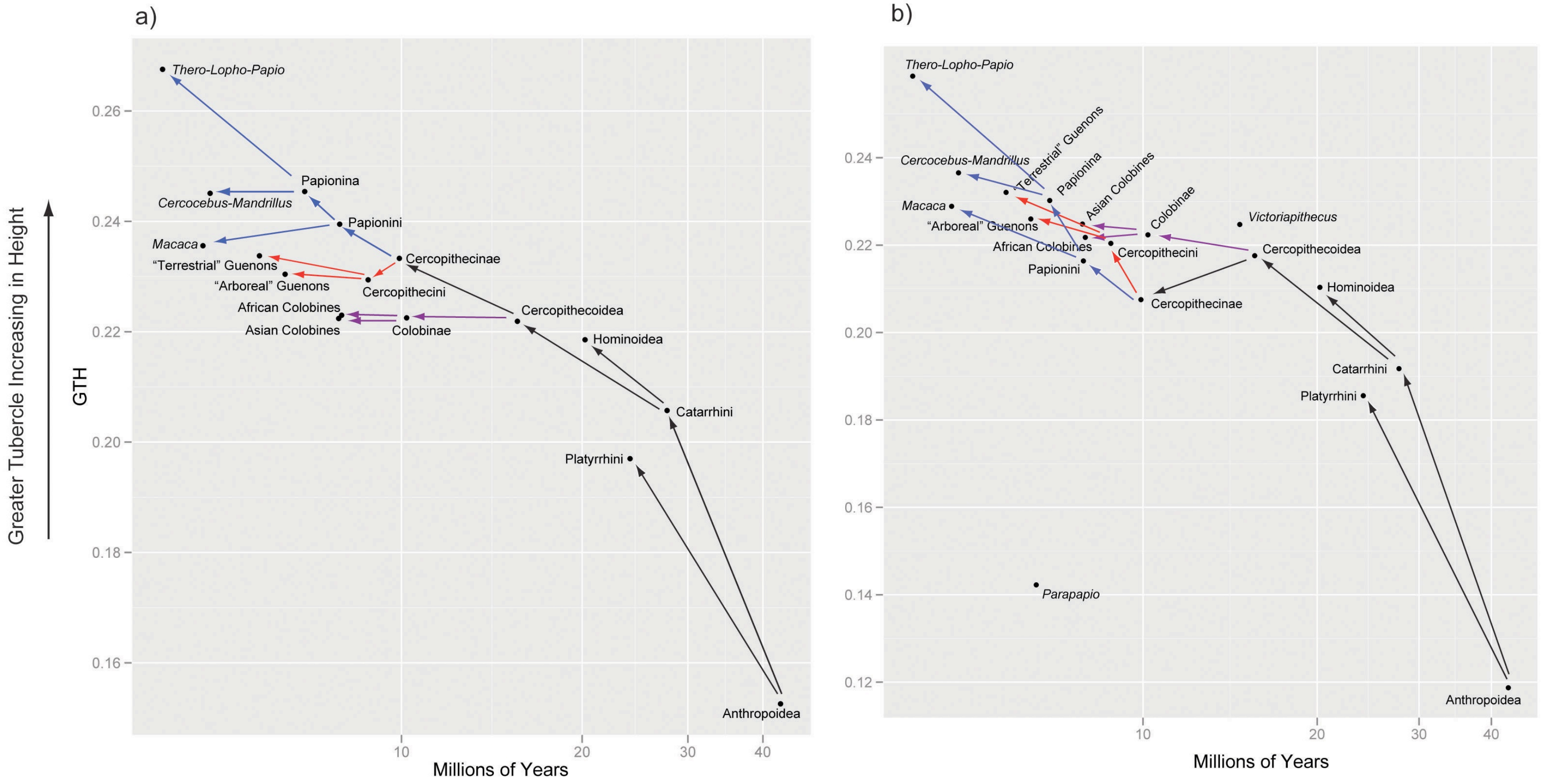


Figure 4.6. Character trait evolution for the angle of the medial epicondyle (AME) along a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

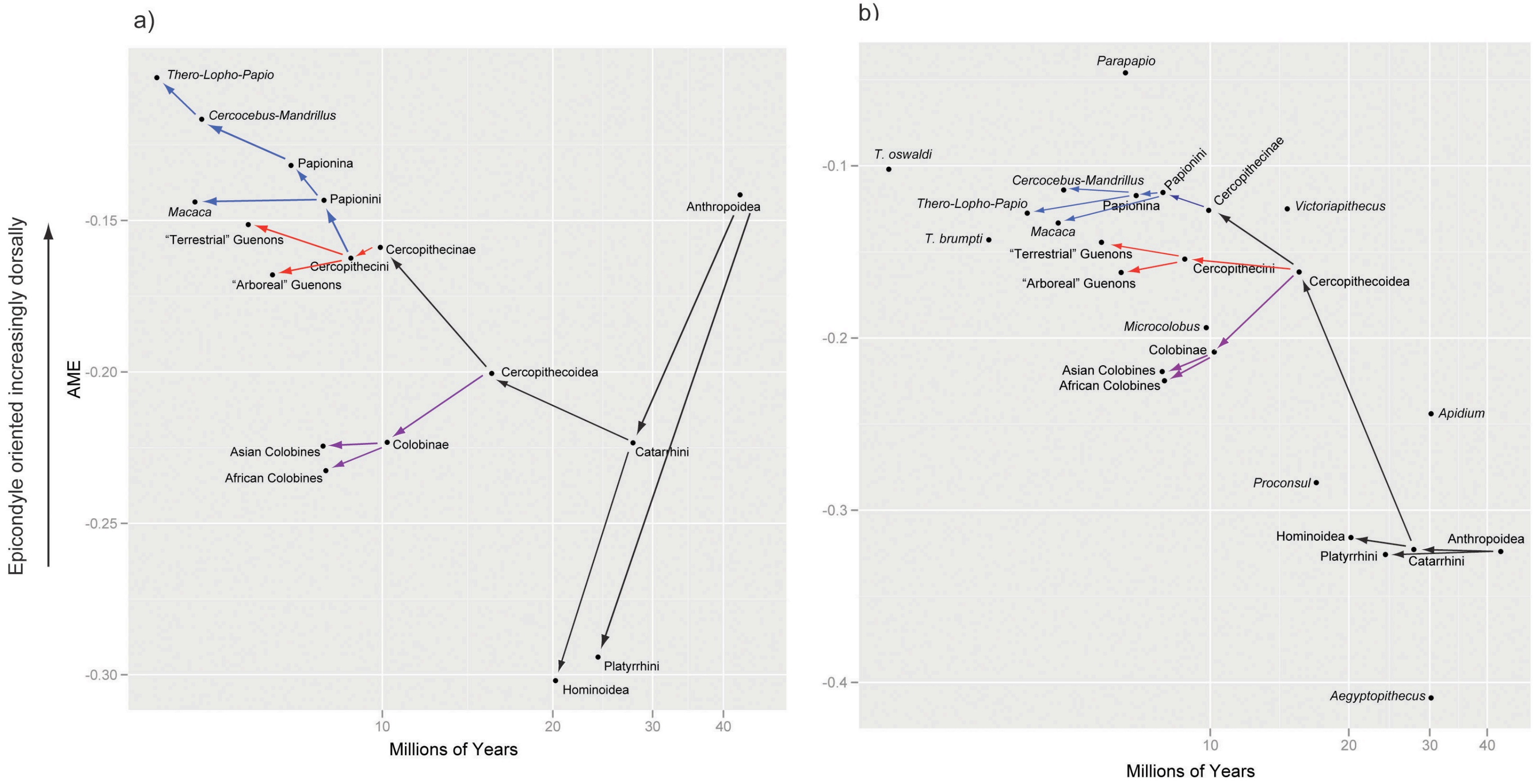


Figure 4.7. Character trait evolution for the overall length of the astragalus (AL) along a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

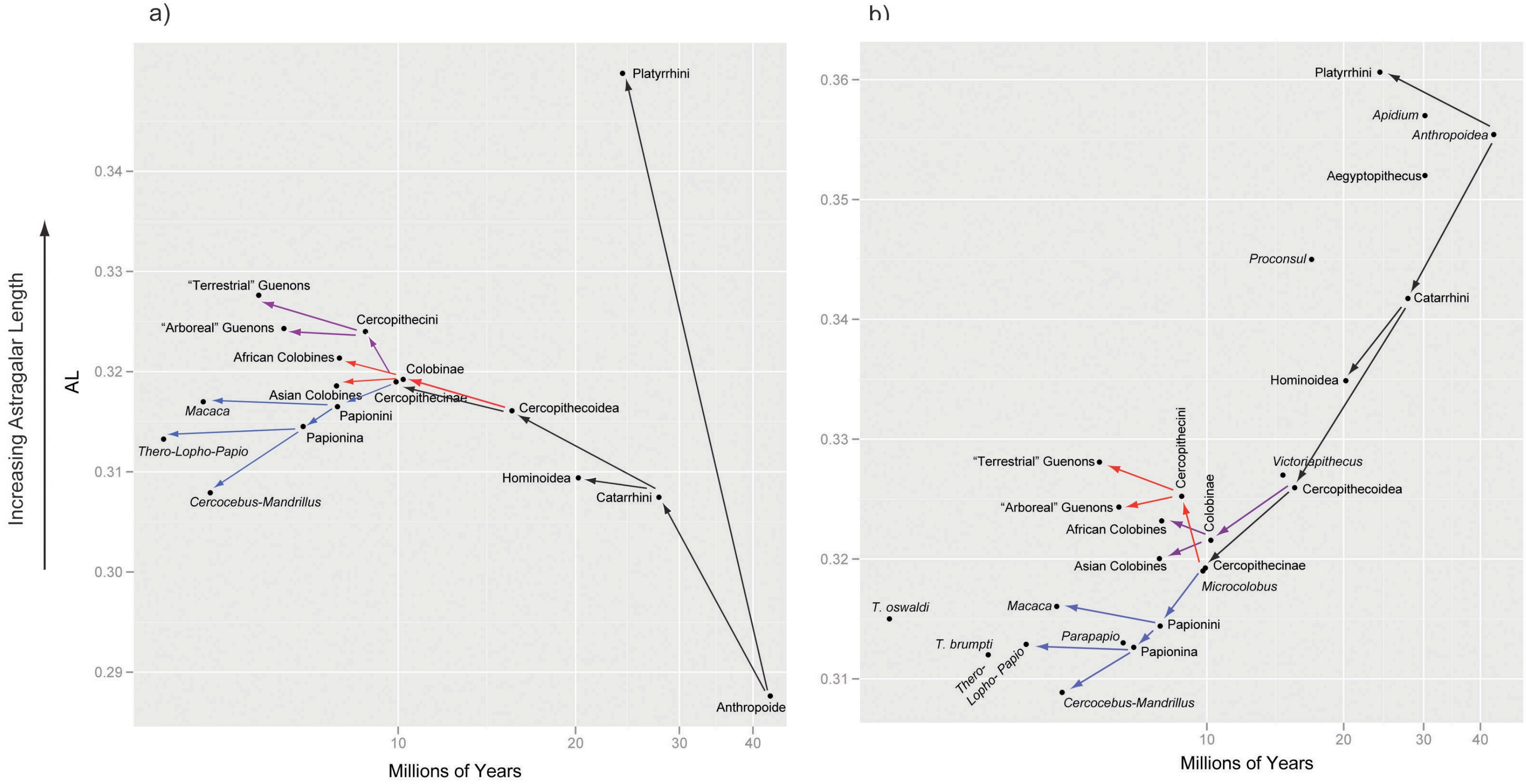


Figure 4.8. Character trait evolution for the ectal facet length (EL) along a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

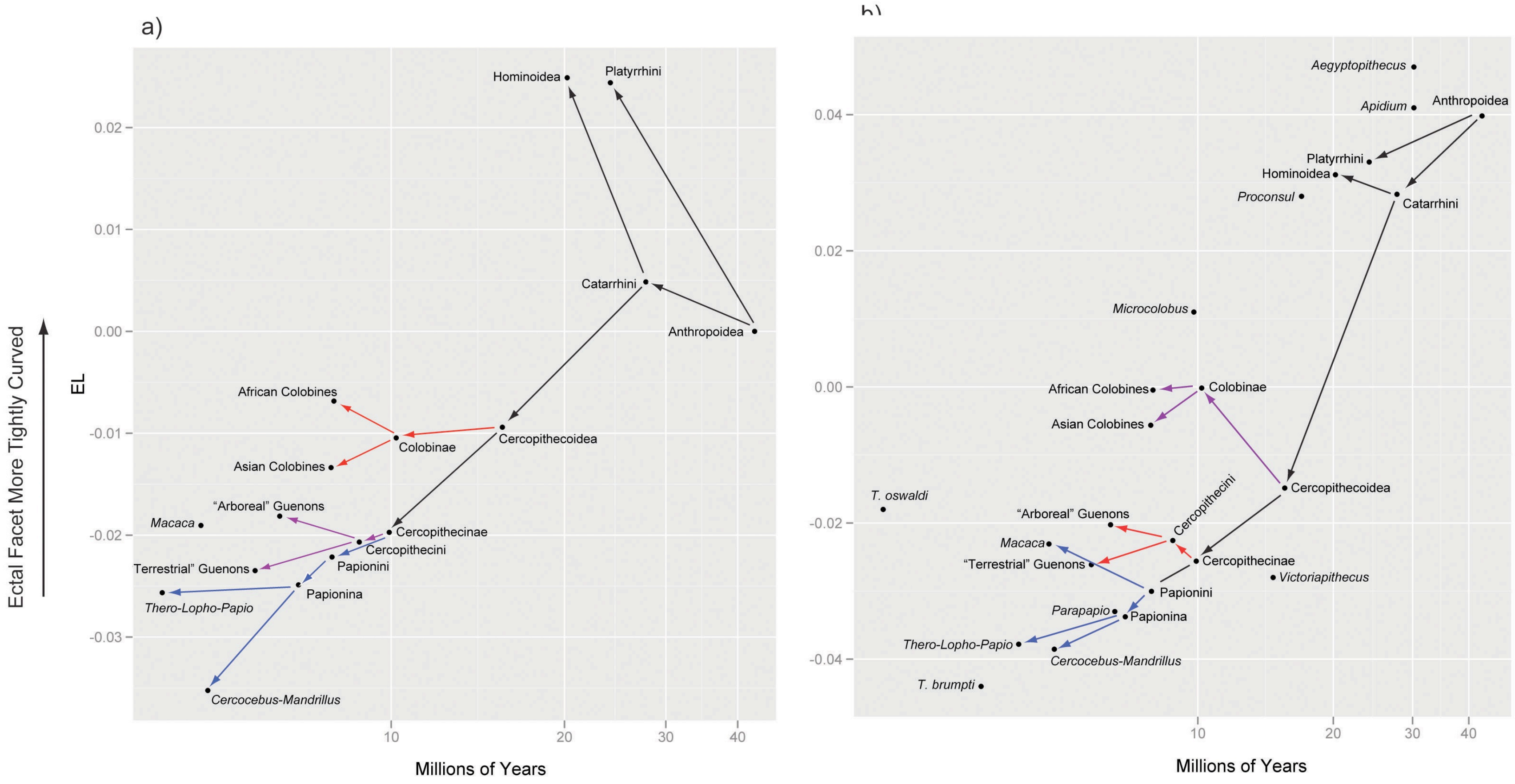


Figure 4.9. 95% confidence intervals for HHI for 15 reconstructed nodes for a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

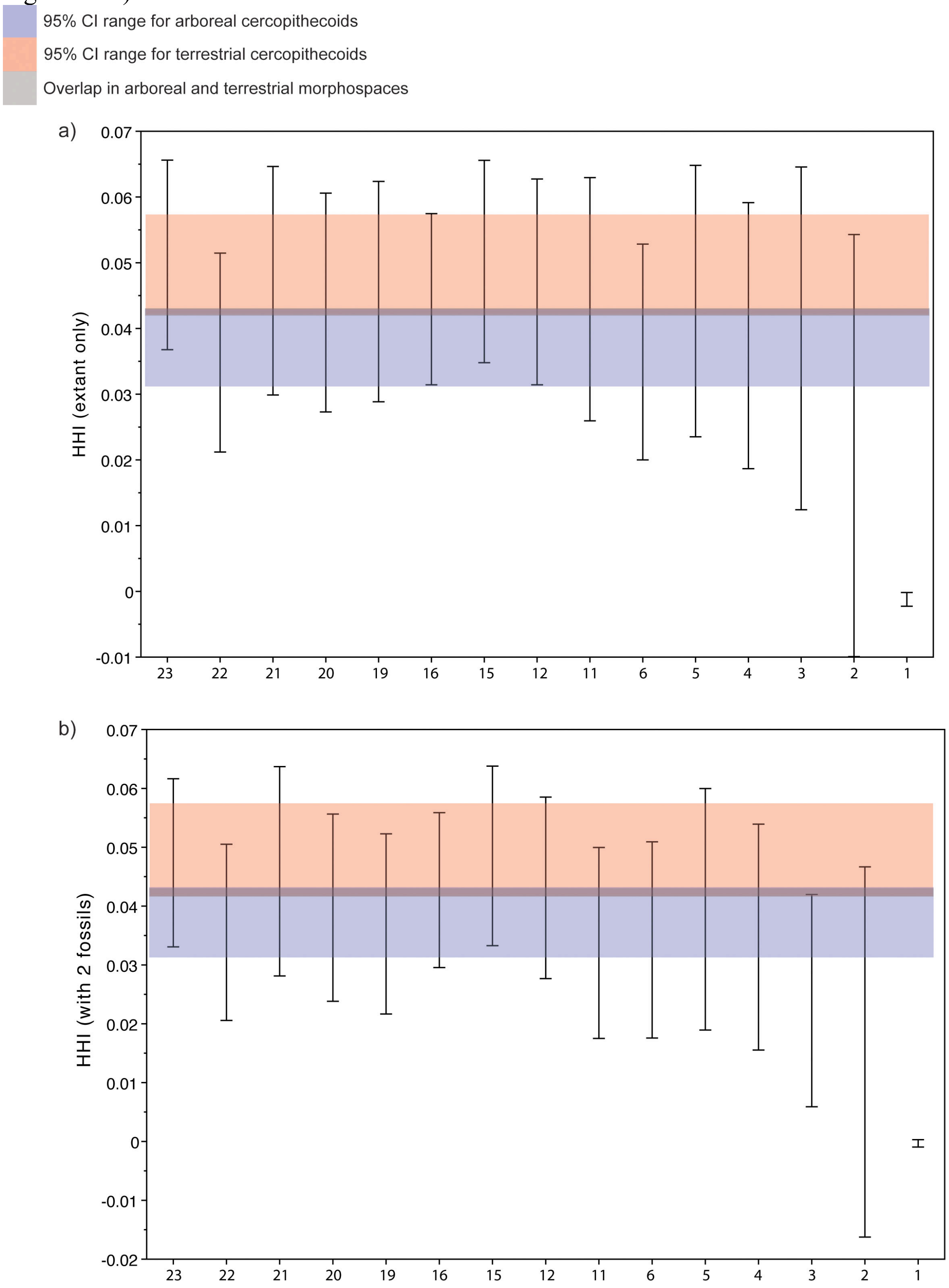


Figure 4.10. 95% confidence intervals for GTH for 15 reconstructed nodes for a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

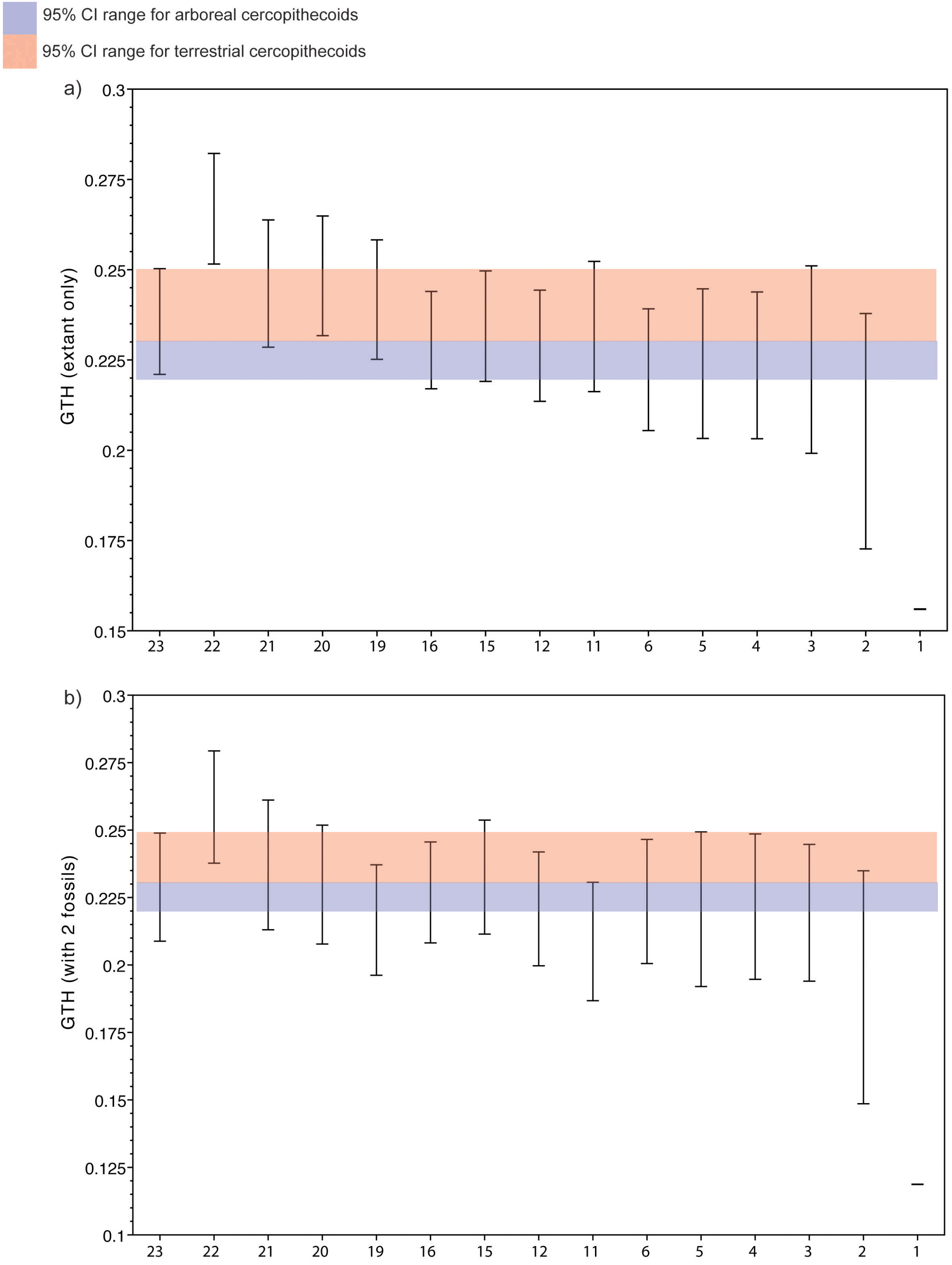


Figure 4.11. 95% confidence intervals for AME for 15 reconstructed nodes for a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

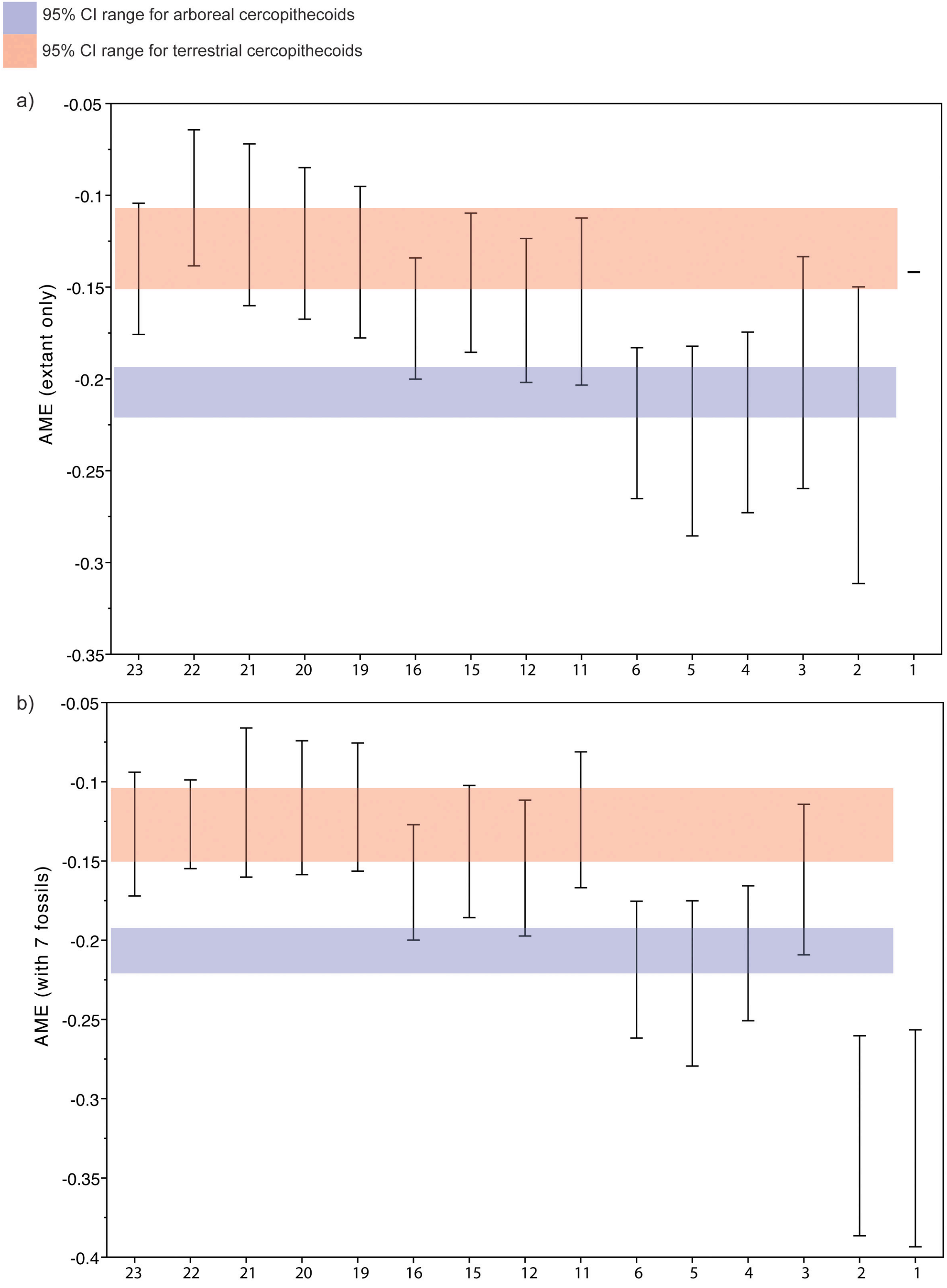


Figure 4.12. 95% confidence intervals for AL for 15 reconstructed nodes for a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

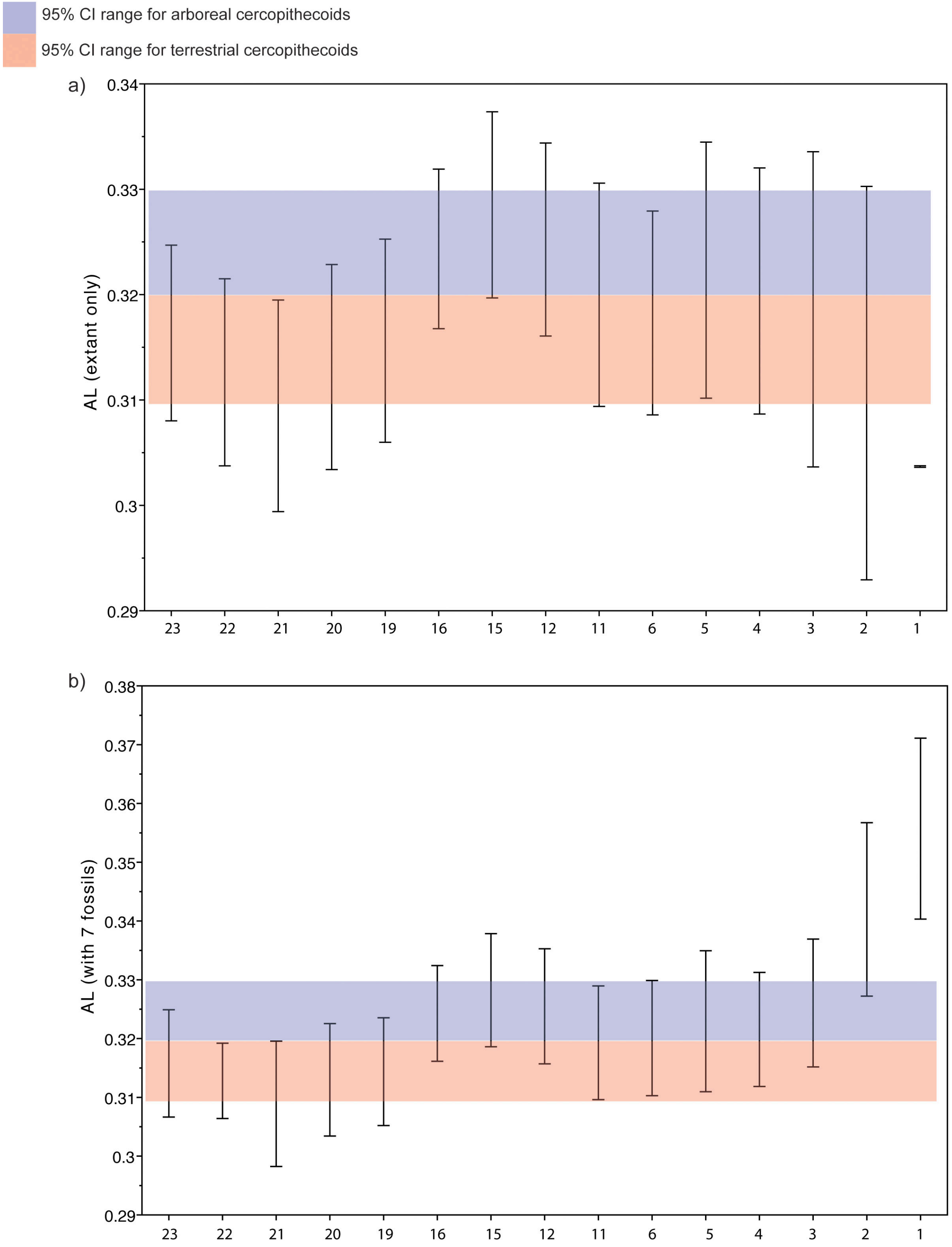


Figure 4.13. 95% confidence intervals for EL for 15 reconstructed nodes for a) the extant-only modified Springer phylogeny and b) the Springer phylogeny with 7 added fossils (y-axis is in log10 scale)

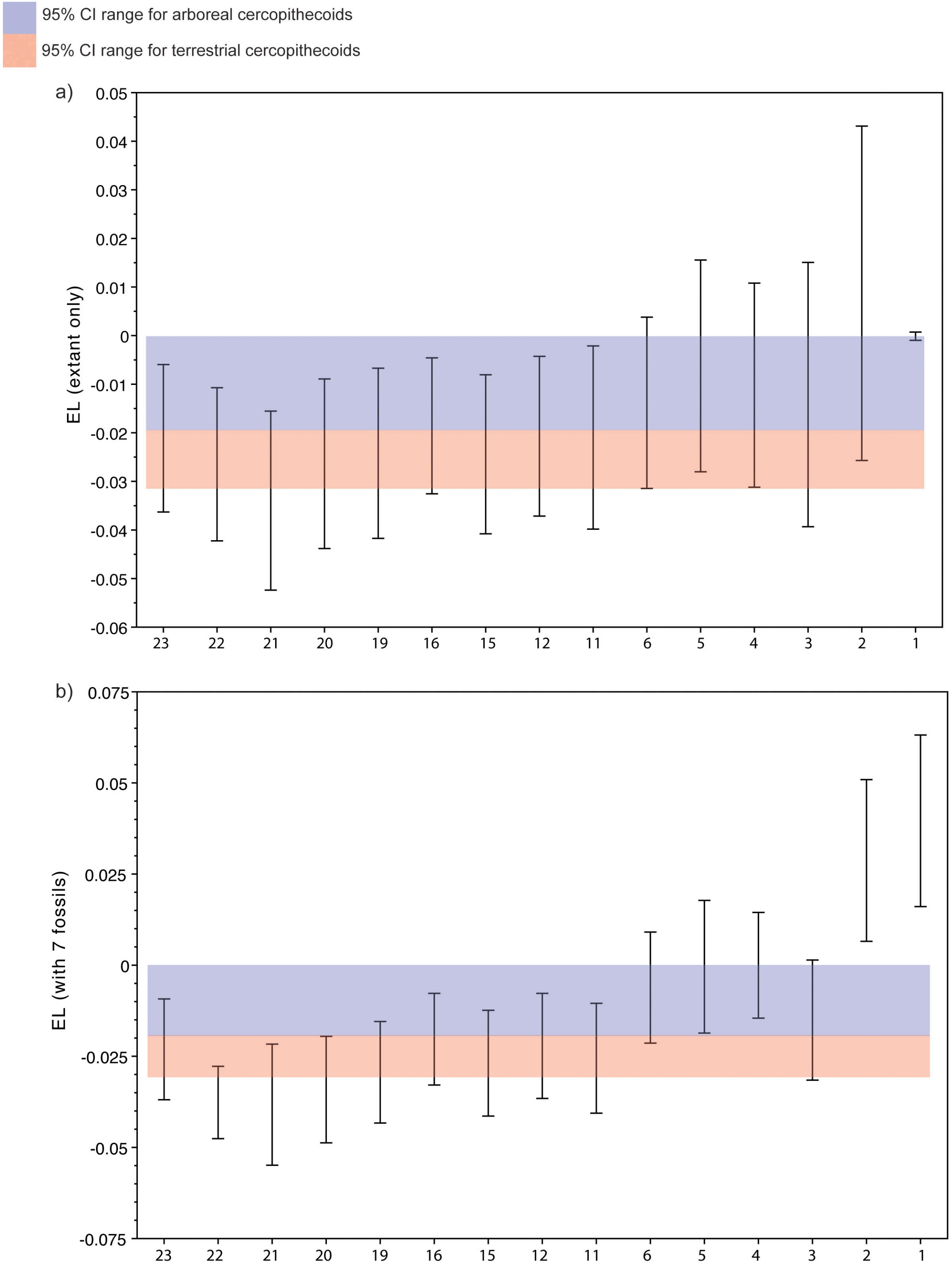
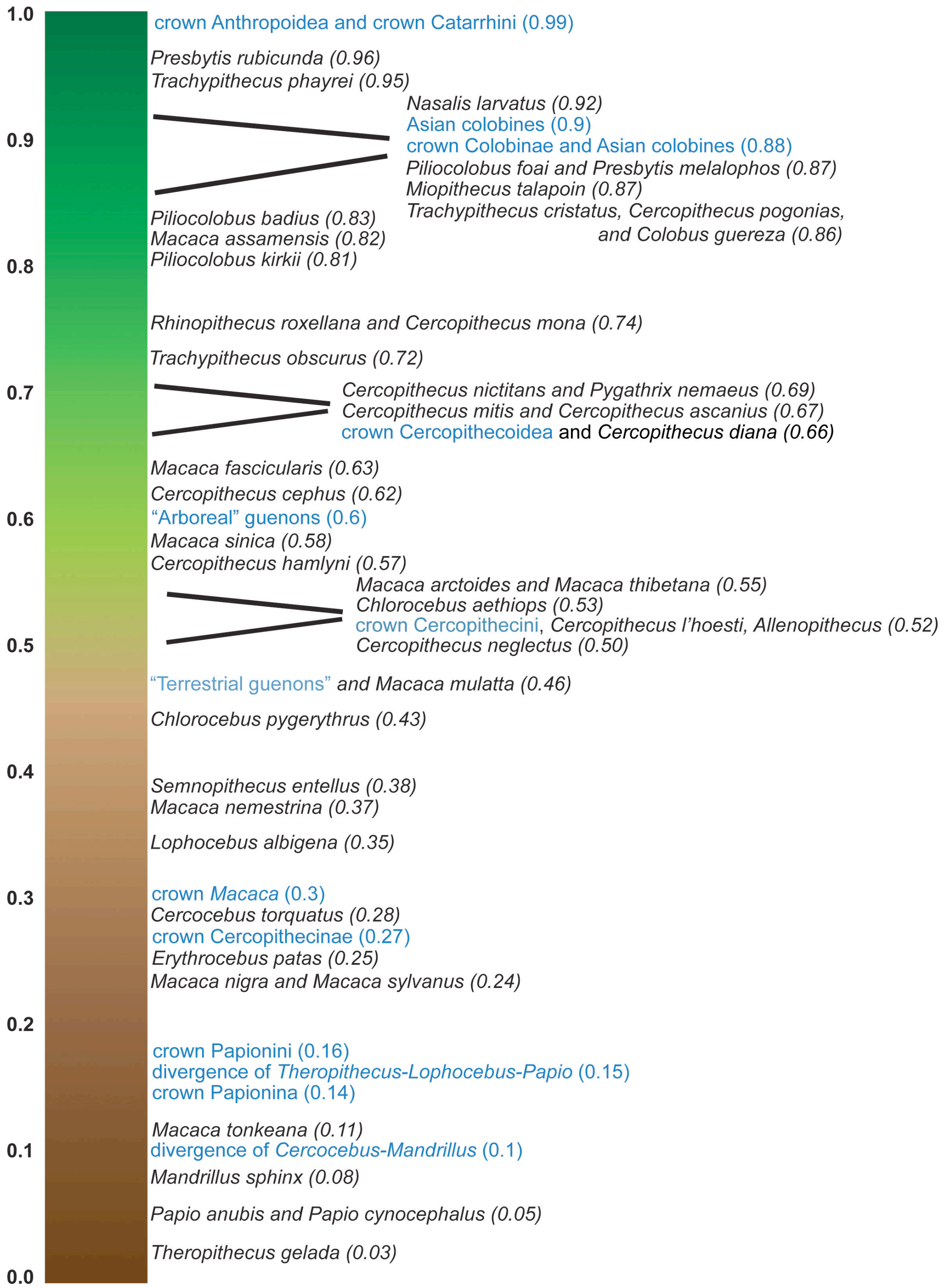


Figure 4.14. Posterior probabilities of being assigned to the arboreal group using a combination of the distal humerus and astragalus along a color gradient. 1.0 = 100% probability of being assigned to the arboreal group and 0.0 = 0% probability of being assigned to the arboreal group.



Chapter 5
Conclusions

The aim of this dissertation was to examine postcranial diversity of cercopithecoids within an explicitly phylogenetic framework and to reassess hypotheses of locomotor evolution in this clade. Although much previous work on the cercopithecoid postcranium has been successful in documenting associations between morphology and behavior (Jolly 1967; Etter 1973; Manaster 1979; Rodman 1979; Strasser 1988; Harrison 1989; Ciochon 1993; Larson 1993; Gebo and Sargis 1994; Nakatsukasa 1994; Elton 2002; Su and Jablonski 2009; Patel 2010), recent advances in phylogenetic comparative methods necessitated a reexamination of this work to determine if these associations still hold under phylogenetically informed statistical models. The analyses undertaken in this dissertation improve upon previous studies by identifying features that are well-associated with locomotor behavior regardless of the shared evolutionary history among species. In addition, recent discoveries of cercopithecoid postcrania (Frost and Delson 2002; Hlusko 2006; Nakatsukasa et al. 2010) have added complexity to the hypothesized pattern of locomotor transitions in Cercopithecoidea. This dissertation sought not only to reconstruct locomotor behavior of stem and crown fossil cercopithecoids, but also to incorporate fossil material in ancestral state reconstruction (ASR) analyses to better inform the evolution of morphological traits associated with behavior and the ancestral condition within important crown groups in Cercopithecoidea. This chapter summarizes the major findings of the dissertation and its significance to the fields of primate evolution and physical anthropology generally.

The main goal of Chapter 2 was to document postcranial diversity of 44 cercopithecoid species, including 16 papionin, 13 colobine, and 15 guenon species using standard and phylogenetically informed univariate statistics to determine morphological features that best separated species according to either substrate preference or phylogeny. Analyses examined a cercopithecoid-only dataset using two different behavioral codings. Coding 1 assigned species to 3 *a priori* groups – arboreal, semi-terrestrial, and terrestrial. This coding sought to determine which morphological features, if any, best differentiated semi-terrestrial species from primarily arboreal and primarily terrestrial species. Coding 2 assigned species to 2 *a priori* groups of arboreal and terrestrial (with all semi-terrestrial species from Coding 1 included in the terrestrial group). Coding 2 sought to identify morphological features that separated primarily arboreal species from those that engaged in at least a moderate amount of terrestrial behavior. Finally, multivariate analyses sought to determine if a combination of weighted variables separated locomotor groups better than individual variables alone.

The univariate analyses document several features that are associated with locomotor behavior in cercopithecoids (see Table 2.3). Generally these features separated primarily arboreal from primarily terrestrial cercopithecoids, but behaviorally semi-terrestrial cercopithecoids overlapped with both groups in the morphospace. Multivariate analyses also document a similar morphological continuum. Although the behaviorally "semi-terrestrial" cercopithecoids occupied an intermediate space between primarily arboreal and primarily terrestrial species, this space substantially overlapped with the two other locomotor groups and suggests the absence of a unique "semi-terrestrial" morphology. Semi-terrestrial cercopithecoids may be intermediate in their morphology but the variation among species is wide as can be seen in Figures from Chapter 2. Semi-terrestrial species may resemble primarily arboreal species, primarily terrestrial species, or fall between the ranges of these groups. Arguably, all cercopithecoids are "semi-terrestrial" and even the morphology of the most arboreal cercopithecoids does not prohibit them from utilizing the ground if necessary; even different species of *Papio* are known to engage in different amounts of climbing and arboreal behavior (See Appendix A). However, Chapter 2 illustrates the utility of using a three group *a priori* classification for purposes of differentiating primarily arboreal from primarily terrestrial cercopithecoids. When "semi-terrestrial" and primarily terrestrial cercopithecoids are combined into one locomotor group (i.e., Coding 2), substantial overlap exists with the arboreal group because there is greater variation in the "expanded" terrestrial group. As can be seen in the Figures from Chapter 2, the morphospaces of these two groups overlap substantially both in univariate and multivariate analyses. Therefore, although reconstruction of locomotor behavior in fossil cercopithecoids may not be able to specify the amount of time a species likely spent on the ground, use of Coding 1 can determine if a fossil species was primarily arboreal or primarily terrestrial. Additionally, if a fossil species is reconstructed as "semi-terrestrial" then we can be confident that this species was as adept at utilizing both arboreal substrates and the ground as many cercopithecoids are today.

Overall, the results from Chapter 2 were consistent with previous studies of cercopithecoid postcranial morphology that have documented associations between morphology and behavior (Strasser 1988; Harrison 1989; Ciochon 1993; Larson 1993; Nakatsukasa 1994; Elton 2002). The use of phylogenetically informed statistics in Chapter 2 strengthens these associations. These features are used in Chapter 3 to determine whether discriminant function analyses could classify individuals to their *a priori* locomotor grouping, thereby providing a quantitative means by which locomotor behavior might be reconstructed in fossil stem and crown cercopithecoids. These features are also used in ASR analyses in Chapter 4 to study trait evolution and to reconstruct the ancestral locomotor mode at important divergences in cercopithecoid evolution.

The aim of Chapter 3 was twofold. First, discriminant function analyses sought to determine which combinations of variables best classified individuals to *a priori* groups. DFAs were run using variables from single elements (i.e., the humerus, femur, astragalus, and calcaneus alone) and using variables from a combination of elements (i.e., all four elements combined; or a combination of the humerus, astragalus, and calcaneus; or a combination of the distal humerus and astragalus). Second, the discriminant function analyses were used to reconstruct locomotor behavior in fossil stem and crown cercopithecoids. Of particular interest in this chapter were the behavioral reconstructions of *Victoriapithecus* and *Microcolobus*, which both influence our understanding of locomotor behavior early in cercopithecoid evolution. Previous reconstructions of *Victoriapithecus* as partly terrestrial have largely supported the hypothesis that the LCA of crown cercopithecoids regularly engaged in terrestrial behavior (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a; Leakey et al. 2003). The recent description of *Microcolobus*, a probable stem colobine (Rossie et al. 2013), as primarily arboreal suggests that colobines inherited their arboreal behavior from the LCA of crown Colobinae (Nakatsukasa et al. 2010). The appearance of arboreality on the colobine stem lineage also suggests an alternative evolutionary scenario in which arboreality was inherited from the LCA of crown Cercopithecoidea and that terrestriality evolved later in the group's evolution.

The DFAs in Chapter 3 show patterns that are similar to those of the univariate and multivariate analyses in Chapter 2. Arboreal and terrestrial individuals are generally well-separated in the morphospace with behaviorally "semi-terrestrial" species overlapping with both groups. When two *a priori* groups are used in the DFAs, the arboreal and terrestrial groups (i.e., semi-terrestrial and terrestrial individuals) show substantial overlap. Generally, analyses were successful in classifying arboreal individuals to their *a priori* grouping (posterior probabilities generally above 0.8). However, classification of semi-terrestrial and terrestrial individuals varied widely depending on which element, or combination of elements, were used. The best classification rates for these groups were in analyses that included either a combination of elements, or the complete humerus alone. Variables from the proximal humerus and astragalus had the lowest classification rates for these groups, suggesting that locomotor reconstructions based solely on these elements should be considered with caution and reevaluated when additional fossil material is available.

Another set of DFAs examined classification rates when behaviorally semi-terrestrial individuals were left as unknown. Overall classification rates improved, with arboreal individuals correctly classified at a rate above 90%. Classification of terrestrial individuals improved, especially when using the humerus or a combination of elements, with individuals correctly classified at a rate of over 80%. The proximal humerus and astragalus still provided low classification rates of 40% and 44%, respectively. Classification of semi-terrestrial species left as unknown showed that most species are assigned to the arboreal group. This result is likely because the terrestrial group included only the species most committed to terrestrial behavior, and the morphology of semi-terrestrial species probably more closely resembles arboreal species than these committed terrestrial species. *Papio anubis* is consistently assigned to the terrestrial group, which reveals that, despite having a "terrestrial" morphology, this species is nevertheless adept at climbing and arboreal behavior (Appendix A). A few species, such as *Cercocebus torquatus*, *Erythrocebus patas, Macaca nigra, Macaca tonkeana,* and *M. sylvanus*, are inconsistently assigned to the arboreal and terrestrial group depending on which element, or groups of elements, are used. These results show that some "semi-terrestrial" species may have morphological adaptations for both arboreal or terrestrial behavior in different regions of the postcranium.

Although some of the DFAs presented in Chapter 3 have low classification rates, the results show that either the humerus considered alone, or a combination of variables from different elements, can be used with some confidence in reconstructing locomotor behavior in fossil cercopithecoids. Elements from 15 species of fossil stem or crown cercopithecoids were classified by the DFAs using single elements and composite specimens and associated postcrania were classified by the DFAs using a combination of elements. One of the most important findings of Chapter 3 is that *Victoriapithecus* probably engaged in more arboreal behavior than previously thought. *Victoriapithecus* was classified as arboreal by most single elements and the composite specimen was classified as arboreal by all DFAs. Most distal humeri of *Victoriapithecus* are classified as semi-terrestrial. Given that the angle of the medial epicondyle is the highest loading variable in the DFA on the distal humerus and that *Victoriapithecus* has a more dorsally oriented medial epicondyle than arboreal cercopithecoids (see Figures 3.10 and 3.12), it is possible that *Victoriapithecus* engaged in a limited amount of terrestrial behavior. However, all other analyses are suggestive of a primarily arboreal lifestyle for *Victoripithecus*. Figure 3.8 shows the posterior probability of being placed in the arboreal group along a color gradient and *Victoriapithecus* (0.75) falls near *Macaca fascicularis* (0.72), *Cercopithecus mona* (0.76), *Cercopithecus ascanius*, *Ceropithecus cephus*, and *Miopithecus talapoin* (0.77). *Semnopithecus* was classified as arboreal by all analyses in which behaviorally "semi-terrestrial" individuals were left as unknown (see also Figures 3.7-3.9), but this species was an outlier among colobines in plots of phylogenetic differences in AME in Chapter 2 (Figure 2.3a). *Semnopithecus* is seasonally terrestrial, spending approximately 34% of its time on the ground during the dry season (see Appendix A). Although, the results from Chapter 3 show that the postcranial morphology of *Semnopithecus* is primarily adapted to arboreal behavior, it appears that a more dorsally directed medial epicondyle might be an important adaptation for the limited amount of time this species spends on the ground during the dry season. These results do not suggest that *Victoriapithecus* was necessarily seasonally terrestrial (although that is a possibility) but rather provides an example of a species with a relatively dorsally directed medial epicondyle that is nevertheless primarily arboreal.

The results from Chapter 3 also support the reconstruction of *Microcolobus* as primarily arboreal by Nakatsukasa et al (2010). Given that *Victoriapithecus* was likely more arboreal than previously thought (McCrossin et al. 1998; Benefit 1999b; Benefit 1999a) it is likely that colobines inherited this locomotor behavior from the LCA of crown cercopithecoids. Although colobines may have become more dedicated to arboreality, based on the classification of *Microcolobus* to the arboreal group by all sets of analyses, they most likely inherited a *bauplan* largely adapted for life in an arboreal setting.

If the LCA of crown Cercopithecoidea was primarily arboreal, then terrestriality in various colobines, guenons, and papionins would be a specialized condition. The timing of these locomotor transitions is the subject of Chapter 4. This chapter presents ASR analyses and patterns of trait evolution to determine the most likely ancestral locomotor mode at important divergences in cercopithecoid evolution, and the pattern of locomotor evolution across the clade. ASR analyses were run across extant-only phylogenies and phylogenies with added fossil taxa. Overall all ASR analyses recovered similar patterns of trait evolution and consistently reconstructed locomotor behavior for ancestral nodes despite differences in branch lengths among the phylogenies used. However, the results clearly show that adding fossil taxa, especially near deep divergences, is important for reconstructing an accurate root node. The root node, in the case of these phylogenies, is crown Anthropoidea, and the extant-only phylogenies and the phylogenies with two added fossils generally recovered a "cercopithecoid-like" morphology for crown Anthropoidea. However, when the phylogeny with eight added fossils (including Oligocene *Aegyptopithecus* and *Apidium*) was used, the morphology for crown Anthropoidea was more similar to the morphologies reconstructed for crown Platyrrhini and crown Catarrhini.

ASR reconstructions and patterns of trait evolution show that arboreality was likely the primary locomotor behavior in crown Cercopithecoidea and crown Colobinae. Generally, crown colobines retained a similar character state to that of crown Cercopithecoidea. Morphologies associated with terrestrial behavior are likely to have evolved in the LCA of crown Cercopithecinae. This result suggests that terrestrial behavior of guenons and papionins was inherited from their LCA and that the primarily arboreal behavior in some guenons and macaques was secondarily evolved. The evolution of committed terrestriality likely evolved independently along the *Macaca thibetana*, *Mandrillus*, *Papio*, and *Theropithecus* lineages and an increase in arboreality evolved convergently along the *Cercocebus* and *Lophocebus* lineages. Finally, Crown *Macaca* diverged from Papionina around 4.7 mya (see autocorrelated hard-bounded tree from Springer et al. 2012) and underwent a fairly diversification throughout Asia. Figure 5.2 shows that although Crown *Macaca* has a probability of being assigned to the arboreal group of 0.3, by the present day this genus is represented by an ecological diverse set of species, which range their probabilities of being assigned to the arboreal group from 0.11 (*Macaca tonkenana*) to 0.82 (*Macaca assamensis*). These reconstructions provide a new framework for locomotor evolution in cercopithecoids and new hypotheses that can be tested with future fossil discoveries. Discovery of stem cercopithecines would be particularly important for testing the hypothesis that a shift to increased use of terrestrial substrates occurred along the cercopithecine stem lineage.

This dissertation focused on the humerus, femur, astragalus, and calcaneus because of their previously demonstrated utility in predicting locomotor behavior and their prevalence in the fossil record. However, other aspects in the cercopithecoid postcranium, such as the forearm and digit proportions (Jolly 1967; Etter 1973; Rose 1988; Harrison 1989; Ciochon 1993; Patel 2010), have been demonstrated to be associated with locomotor behavior. Future study of elements such as the ulna, radius, and digits may improve upon the classification analyses presented here and provide more complete behavioral reconstructions of fossil taxa. Further, as was shown in Chapter 3, the inclusion of multiple elements across the postcranium in discriminant functional analyses improves classification rates. Therefore, the addition of morphological features to DFAs may give more confidence in our ability to correctly classify extant individuals to their correct locomotor group, and increase confidence in reconstructions of fossil taxa and ancestral nodes.

This dissertation advances the understanding of cercopithecoid evolution, but the results presented here also fit into the broader context of environmental change, faunal change, and primate evolution. Using deep-sea and carbon isotope dating, Zachos et al. (2001) document that a global cooling event that begins after 15 ma and continues until the early Pliocene. Figure 5.1 shows that association between this period of global cooling and increasing terrestriality in cercopithecines. A brief warming period begins in the late Miocene (around 6 ma) and continues until 3.2 ma and this interval coincides with the appearance of the large-bodied colobine genera in east Africa – *Paracolobus*, *Cercopithecoides,* and *Rhinocolobus* (for a review see Jablonski and Frost 2010). These three genera are presumably extinct by 1.5 ma (Jablonski and Frost 2010), which is subsequent to the second cooling period beginning at 3.2 ma that results in the Northern Hemisphere Glaciation (Zachos et al. 2001). *Paracolobus chemeroni* and *Rhinocolobus* are reconstructed as primarily arboreal by this study and previous work (Birchette 1982; Ciochon 1993; Frost and Delson 2002; Jablonski et al. 2008b) and recent work has documented a shift in East African ecosystem towards a more variable climate with greater seasonality and an increase in savannah grassland environments over the period of 4 – 1 ma (Bobe and Behrensmeyer 2004; deMenocal 2004; Hernandez Fernandez and Vrba 2006; Cerling et al. 2011). deMenocal (2004) specifically documents an increase in climate variation and aridification in East Africa at 1.7 ma, which precedes the extinction of all large-bodied colobines by 300 ky. Given the arboreal lifestyle of *Paracolobus* and *Rhinocolobus*, this relatively rapid habitat shift may have been one factor leading to their extinction.

All three species of *Cercopithecoides* are reconstructed as having engaged in terrestrial behavior (this study; Birchette 1982; Frost and Delson 2002; Jablonski et al. 2008b) and yet these species are also presumably extinct by 1.5 ma (Jablonski and Frost 2010). However, *Cercopithecoides* may also have used some arboreal behavior (see Chapter 3) and therefore changes in habitat may also have affected this lineage. In addition to increasing aridification over the 4 – 1 ma period in East Africa, the environment was increasingly made up of grasses using the C_4 photosynthesis pathway (Cerling et al. 2005; Cerling et al. 2011). Cerling et al. (2005; 2013) has shown that suids and *Theropithecus* had made dietary shifts such that these lineages were consuming exclusively C_4 plants by 1 ma. Therefore, it is possible that the large bodied Pliocene colobines may have experienced competitive exclusion from other mammalian groups in addition to changes in their preferred habitats (see also, Jablonski and Frost 2010).

The evolution of the *Theropithecus* lineage is also interesting to examine in the context of climate change in East Africa (for a review see Jablonski and Frost 2010). *Theropithecus* *brumpti*, the most basal member of the *Theropithecus* lineage (Gilbert 2013) appears around 3.4 mya (Jablonski and Frost 2010) prior to the cooling event that begin in the Pleistocene at 3.2 ma (Zachos et al. 2001). *Theropithecus brumpti* is reconstructed by this study and others (e.g., Guthrie 2011) as a mostly terrestrial species but probably engaging in more arboreal behavior than modern day geladas or *Theropithecus oswaldi*. *Theropithecus oswaldi*, which appears at 2.5 ma (Jablonski and Frost 2010), is larger than *Theropithecus brumpti* (Delson et al. 2000) and most likely was highly committed to terrestrial behavior (this study; Ciochon 1993; Krentz 1993; Jablonski et al. 2008a; Guthrie 2011). Cerling et al. (2013) show that while *T. brumpti* had a diet made up primarily of C_4 plants (around 64% of the diet) by 1 ma *T. oswaldi* was consuming exclusively C_4 plants. Thus, the *Theropithecus* lineage was highly successful during the climate shifts that occurred between 4 – 1 ma in East Africa (or a review of abundance of *Theropithecus* see Frost 2007), evolving from a mixed browser-grazer with arboreal capabilities of to a committed terrestrial grazer (Cerling et al. 2013).

Parallels have been drawn between the *Theropithecus* and hominin lineages since it has been argued that both became increasingly adapted for terrestrial travel (for a review see Elton 2006) and are the only African catarrhines to migrate into Eurasia during the Plio-Pleistocene (for a review see Jablonski 2002). The temporal range of the *Theropithecus* lineage (~ 3.5 ma to the present) is contemporaneous with the diversification of definitively bipedal hominins in the fossil record (for a review see Ward 2002). Results from the ASR analyses support these ideas, documenting an increasing "terrestrial morphology" in the lineage leading from Papionini to the divergence of *Theropithecus-Lophocebus-Papio*. Additionally, fossil reconstructions of *Theropithecus brumpti* and *Theropithecus oswaldi* confirm previous suggestions that the former, earlier species is likely to have engaged in more arboreal behavior than the latter and modern geladas (e.g., Guthrie 2011).

In conclusion, this dissertation documents cercopithecoid postcranial diversity in phylogenetic context and shows that associations between morphology and behavior are supported when taking shared evolutionary history into consideration. The dissertation strongly supports an arboreal LCA for crown Cercopithecoidea with the LCA of crown Colobinae inheriting this locomotor behavior. This work suggests that guenons and papionins inherited "semi-terrestrial" behavior from the LCA of crown Cercopithecinae with some lineages – *Theropithecus*, *Papio*, *Mandrillus*, and *Macaca thibetana* – becoming more committed to terrestriality much more recently and other lineages – *Cercopithecus*, *Lophocebus*, and *Cercocebus* evolving arboreality secondarily. Finally, transitions to terrestriality likely occurred multiple times in cercopithecoid evolution given that the colobine genera *Mesopithecus*, *Cercopithecoides*, and *Semnopithecus* engage(d) in at least a modest amount of terrestrial behavior. The framework outlined in this dissertation can be considered a new hypothesis for cercopithecoid locomotor evolution that can be further tested in the future with additional fossil material.

Figure 5.1. Probability of being placed in the arboreal group from the Springer et al. phylogeny with eight added fossils (using the DFA with two elements and two groups *a priori* with "semi-terrestrialists" included in the terrestrial group) mapped against an oxygen istope curve modified from Zachos et al. (2001).

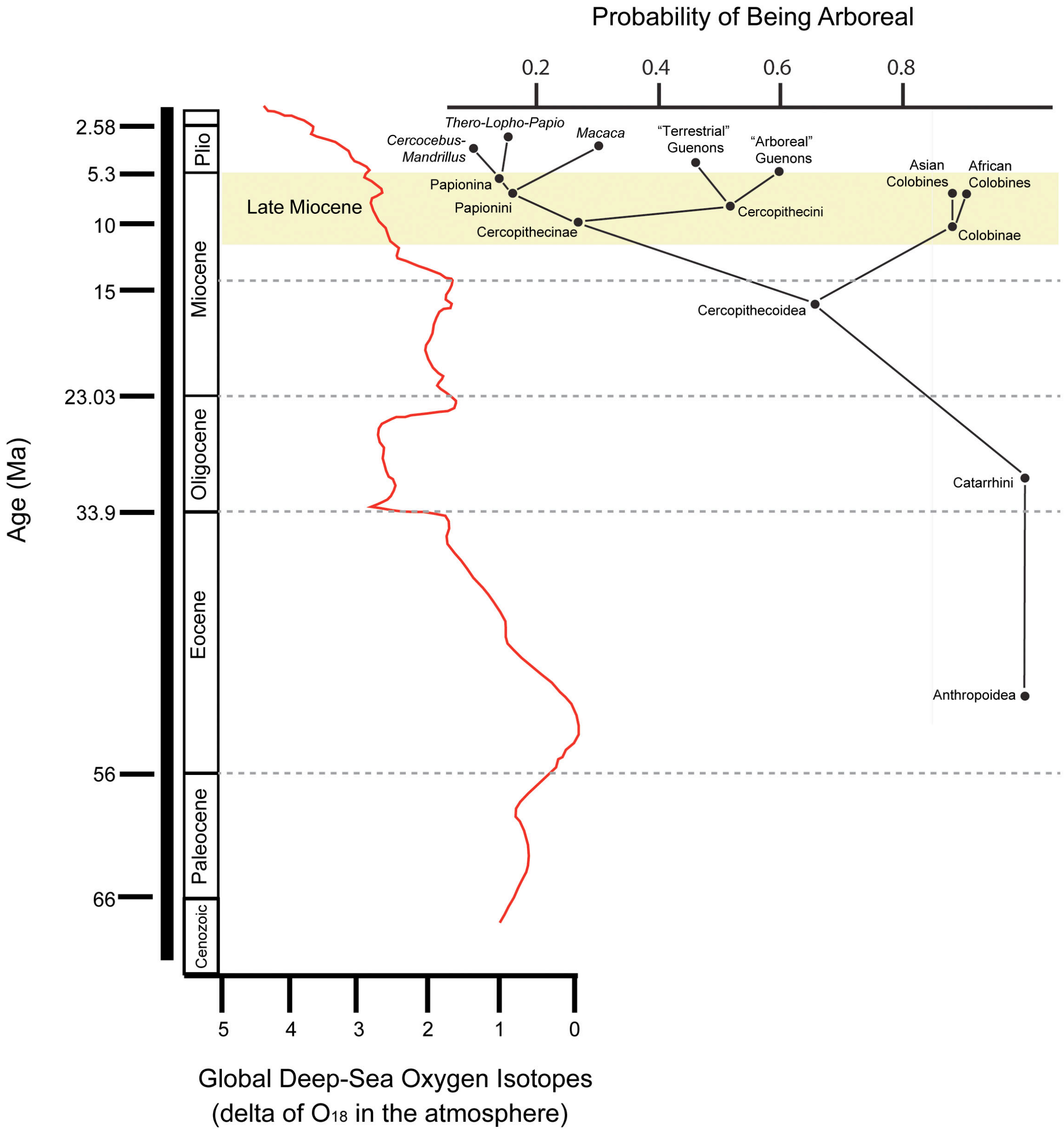
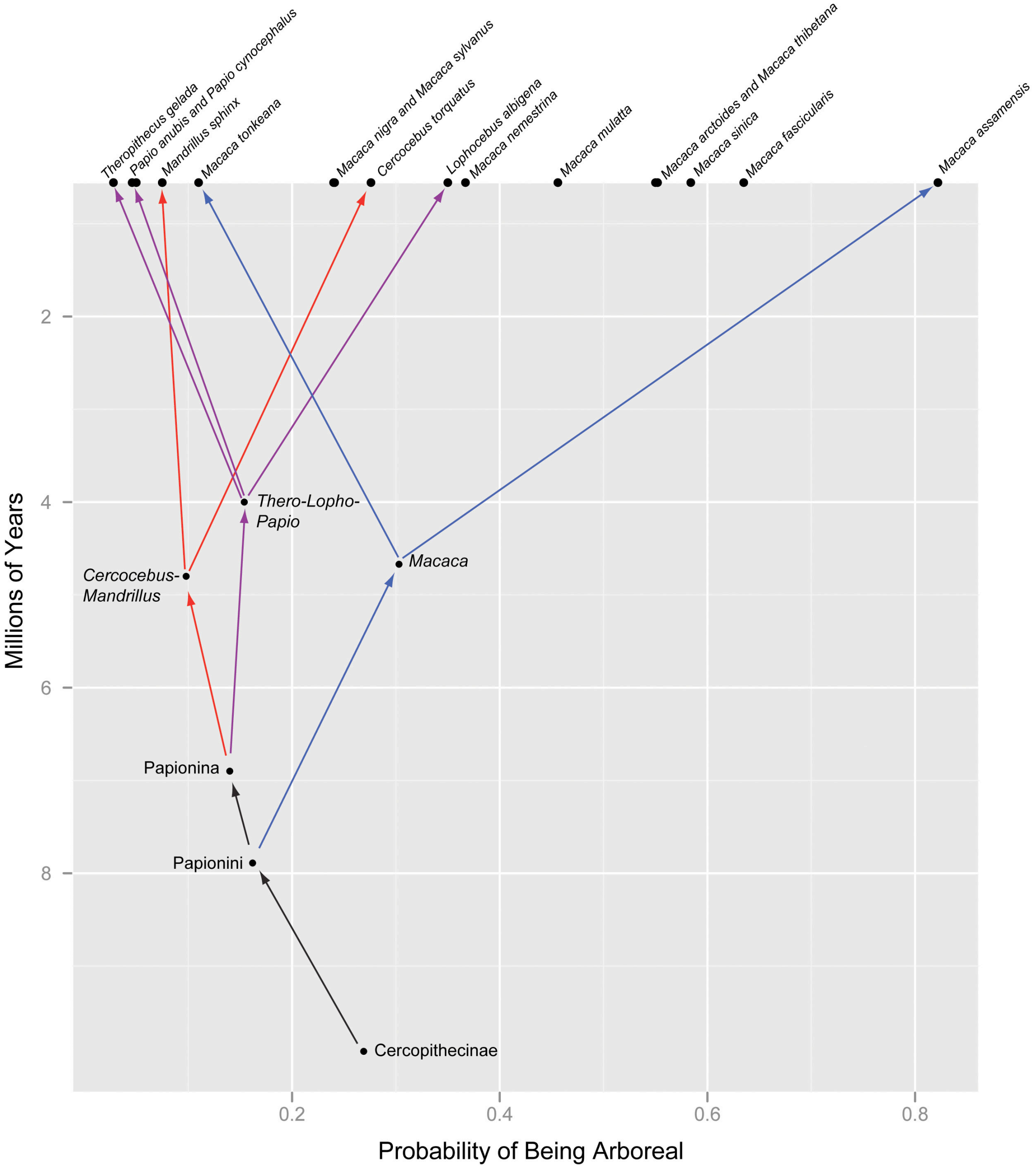


Figure 5.2. Probability of being placed in the arboreal group from the Springer et al. phylogeny with eight added fossils (using the DFA with two elements and two groups *a priori* with "semi-terrestrialists" included in the terrestrial group) for the papionins.



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Appendix A. Sources and locomotor assignments for 52 anthropoid species included in the study.

Species	Coding	Source	Assessment
PLATYRHINES			
Aotus azarai	A	E. Fernandez-Duque in (Rowe and Myers 2013)	Arboreal; will travel on ground for 50 - 100 meters between patches of forest
Cebus apella	A	(Mittermeier and van Roosmalen 1981)	Arboreal
GUENONS			
Allenopithecus nigroviridis	ST	(McGraw 1994)	Most often observed on the ground
Allochrocebus lhoesti	ST	(Kaplin and Moermond 2000)	~38% of time on ground
Cercopithecus ascanius	A	pers comm. J. Rothman (Assessment)	Rarely or never on ground
	A	(Gebo and Chapman 1995b)	Not observed on the ground
	A	(Thomas 1991)	~10% of time on ground
	A/ST	(McGraw 1994)	Observed on ground sometimes
Cercopithecus cephus	A	Z. Tooze & S. Seymour in (Rowe and Myers 2013)	Not observed on ground
Cercopithecus diana	A	(Buzzard 2006)	1.8% ground (more detailed breakdown of forest strata in Table 4)
	A	(McGraw 1998; Bitty and McGraw 2007)	2.2% of time on ground (1.7% of time on ground when traveling)
	A	(McGraw 2000)	1.7% of time on ground (1.7% when traveling)
	A	(Eckardt and Zuberbuhler 2004)	Prefer upper canopy forest
Cercopithecus hamlyni	ST	R. Goodwin & B. Kaplin in (Rowe and Myers 2013)	61% of time on ground
Cercopithecus mitis	A	pers. comm. Marina Cords (Assesment)	Most of time in trees with brief periods on ground
	A	(Thomas 1991)	~5% of time on ground
	A	(Kaplin and Moermond 2000)	~2% of time on ground
	A	(Gebo and Chapman 1995b)	Not observed on the ground
Cercopithecus mona	A	pers. comm. Mary Glenn (Assessment)	Rare to see on ground but all male groups may forage on ground
	A	R. Goodwin & Z. Tooze in (Rowe and Myers 2013)	2-3% of time on ground
Cercopithecus neglectus	ST	(McGraw 1994)	Most often observed on the ground
	ST	R Goodwin in (Rowe and Myers 2013)	15-20% of time on ground
Cercopithecus nictitans	A	(Eckardt and Zuberbuhler 2004)	Prefer upper canopy forest
	A	(Bitty and McGraw 2007)	1% of time on ground (0.3% when traveling)
Cercopithecus pogonias	A	(Thomas 1991)	~1 or 2% of time on ground
Chlorocebus aethiops	ST	pers comm. D. Cheney (Assessment)	Equal amounts of time in tree and ground
	ST	pers comm R. Seyfarth (Assessment)	Equal amounts of time in tree and ground

	ST	L.A Isbell, unpub. data (Assessment)	16.6% of time on ground over year; 31% of time on ground in wet season; most of time in tree with bried periods on ground
	ST	(Rose 1979)	19.4% of time on ground
	ST	Dunbar and Dunbar 1974	43.4% of time on ground
Chlorocebus pygerthrus	ST	Based on data from *Chlorocebus aethiops*	
Erythrocebus patas	ST	(Nakagawa 1989)	59.6% of time on ground; 90.5% of time on ground when feeding
Miopithecus talapoin	A	(Fleagle 1999)	Riverine forest habitat
MACAQUES			
Macaca arctoides	ST	(Fooden 1990)	Travels and forages on the ground
Macaca assamensis	A	M. Chalise, et al. in (Rowe and Myers 2013)	12.75% of time on ground
	A	(Schulke et al. 2011)	~10% of time on ground
Macaca fascicularis	A	(Cant 1988)	> 80% on arboreal supports
	A	(Rodman 1979)	2% of time on ground
Macaca mulatta	ST	pers comm. C. Berman (Assessment: Cayo Santiago population; provisioned)	Most of time on ground in trees for brief periods of time
	ST	(Wells and Turnquist 2001): (provisioned population)	~55% of time on ground (broken down by age in the paper)
	ST	(Rowe and Myers 2013) C. Southwick	50% of time on ground
	T	pers comm. J. Higham	Mostly terrestrial but enter trees; study site not heavily forested
Macaca nemestrina	ST	(Rodman 1979)	Qualitative described as travling on the ground but feeding in the trees
Macaca nigra	ST	(O'Brien and Kinnaird 1997)	>60% of time on ground
	ST	pers comm. J. Higham	Travel on ground but will enter trees to eat and sleep
Macaca sinica	A	(Rowe and Myers 2013) W. Dittus	Not observed on ground
Macaca sylvanus	ST	(Machairas et al. 2003)	70% of time on ground
Macaca thibetana	T	pers comm. C. Berman (Assessment: provisioned population)	Most of time on ground in trees for brief periods of time
Macaca tonkeana	ST/A	(Riley 2008)	1 group spend most time in trees (0.47% on ground), other group in disturbed habitat spent more time on ground (21.58% on ground)
	A	(Pombo et al. 2004)	Most of time in trees
PAPIONINANS			
Cercocebus torquatus	ST	(Cooke 2012)	39.4% of time on the ground (although this may have a seasonality component)
	ST	(Mitani 1989)	~50% of time on ground when traveling, resting, and engaging on social activity. ~25% of time on ground when feeding
	ST	(Jones and Sabater Pi 1968)	"terrestrial as well as arboreal"
Lophocebus albigena	A	(Gebo and Chapman 1995b)	Not observed on the ground
	A	(Thomas 1991)	Not observed on the ground
	A	(Janmaat and Chancellor 2010)	Males spent 8% of time on ground; females spent 1% of time on ground

	A	(Jones and Sabater Pi 1968)	"Entirely arboreal"
	A	M. Arlet et al. (Rowe and Myers 2013)	Occasionally on ground
Mandrillus sphinx	T	pers. comm. J. Setchell (Assessment: semi-free ranging population)	Most of time on ground in trees for brief periods of time
	T	(Norris 1988)	80% terrestrial (population was free-ranging within a forested 1.4- ha enclosure)
	T	(Sabater Pi 1972)	Most of time on ground
Papio anubis	T	pers. comm. J. Rothman (Assessment)	Most of time on ground in trees for brief periods of time
	ST	(Dunbar and Dunbar 1974)	72.1% of time on ground; better able to climb and move arboreally compared to geladas
	ST	pers comm. J. Higham	Populations living in savannah are more terrestrial; populations living in forested areas more arboreal
Papio cynocephalus	T	pers. comm N. Nguyen (Assessment)	Most of time on ground in trees for brief periods of time
	T	V. Bentley-Condit in (Rowe and Myers 2013)	Usually terrestrial
Theropithecus gelada	T	pers. comm N. Nguyen (Assessment)	Rarely or never in trees
	T	(Dunbar and Dunbar 1974)	98.4% of time on ground
COLOBINES			
Colobus guereza	A	(Rose 1979)	4.4% of time on ground
	A	(Gebo and Chapman 1995b)	Not observed on the ground
Nasalis larvatus	A	(Boonratana 2000)	Occasionally traveled on ground (< 20 meters)
Piliocolobus badius	A	(McGraw 1998)	< 1% of time on ground
	A	(Gebo and Chapman 1995b)	Not observed on the ground
	A	(Thomas 1991)	Not observed on the ground
Piliocolobus foai	A	Based on data from *P. badius* and *P. kirkii*	
Piliocolobus kirkii	A	K. Siex in (Rowe and Myers 2013)	2% of time on ground
Presbytis melalophos	A	Based on sources for other *Presbytis* species	
Presbytis rubicunda	A	Based on sources for other *Presbytis* species	
Pygathrix nemeaus	A	(Lippold 1998)	Not observed on the ground
	A	L. Lippold & T. Vu in (Rowe and Myers 2013)	0% of time on ground
Rhinopithecus roxellana	A	(Su et al. 1998)	Occasionally traveled on ground
	ST	(Ren et al. 2001)	15.3% of time on ground
	A	(Li 2007)	2.9% of time on ground
Semnopithecus entellus	ST	pers. comm K. Sayers (Assessment)	Equal amounts of time in tree and ground
	ST/A	pers. comm C. Borries & A. Koenig (Assessment)	15.7% of time on ground over year; 34% of time on ground during dry season; Most of time in trees with brief periods on ground
Trachypithecus cristatus	A	pers. comm John Fleagle	

Trachypithecus obscurus	A	(Md-Zain and Ch'ng 2011)	Uses all levels of canopy
Trachypithecus phayrei	A	pers. comm C. Borries & A. Koenig (Assessment)	Most of time in trees with brief periods on ground
<u>HOMINOIDS</u>			
Hylobates lar	Sus	(Fleagle and McGraw 1999)	Use frequent two-arm brachiation
Pan troglodytes	Sus	(Hunt 1992)	Engages in unimodal suspension
	Sus	(Doran 1992)	Infant chimpanzees engage in frequent suspensory behavior
	Sus	(Doran 1993)	Engage in suspensory behavior during arboreal feeding
Pongo pygmeaus	Sus	(Cant 1987)	Suspension by forelimbs occurs in 80% of travel

Appendix B. Measurements taken on the humerus, femur, astragalus, and calcaneus

<u>Humerus</u> (see Figures B.1 and B.2)

1) Proximodistal length of the humerus (HL)
    a. Taken using a bone board from the most proximal point to the most distal point with the humerus positioned dorsal side up
2) Mediolateral breadth of humeral head (MLHH)
    a. Taken from the edge of the lesser tubercle to the edge of the greater tubercle
3) Superoinferior length of humeral head (SIHH)
    a. Taken from the most superior point to the distal rim on humeral head
4) Humeral head index (HHI)
    a. MLHH/SIHH
5) Maximum diameter of greater tubercle (MGT)
    a. Taken along the widest points of the greater tubercle
6) Maximum diameter of lesser tubercle (MLT)
    a. Taken along the widest points of the lesser tubercle
7) Biccipital groove width (BGW)
    a. Taken between the lesser and greater tubercles at the superior opening of the groove
8) Maximum mediolateral breadth of olecranon fossa (MLOF)
    a. Taken at the base of the olecranon fossa
9) Maximum proximodistal height of olecranon fossa (PDOF)
    a. Taken from the superior edge of the articular surface to the most superior point in the olecranon fosaa
10) Proximodistal height of capitulum (PDC)
    a. Taken along the widest margin of the capitulum
11) Mediolateral width of the capitulum (MLC)
    a. Taken from the most lateral edge of the capitulum to the beginning of the trochlea; does not include a flange of the capitlulum when present
12) Depth of the trochlea (PDT)
    a. Taken from the medial margin of the trochlea to the termination of the trochlea on the dorsal side of the humerus
13) Mediolateral width of the trochlea (MLTR)
    a. Taken from the edge of the capitulum to the most medial point along the medial margin of the trochlea
14) Width of the distal articular surface (MLCT)
    a. Taken along widest margin of the articular surface; not including any flanges when present
15) Biepicondylar breadth (BB)
    a. Taken from the medial epicondyle to the lateral epicondyle
16) Height of the greater tubercle
    a. Height of the greater tubercle (GTH)
        i. Taken from a photograph: a line measured from the base of the humeral head to a line tangent to the greater tubercle
    b. Humeral head length (HHL)

        i. Taken from a photograph: a line measured from the base of the humeral head to point where the greater tubercle meets the humeral head
    c. Greater tubercle index (GTI)
        i. GTH/HHL

17) Direction of the medial epicondyle
    a. Dorsal projection of medial epicondyle (DL)
        i. Taken from a photograph: A line tangent to the medial edge of the trochlea and parallel to a reference line drawn based on the lateral edge of the olecranon fossa. The length is taken from the second reference line (perpendicular to the first reference line and tangent to the ventral aspect of the capitulum) to EL (see below).
    b. Epicondyle length (EL)
        i. Taken from a photograph: Length between a line tangent to DL and a second line tangent to the medial edge of the medial epicondyle and parallel to DL.
    c. Medial epicondylar index (MEI)
        i. EL/DL
    d. Angle of medial epicondyle (AME)
        i. Taken from a photograph: An angle created by the second reference line to the point where the medial epicondyle meets the dorsal aspect of the medial epicondyle

Femur (see Figures B.3-B.6)

1) Proximodistal length of the femur (FL)
    a. Taken using a bone board from the most proximal point to the most distal point with the femur anterior side up
2) Anteroposterior width of the femoral head (APFH)
    a. Taken along the widest diameter
3) Proximodistal height of the femoral head (PDFH)
    a. Taken from the most superior point to the inferior rim of the femoral head
4) Proximodistal height of the lesser trochanter (PDLT)
    a. Using the smoothened muscle attachment, measurement is taken from the most inferior point to the most superior point on the lesser trochanter
5) Anteroposterior width of the medial femoral condyle (APMC)
    a. Taken from the medial ridge of the patellar groove to the posterior most point on the medial condyle
6) Proximodistal height of the medial femoral condyle (PDMC)
    a. Taken from the superior ridge of the condyle to the most inferior point
7) Mediolateral width of the medial femoral condyle (MLMC)
    a. Diameter taken midway down the medial condyle
8) Anteroposterior width of the lateral femoral condyle (APLC)
    a. Taken from the lateral ridge of the patellar groove to the posterior most point on the lateral condyle
9) Proximodistal height of the lateral femoral condyle (PDLC)
    a. Taken from the superior ridge of the condyle to the most inferior point

10) Mediolateral width of the lateral femoral condyle (MLLC)
    a. Diameter taken midway down the lateral condyle
11) Anteroposterior depth condylar index (API)
    a. APMC/APLC
12) Proximodistal height condylar index (PDI)
    a. PDMC/PDLC
13) Mediolateral condylar width index (MLI)
    a. MLMC/MLLC
14) Bicondylar breadth (BB)
    a. Taken on the superior end of the condyles
15) Height of the patellar groove (PH)
    a. Taken from the inferior rim between the medial and lateral condyles to the most superior point on the groove
16) Width of the patellar groove (PW)
    a. Taken at the widest diameter of the groove
17) Femoral neck angle (FNA)
    a. Taken from a photograph: An angle created by 1) a line defining the midline of the shaft and the intersection of 2) a line tangent to the medial aspect of the femoral head and parallel to the midline, 3) two lines tangent to the superior aspect of the femoral head and tangent to the superior aspect of the femoral neck and perpendicular to the midline
18) Condylar asymmetry (ACON)
    a. Taken from a photograph: An angle created by 1) a line defining the midline of the shaft and 2) a line tangent to the distal aspect of the medial and lateral condyles

<u>Astragalus</u> (see Figures B.7 and B.8)

1) Maximum proximodistal length of the talus (AL)
    a. Taken from the most distal point on the talar head to the most proximal point on the lateral trochlear ridge
2) Proximodistal length of the talar body (MBD)
    a. Taken from the most distal point to the most proximal point on the lateral trochlear ridge
3) Proximodistal length of the head and neck (HNPD)
    a. Taken from the most proximal point on the sustentaculum facet (excluding medial expansion if present) to the most distal point on the talar head
4) Maximum dorsoplantar height of the medial tibial facet (DHTF)
    a. Taken from the most plantar point on the facet to the most dorsal point on the lateral ridge of the trochlea
5) Maximum trochlear width (TW)
    a. Taken from most medial point to most lateral point on the medial ridge of the trochlea
6) Height of the medial trochlear ridge (HMR)
    a. Taken from base of astragalar head to most dorsal aspect of the medial trochlear ridge

7) Height of the lateral trochlear ridge (HLR)
    a. Taken from base of astragalar head to most dorsal aspect of the lateral trochlear ridge
8) Asymmetry index (ASM)
    a. HMR/HLR
9) Maximum dorsoplantar height of the fibular facet (DHFF)
    a. Taken from the most plantar point to the most dorsal point on the medial ridge of the trochlea
10) Maximum proximodistal length of the fibular facet (PDFF)
    a. Taken from the most distal point to the most proximal point on the medial tibial facet
11) Ectal facet width (EW)
    a. Taken along the widest margin of the ectal facet
12) Ectal facet length (EL)
    a. Taken along long axis of ectal facet
13) Mediolateral width of the talar head (WTH)
    a. Taken along widest margin
14) Width of proximal trochlea (PT)
    a. Mediolateral width at the proximal end of trochlea
15) Width of distal trochlea (DT)
    a. Mediolateral width at the distal end of trochlea
16) Trochlear wedge index (WED)
    a. DT/PT
17) Angle of the talar head (ATH)
    a. Taken from a photograph: An angle created by 1) a line tangent to the lateral aspect of the lateral ridge of the trochlea and 2) a line that passes through the widest diameter of the astragalar head
18) Trochlear asymmetry (TAS)
    a. Taken from a photograph: An angle created by the intersection of 1) a line tangent to the lateral aspect of the lateral ridge and a perpendicular line tangent to the dorsal aspect of the lateral ridge and 2) a line tangent to the medial aspect of the medial ridge and (parallel to the first line along the lateral ridge) and a perpendicular line tangent to the dorsal aspect of the medial ridge

<u>Calcaneus </u>(see Figures B.9 and B.10)

1) Proximodistal length of the calcaneus (CL)
    a. Taken using a bone board from the most proximal point to the most distal point with the calcaneus plantar side up
2) Proximodistal length of distal segment of calcaneus (PDA)
    a. Taken from the proximal end of the astragalar facet to the superior rim of the navicular facet
3) Proximodistal length of the calcaneal tuber (CTL)
    a. Taken from the proximal end of the astragalar facet to the superior rim of the calcaneal tuber
4) Proximodistal length of distal articular facet (PDF)

    a. Taken from the most proximal point to the most distal point on the facet
5) Mediolateral breadth of the distal articular facet (MLF)
    a. Taken along widest margin
6) Mediolateral breadth of the sustentaculum tali (MLS)
    a. Taken in plantar view; from where the sustentaculum tali contacts the body of the calcaneus to the most medial point
7) Dorsoplantar breadth of the cuboid facet (HCF)
    a. Taken from the most plantar point to most dorsal point on the facet
8) Mediolateral breadth of calcaneal tuberosity (CTW)
    a. Taken along the widest margin of the roughened end of the tuber

Figure B.1. Proximal humerus of *Chlorocebus aethiops* (AMNH 216258) in a) dorsal view, b) medial view, and c) lateral view

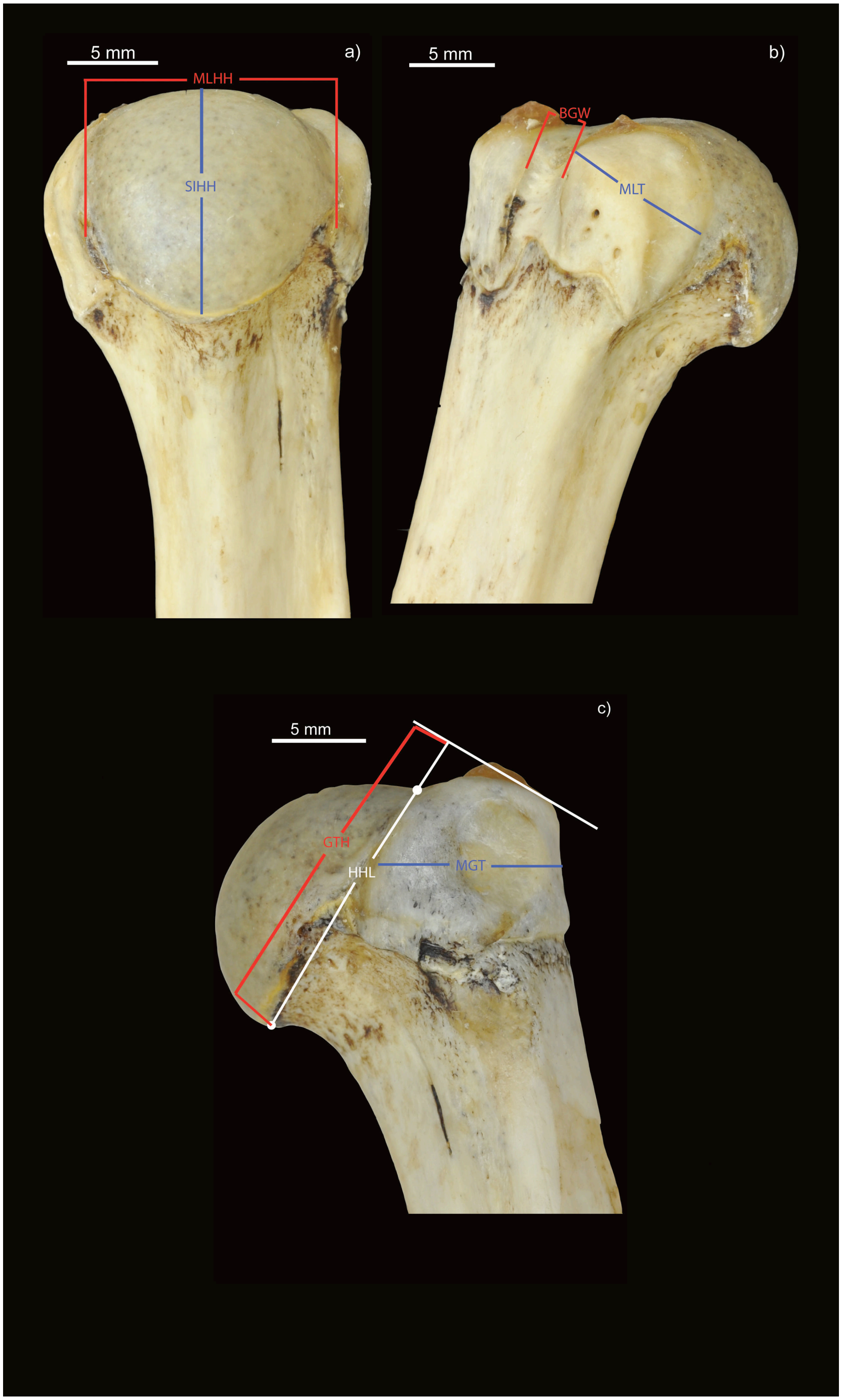


Figure B.2. Distal humerus of *Chlorocebus aethiops* (AMNH 216258) in a) ventral view, b) dorsal view, and c) distal view

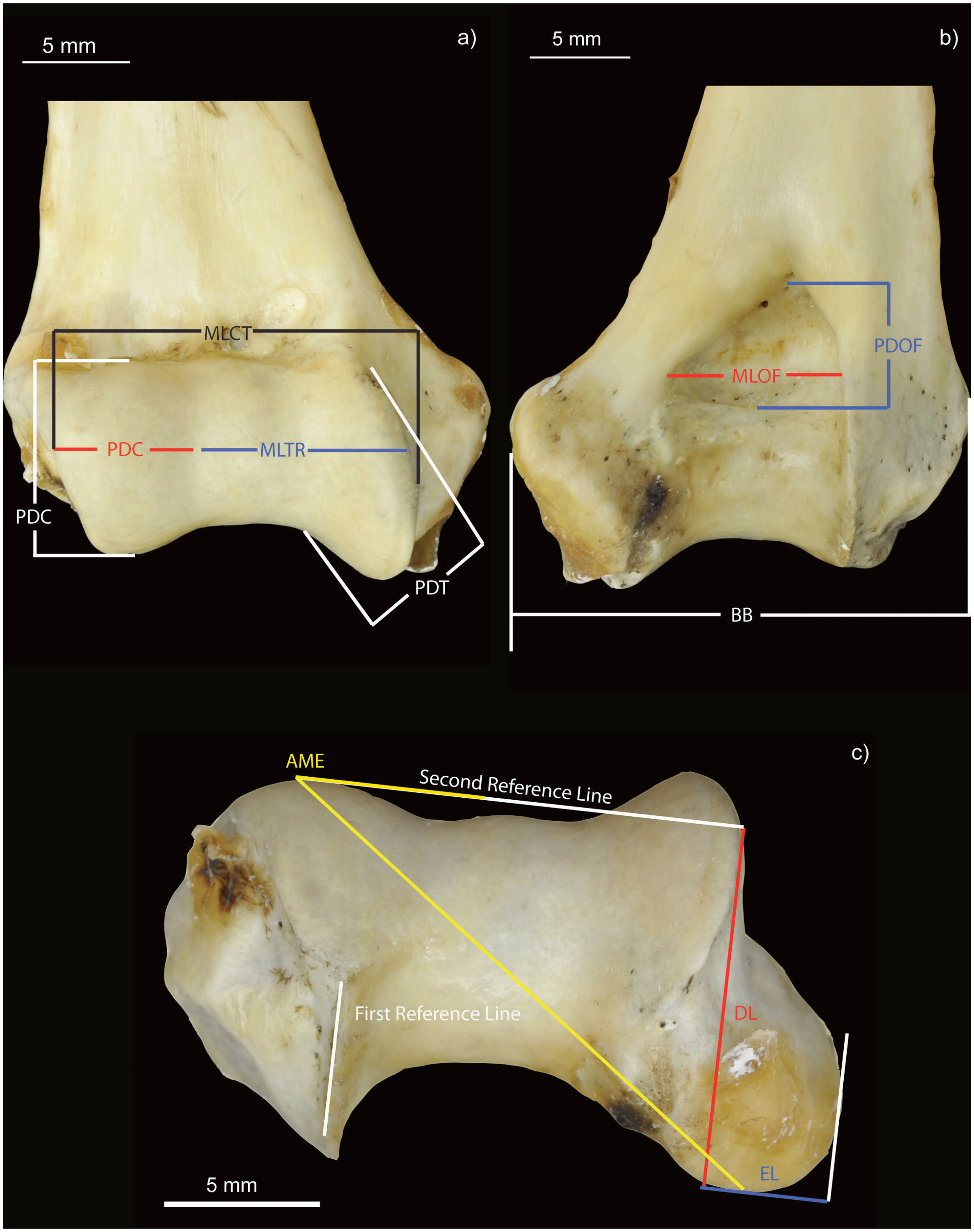


Figure B.3. Proximal femur of *Chlorocebus aethiops* (AMNH 216258) in a) lateral view and b) medial view

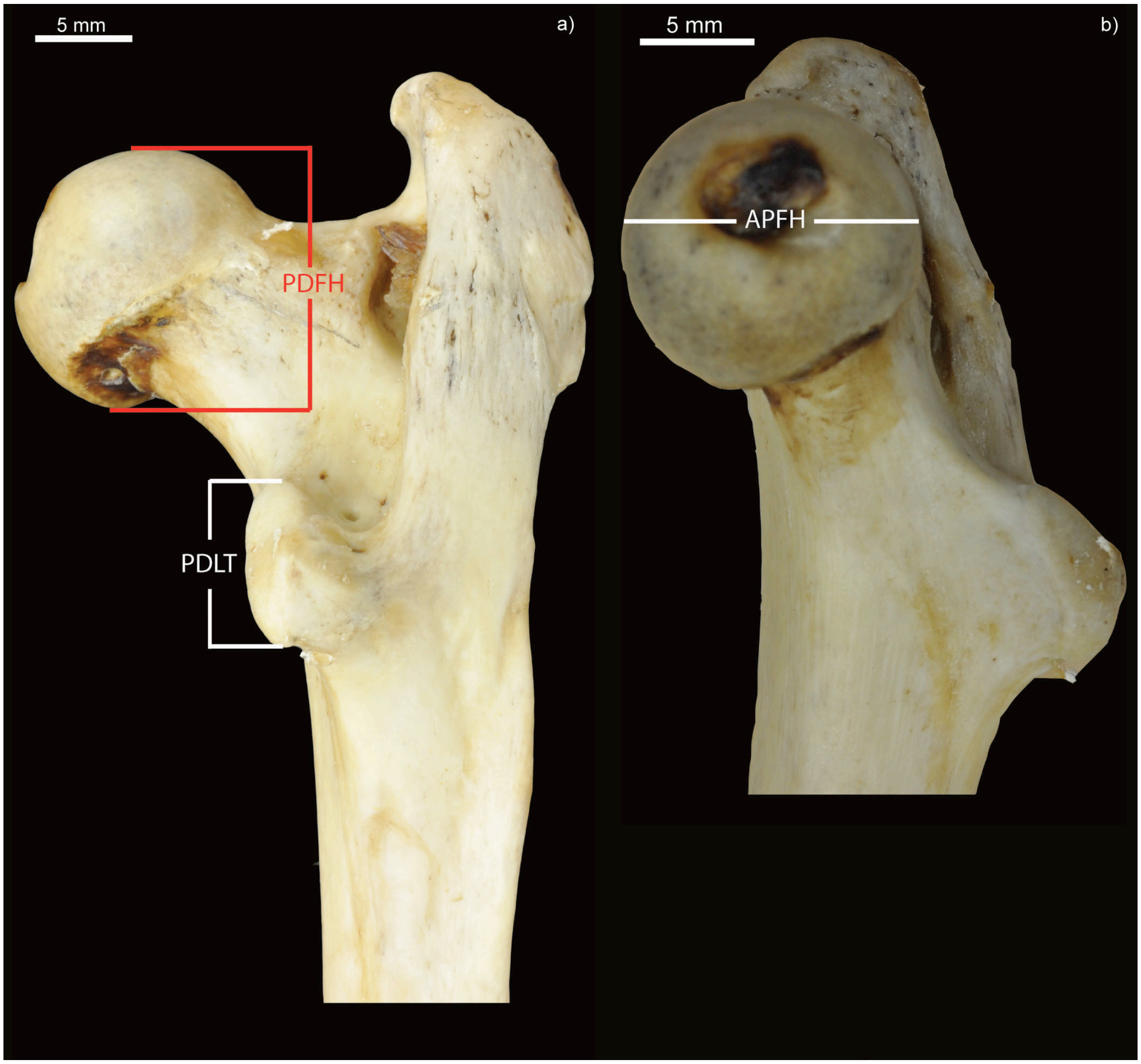


Figure B.4. Femur of *Chlorocebus aethiops* (AMNH 216258) in lateral view

Figure B.5. Distal femur of *Chlorocebus aethiops* (AMNH 216258) in a) medial veiw, and b) lateral view

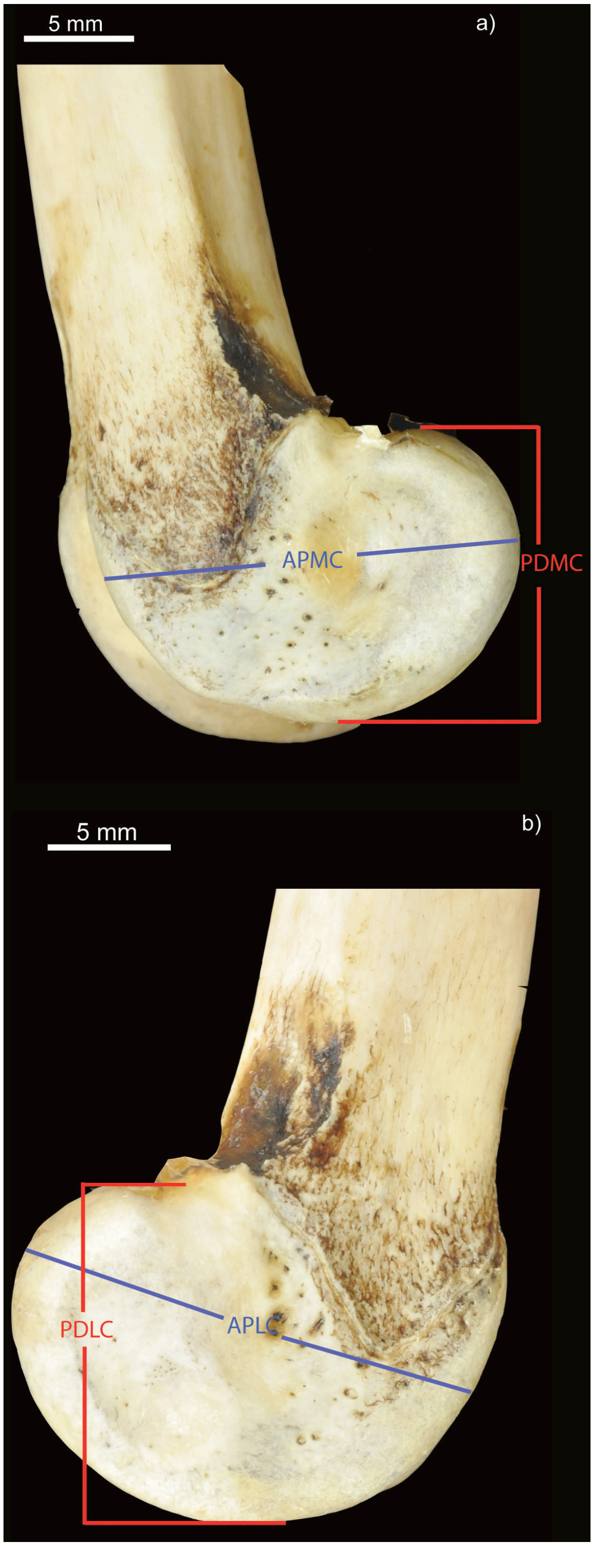


Figure B.6. Distal femur of *Chlorocebus aethiops* (AMNH 216258) in a) dorsal view and b) ventral view

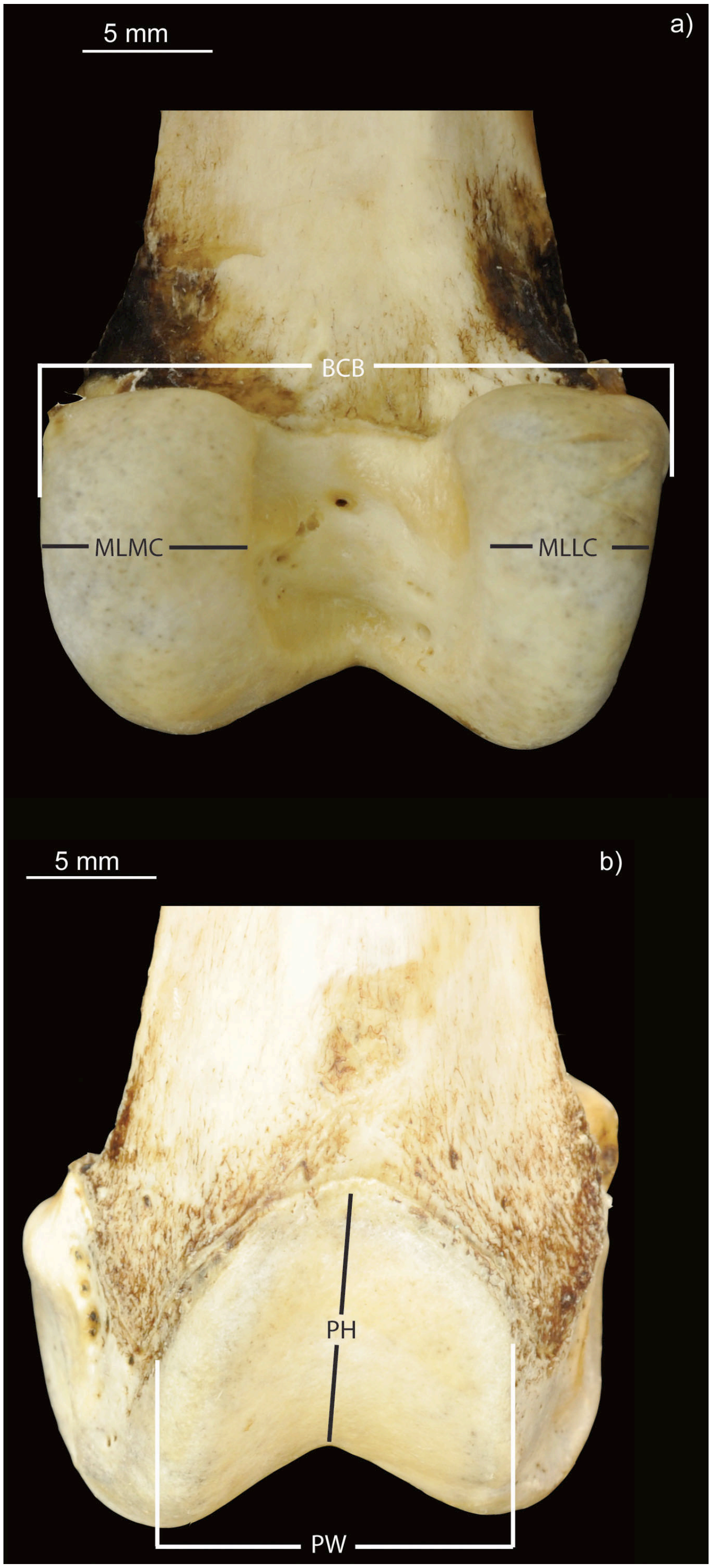


Figure B.7. Astragalus of *Chlorocebus aethiops* (AMNH 216258) in a) dorsal view, b) medial view, c) plantar view, and d) lateral view

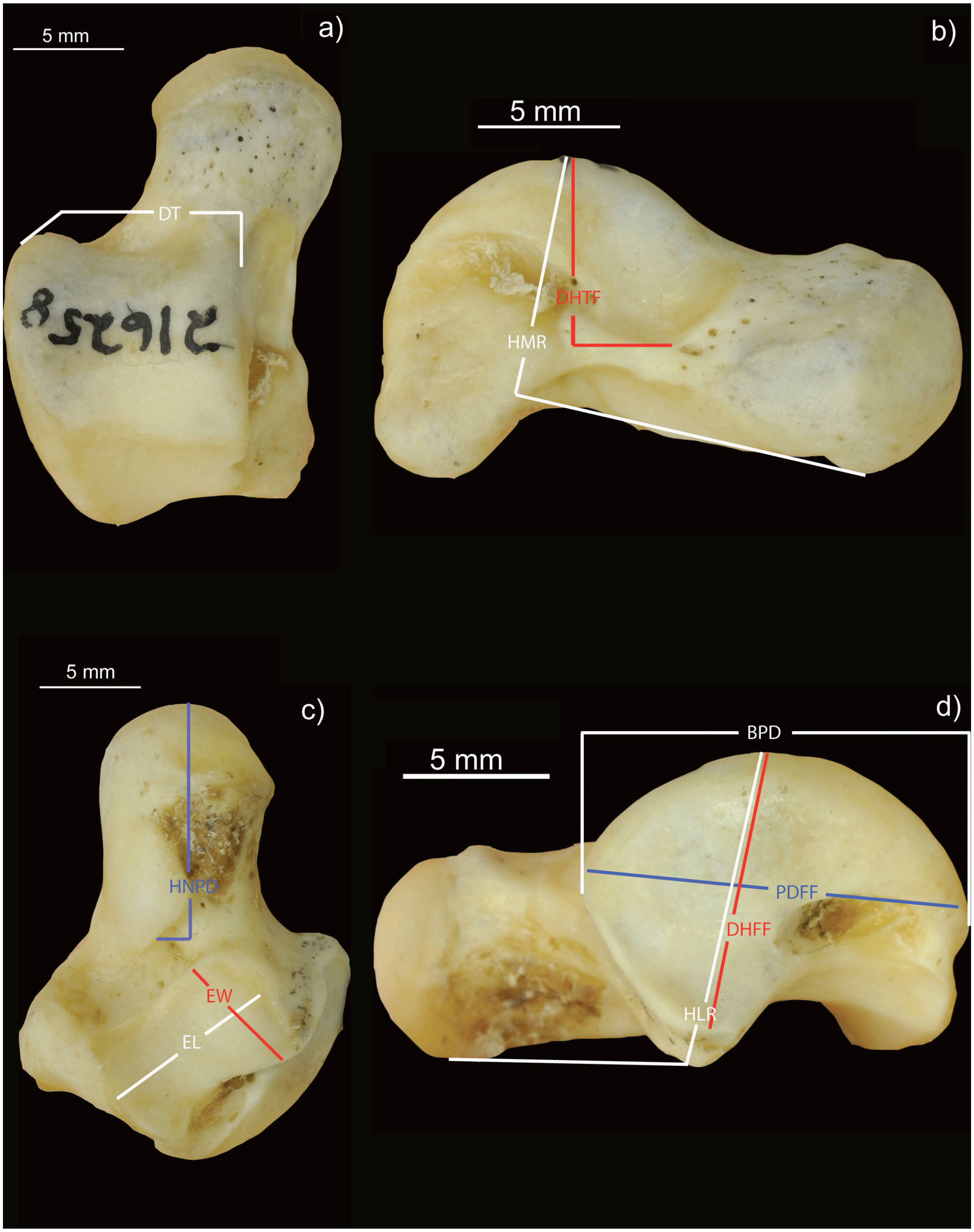


Figure B.8. Astragalus of *Chlorocebus aethiops* (AMNH 216258) in a) distal view, b) distal view, and c) proximal view

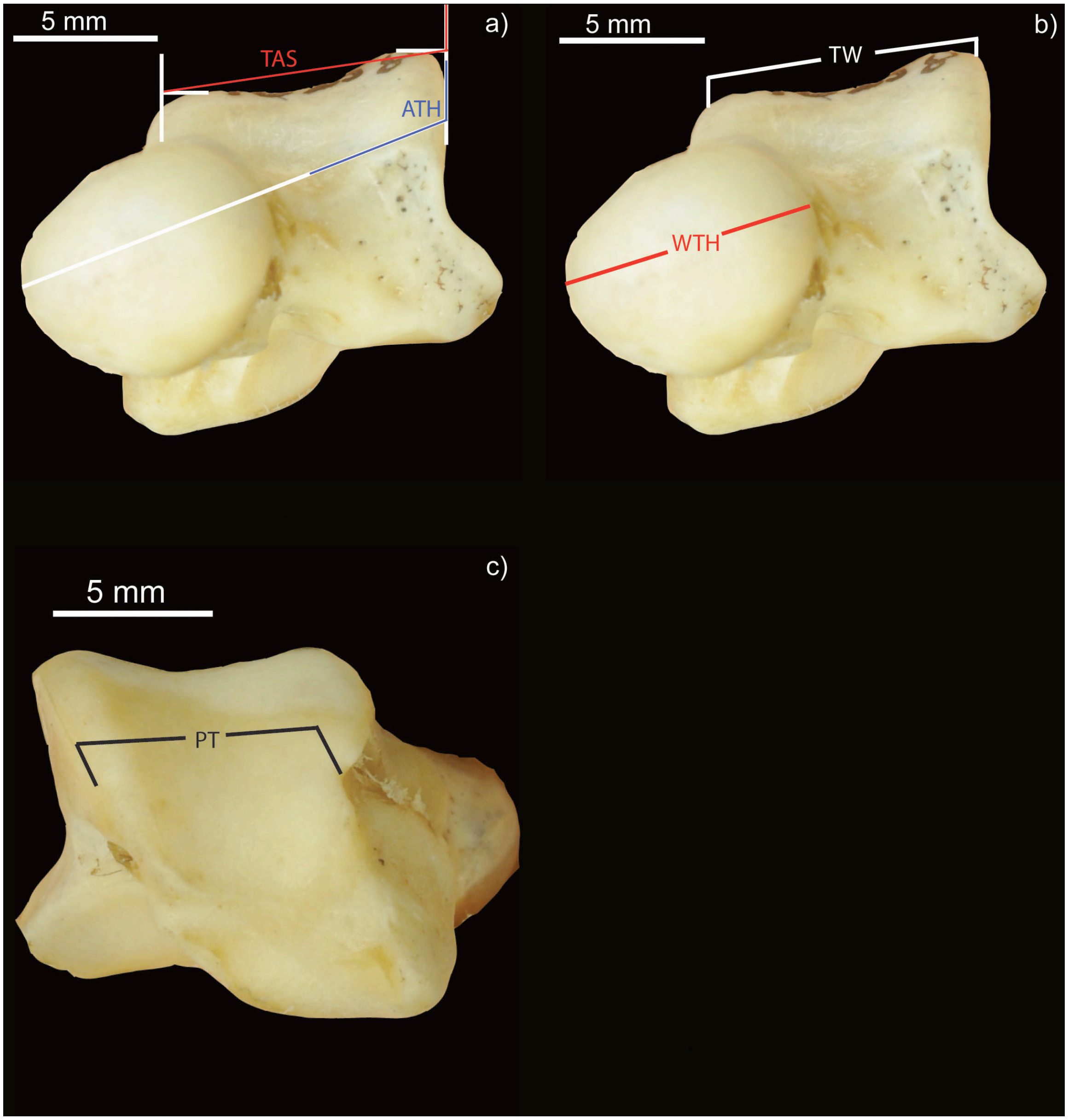


Figure B.9. Calcaneus of *Chlorocebus aethiops* (AMNH 216258) in a) dorsal view, b) plantar view, and c) medial view

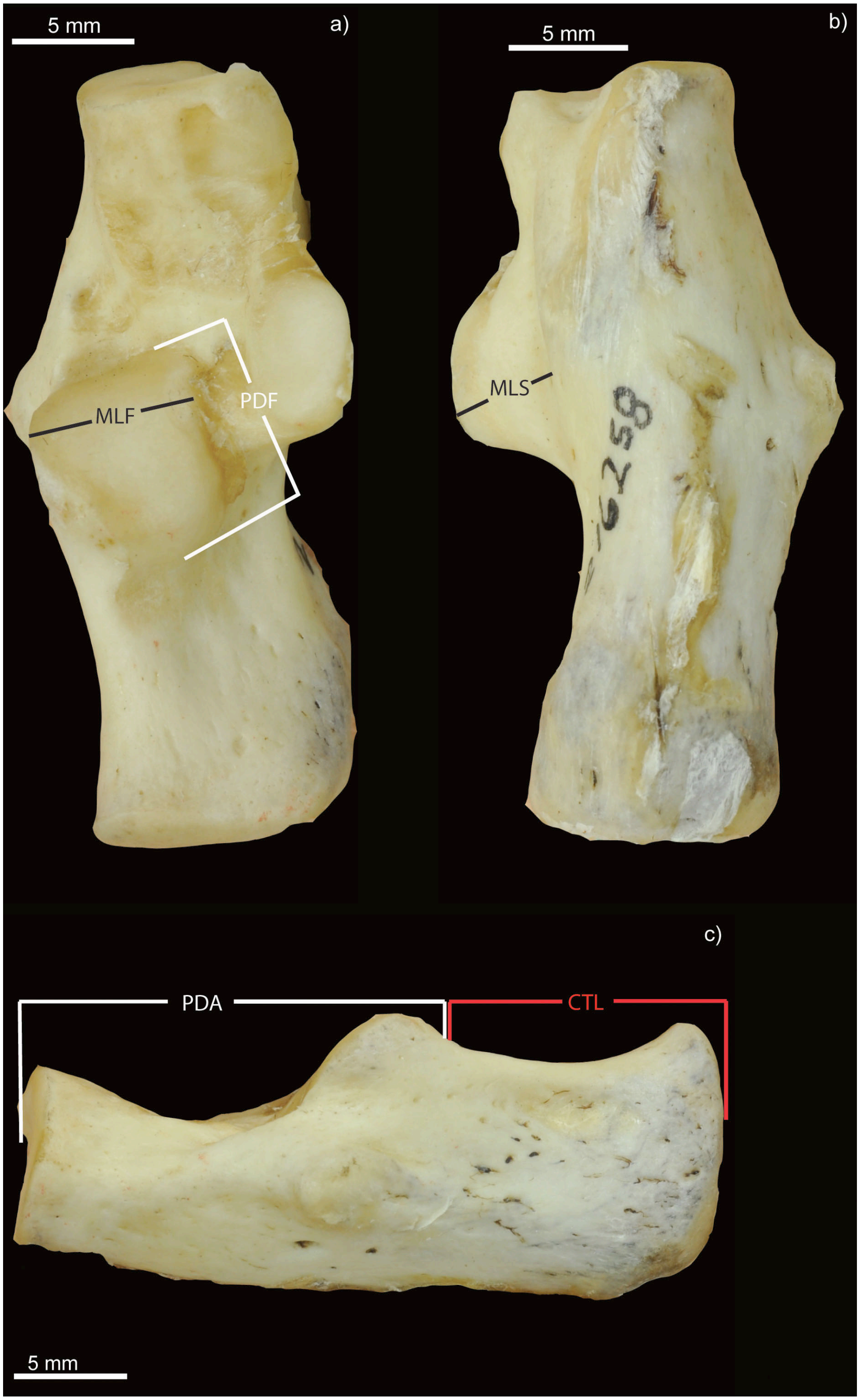
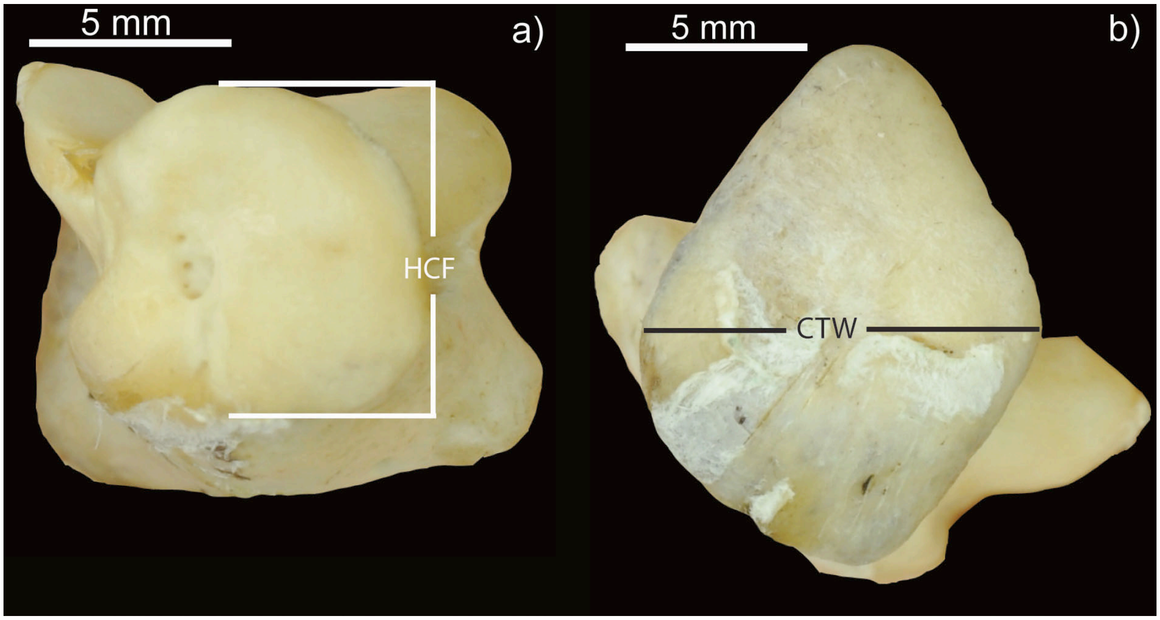


Figure B.10. Calcaneus of *Chlorocebus aethiops* (AMNH 216258) in a) distal view and b) proximal view



Appendix C. Extant sample. Note that although the genera *Semnopithecus*, *Trachypithecus*, and *Chlorocebus* are listed here, many museums still list *Trachypithecus* species as *Presbystis* and *Chlorocebus* species as *Cercopithecus*. **Allochrocebus lhoesti* is listed here according to its generic assignment at the RMCA (i.e., *Ceropithecus lhoesti*)

Species	Catalogue	Sex
Allenopithecus nigroviridis	AMNH 86856	M
Allenopithecus nigroviridis	NMNH 395131	F
Alouatta palliata	NMNH 240407	M
Alouatta palliata	NMNH 240408	M
Alouatta palliata	NMNH 257307	F
Alouatta palliata	NMNH 258313	F
Alouatta palliata	NMNH 282798	F
Alouatta palliata	NMNH 338104	F
Alouatta palliata	NMNH 338105	M
Alouatta palliata	NMNH 338108	M
Alouatta palliata	NMNH 338109	M
Aotus azarai	AMNH 211457	M
Aotus azarai	AMNH 211458	M
Aotus azarai	AMNH 211476	F
Aotus azarai	AMNH 211481	F
Aotus azarai	AMNH 211482	M
Aotus azarai	AMNH 211486	M
Aotus azarai	AMNH 215048	F
Aotus azarai	AMNH 215053	F
Aotus azarai	AMNH 215054	M
Aotus azarai	AMNH 215056	F
Aotus azarai	AMNH 215058	F
Aotus azarai	AMNH 215059	M
Cebus apella	AMNH 133622	M
Cebus apella	AMNH 133623	M
Cebus apella	AMNH 133626	F
Cebus apella	AMNH 133628	M
Cebus apella	AMNH 133631	F
Cebus apella	AMNH 133633	M
Cebus apella	AMNH 133635	F
Cebus apella	AMNH 133674	F
Cebus apella	AMNH 133677	F
Cebus apella	AMNH 133681	F
Cebus apella	AMNH 133815	M
Cebus apella	AMNH 133851	M
Cercocebus torquatus	BMNH 1938.12.6.1	F
Cercocebus torquatus	BMNH 1938.7.7.3	M
Cercocebus torquatus	BMNH 1948-450	M
Cercocebus torquatus	PCM M102	F
Cercocebus torquatus	PCM M103	M
Cercocebus torquatus	PCM M115	M
Cercocebus torquatus	PCM M39	M
Cercocebus torquatus	PCM M59	M
Cercocebus torquatus	PCM M69	M
Cercocebus torquatus	PCM M71	M
Cercocebus torquatus	PCM M77	F
Cercocebus torquatus	PCM M80	M
Cercocebus torquatus	PCM M81	F
Cercocebus torquatus	PCM M84	F
Cercopithecis mitis	AMNH 52368	M
Cercopithecis mitis	AMNH 52398	M
Cercopithecis mitis	AMNH 52401	M
Cercopithecis mitis	AMNH 52402	M
Cercopithecus ascanius	BMNH 72.4	F
Cercopithecus ascanius	BMNH 1977.315	M
Cercopithecus ascanius	RMCA 646	U
Cercopithecus ascanius	RMCA 972	F
Cercopithecus ascanius	RMCA 1283	M
Cercopithecus ascanius	RMCA 1778	M
Cercopithecus ascanius	RMCA 1779	M
Cercopithecus ascanius	RMCA 5397	U
Cercopithecus ascanius	RMCA 18043	M
Cercopithecus ascanius	RMCA 25470	U
Cercopithecus ascanius	RMCA 25515	M
Cercopithecus ascanius	RMCA 28995	M
Cercopithecus ascanius	RMCA 29115	F
Cercopithecus ascanius	RMCA 37486	F
Cercopithecus ascanius	RMCA 37495	F
Cercopithecus cephus	PCM M213	M
Cercopithecus cephus	PCM M23	M
Cercopithecus cephus	PCM M335	M
Cercopithecus cephus	PCM M381	M
Cercopithecus cephus	PCM M426	F
Cercopithecus cephus	PCM M753	F
Cercopithecus cephus	PCM M754	F
Cercopithecus cephus	PCM M872	M
Cercopithecus cephus	PCM M94	M
Cercopithecus cephus	PCM M972	F
Cercopithecus diana	FM 51517	F
Cercopithecus diana	FM 62266	M
Cercopithecus diana	NMNH 282554	M
Cercopithecus diana	NMNH 314971	F
Cercopithecus diana	NMNH 361889	F
Cercopithecus diana	NMNH 477295	F
Cercopithecus hamlyni	RMCA 1500	U
Cercopithecus hamlyni	RMCA 26597	F

Species	Catalogue	Sex	Species	Catalogue	Sex
Cercopithecus hamlyni	RMCA 28411	U	*Cercopithecus neglectus*	RMCA 20169	U
Cercopithecus hamlyni	RMCA 29113	F	*Cercopithecus nictitans*	BMNH 1938.7.7.12	M
Cercopithecus hamlyni	RMCA 88046	M	*Cercopithecus nictitans*	BMNH 1938.7.7.13	M
Cercopithecus hamlyni	RMCA A3040M0013	F	*Cercopithecus nictitans*	BMNH 1938.7.7.14	F
*Cercopithecus lhoesti**	RMCA 1271	M	*Cercopithecus nictitans*	PCM M232	M
*Cercopithecus lhoesti**	RMCA 23702	F	*Cercopithecus nictitans*	PCM M305	M
*Cercopithecus lhoesti**	RMCA 23704	F	*Cercopithecus nictitans*	PCM M336	M
*Cercopithecus lhoesti**	RMCA 23705	M	*Cercopithecus nictitans*	PCM M410	F
*Cercopithecus lhoesti**	RMCA 34197	U	*Cercopithecus nictitans*	PCM M433	M
*Cercopithecus lhoesti**	RMCA 91086M3	F	*Cercopithecus nictitans*	PCM M691	F
*Cercopithecus lhoesti**	RMCA 91086M5	M	*Cercopithecus nictitans*	PCM M792	F
Cercopithecus mitis	NMNH 452530	M	*Cercopithecus nictitans*	PCM M793	F
Cercopithecus mitis	NMNH 452536	M	*Cercopithecus nictitans*	PCM M868	F
Cercopithecus mitis	NMNH 452550	F	*Cercopithecus nictitans*	PCM M990	F
Cercopithecus mitis	NMNH 452551	M	*Cercopithecus pogonias*	PCM M103	F
Cercopithecus mitis	NMNH 452552	F	*Cercopithecus pogonias*	PCM M112	F
Cercopithecus mitis	NMNH 452553	M	*Cercopithecus pogonias*	PCM M152	F
Cercopithecus mitis	NMNH 452554	F	*Cercopithecus pogonias*	PCM M230	M
Cercopithecus mitis	NMNH 452556	F	*Cercopithecus pogonias*	PCM M277	F
Cercopithecus mitis	NMNH 452557	F	*Cercopithecus pogonias*	PCM M297	M
Cercopithecus mitis	NMNH 452559	F	*Cercopithecus pogonias*	PCM M306	M
Cercopithecus mona	AMNH 52482	M	*Cercopithecus pogonias*	PCM M344	M
Cercopithecus mona	AMNH 52485	M	*Cercopithecus pogonias*	PCM M347	F
Cercopithecus mona	AMNH 52508	F	*Cercopithecus pogonias*	PCM M383	M
Cercopithecus mona	AMNH 52521	F	*Cercopithecus pogonias*	PCM M660	F
Cercopithecus mona	BMNH 1938.7.7.8	M	*Cercopithecus pogonias*	PCM M90	M
Cercopithecus mona	BMNH 1948-463	F	*Chlorocebus aethiops*	AMNH 216255	M
Cercopithecus mona	BMNH 1948-475	M	*Chlorocebus aethiops*	AMNH 216256	F
Cercopithecus mona	NMNH 396923	F	*Chlorocebus aethiops*	AMNH 216257	F
Cercopithecus mona	NMNH 481007	U	*Chlorocebus aethiops*	AMNH 216258	M
Cercopithecus mona	PCM M109	M	*Chlorocebus aethiops*	BMNH 72.23	F
Cercopithecus mona	PCM M11	M	*Chlorocebus aethiops*	BMNH 1977.3148	M
Cercopithecus mona	PCM M25	M	*Chlorocebus aethiops*	BMNH 1930.8.1.15	F
Cercopithecus mona	PCM M67	M	*Chlorocebus aethiops*	BMNH 1977.314.9	F
Cercopithecus mona	PCM M94	M	*Chlorocebus aethiops*	MCZ 8302	M
Cercopithecus neglectus	AMNH 52421	M	*Chlorocebus pygerythrus*	AMNH 27705	M
Cercopithecus neglectus	AMNH 52429	M	*Chlorocebus pygerythrus*	AMNH 34716	F
Cercopithecus neglectus	BMNH 72.45	F	*Chlorocebus pygerythrus*	AMNH 187372	M
Cercopithecus neglectus	BMNH 72.47	M	*Chlorocebus pygerythrus*	AMNH 216252	F
Cercopithecus neglectus	BMNH 72.48	F	*Chlorocebus pygerythrus*	AMNH 216253	F
Cercopithecus neglectus	BMNH 72.49	F	*Chlorocebus pygerythrus*	AMNH 216254	M
Cercopithecus neglectus	BMNH 72.5	M	*Chlorocebus pygerythrus*	BMNH 72.27	F
Cercopithecus neglectus	PCM CAM372	M	*Chlorocebus pygerythrus*	BMNH 72.29	M
Cercopithecus neglectus	PCM M195	M	*Chlorocebus pygerythrus*	BMNH 72.3	F
Cercopithecus neglectus	RMCA 1221	U	*Chlorocebus pygerythrus*	BMNH 72.31	M
Cercopithecus neglectus	RMCA 1287	M	*Chlorocebus pygerythrus*	BMNH 72.32	F
Cercopithecus neglectus	RMCA 11526	F	*Chlorocebus pygerythrus*	RMCA 2149	M
Cercopithecus neglectus	RMCA 18231	F	*Chlorocebus pygerythrus*	RMCA 2152	F

Species	Catalogue	Sex
Chlorocebus pygerythrus	RMCA 4023	F
Chlorocebus pygerythrus	RMCA 37479	M
Colobus guereza	PCM FC98	M
Colobus guereza	PCM MER107	M
Colobus guereza	PCM MER277	F
Colobus guereza	PCM MER303	M
Colobus guereza	PCM MER66	F
Colobus guereza	PCM MER749	M
Colobus guereza	PCM MER830	M
Colobus guereza	PCM Sudan32	M
Colobus guereza	RMCA 27.263	M
Colobus guereza	RMCA 2157	F
Colobus guereza	RMCA 5896	F
Colobus guereza	RMCA 5897	F
Colobus guereza	RMCA 27259	M
Colobus guereza	RMCA 27262	M
Colobus guereza	RMCA 36977	F
Erythrocebus patas	CPRC 1031	M
Erythrocebus patas	CPRC 1037	F
Erythrocebus patas	CPRC 1038	F
Erythrocebus patas	CPRC 1042	F
Erythrocebus patas	CPRC 1048	F
Erythrocebus patas	CPRC 1050	F
Erythrocebus patas	CPRC 1065	M
Erythrocebus patas	CPRC 1069	F
Erythrocebus patas	CPRC 1087	M
Erythrocebus patas	CPRC 1116	M
Erythrocebus patas	CPRC 1716	M
Erythrocebus patas	CPRC 3240	M
Hylobates lar	MCZ 35946	M
Hylobates lar	MCZ 41412	F
Hylobates lar	MCZ 41413	M
Hylobates lar	MCZ 41415	M
Hylobates lar	MCZ 41416	F
Hylobates lar	MCZ 41418	F
Hylobates lar	MCZ 41424	F
Hylobates lar	MCZ 41427	M
Hylobates lar	MCZ 41433	M
Hylobates lar	MCZ 41454	F
Hylobates lar	MCZ 41458	F
Hylobates lar	MCZ 41501	M
Lophocebus albigena	AMNH 52596	F
Lophocebus albigena	NMNH 164580	F
Lophocebus albigena	PCM M157	F
Lophocebus albigena	PCM M339	M
Lophocebus albigena	PCM M355	F
Lophocebus albigena	PCM M371	M
Lophocebus albigena	PCM M668	M
Lophocebus albigena	PCM M683	M
Lophocebus albigena	PCM M706	F
Lophocebus albigena	PCM M721	F
Lophocebus albigena	PCM M749	M
Lophocebus albigena	PCM M788	M
Lophocebus albigena	PCM M807	F
Lophocebus albigena	PCM M997	F
Macaca arctoides	AMNH 112727	F
Macaca arctoides	BMNH 1914.8.22.6	F
Macaca arctoides	FM 47570	M
Macaca arctoides	FM 105682	M
Macaca arctoides	FM 105683	M
Macaca arctoides	CPRC 961	F
Macaca arctoides	CPRC 1358	F
Macaca arctoides	CPRC 1359	M
Macaca arctoides	CPRC 1361	F
Macaca arctoides	CPRC 1368	M
Macaca arctoides	CPRC 1371	F
Macaca arctoides	CPRC 1372	M
Macaca arctoides	CPRC 1374	F
Macaca arctoides	CPRC 1378	M
Macaca arctoides	CPRC 1640	M
Macaca assamensis	FM 99622	M
Macaca assamensis	FM 99631	M
Macaca assamensis	FM 99633	F
Macaca assamensis	MCZ 26476	F
Macaca assamensis	MCZ 37704	M
Macaca assamensis	MCZ 37705	F
Macaca assamensis	MCZ 37707	M
Macaca assamensis	MCZ 37708	F
Macaca assamensis	MCZ 37710	M
Macaca assamensis	MCZ 38117	M
Macaca assamensis	MCZ 38118	M
Macaca fascicularis	MCZ 35611	M
Macaca fascicularis	MCZ 35613	M
Macaca fascicularis	MCZ 35626	F
Macaca fascicularis	MCZ 35634	F
Macaca fascicularis	MCZ 35656	M
Macaca fascicularis	MCZ 35658	F
Macaca fascicularis	MCZ 35681	M
Macaca fascicularis	MCZ 35693	F
Macaca fascicularis	MCZ 35724	F
Macaca fascicularis	MCZ 35729	M
Macaca fascicularis	MCZ 35736	M
Macaca fascicularis	MCZ 37663	F
Macaca mulatta	CPRC 469	M
Macaca mulatta	CPRC 495	F
Macaca mulatta	CPRC 496	M

Species	Catalogue	Sex
Macaca mulatta	CPRC 497	F
Macaca mulatta	CPRC 499	M
Macaca mulatta	CPRC 500	M
Macaca mulatta	CPRC 502	F
Macaca mulatta	CPRC 504	M
Macaca mulatta	CPRC 514	F
Macaca mulatta	CPRC 530	M
Macaca mulatta	CPRC 596	F
Macaca mulatta	CPRC 598	F
Macaca nemestrina	MCZ 35602	F
Macaca nemestrina	MCZ 35631	F
Macaca nemestrina	MCZ 35649	F
Macaca nemestrina	MCZ 35670	M
Macaca nemestrina	MCZ 35676	F
Macaca nemestrina	MCZ 35687	F
Macaca nemestrina	MCZ 37420	M
Macaca nemestrina	MCZ 37676	F
Macaca nemestrina	NMNH 49691	M
Macaca nemestrina	NMNH 49874	M
Macaca nemestrina	NMNH 305069	F
Macaca nemestrina	CPRC 3163	F
Macaca nemestrina	CPRC 3247	F
Macaca nemestrina	CPRC 3492	F
Macaca nemestrina	CPRC 3530	F
Macaca nemestrina	CPRC 3806	F
Macaca nigra	AIM 10152	F
Macaca nigra	AIM 10221	M
Macaca nigra	AIM 10560	F
Macaca nigra	AMNH 30597	F
Macaca nigra	BMNH 1896.6.24.5	U
Macaca nigra	FM 31715	M
Macaca nigra	FM 31716	F
Macaca nigra	FM 54301	F
Macaca nigra	FM 60769	M
Macaca nigra	FM 127412	M
Macaca nigra	NMNH 22445	F
Macaca nigra	NMNH 39576	M
Macaca nigra	NMNH 217003	M
Macaca nigra	NMNH 255836	M
Macaca nigra	NMNH 305070	F
Macaca nigra	NMNH 543266	M
Macaca nigra	NMNH 588432	U
Macaca sinica	AIM AS-173	M
Macaca sinica	AIM AS-927	M
Macaca sinica	AIM AS-928	M
Macaca sinica	AIM AS-929	M
Macaca sinica	AIM AS-930	M
Macaca sinica	AIM PAL 51	M
Macaca sinica	AIM PAL 52	M
Macaca sinica	AIM PAL 62	M
Macaca sinica	FM 95021	M
Macaca sinica	FM 98261	M
Macaca sylvanus	AIM 12021	F
Macaca sylvanus	AIM 12022	F
Macaca sylvanus	FM 47398	M
Macaca sylvanus	FM 47409	F
Macaca sylvanus	MCZ 5964	U
Macaca sylvanus	MCZ 15296	M
Macaca sylvanus	NMNH 255979	M
Macaca sylvanus	NMNH 476785	M
Macaca sylvanus	NMNH 476786	F
Macaca thibetana	FM 39499	M
Macaca thibetana	FM 39500	F
Macaca thibetana	FM 39501	F
Macaca thibetana	NMNH 241162	F
Macaca thibetana	NMNH 241163	M
Macaca thibetana	NMNH 254800	M
Macaca thibetana	NMNH 258649	M
Macaca thibetana	NMNH 258650	F
Macaca thibetana	NMNH 258651	M
Macaca thibetana	NMNH 258686	M
Macaca tonkeana	AMNH 152905	M
Macaca tonkeana	AMNH 152906	F
Macaca tonkeana	AMNH 153401	M
Macaca tonkeana	AMNH 153402	M
Mandrillus sphinx	AIM PAL-108	M
Mandrillus sphinx	AIM PAL-109	M
Mandrillus sphinx	AMNH 89358	F
Mandrillus sphinx	AMNH 89361	F
Mandrillus sphinx	AMNH 89364	M
Mandrillus sphinx	AMNH 89365	F
Mandrillus sphinx	AMNH 89367	F
Mandrillus sphinx	AMNH 170364	M
Mandrillus sphinx	AMNH 170366	U
Mandrillus sphinx	BMNH 1948.5.21.2	M
Mandrillus sphinx	BMNH 30.12.15.9	M
Mandrillus sphinx	MCZ 34089	M
Mandrillus sphinx	MCZ 34090	M
Mandrillus sphinx	PCM ZVIII.9	M
Miopithecus talapoin	AIM 7572	M
Miopithecus talapoin	AIM 7602	M
Miopithecus talapoin	AIM 7613	M
Miopithecus talapoin	AIM 7632	F
Miopithecus talapoin	AIM 7674	F
Miopithecus talapoin	AIM 7675	F
Miopithecus talapoin	AIM 7676	M

Species	Catalogue	Sex
Miopithecus talapoin	AIM 7696	F
Miopithecus talapoin	AIM 10328	F
Miopithecus talapoin	AIM 10330	M
Miopithecus talapoin	BMNH 1977.86	M
Miopithecus talapoin	BMNH 1977.861	F
Miopithecus talapoin	BMNH 1977.864	M
Miopithecus talapoin	BMNH 1977.867	F
Miopithecus talapoin	BMNH 1977.874	M
Miopithecus talapoin	BMNH 1977.875	M
Miopithecus talapoin	NMNH 396196	F
Miopithecus talapoin	NMNH 397625	F
Miopithecus talapoin	PCM M346	M
Miopithecus talapoin	PCM M665	M
Nasalis larvatus	MCZ 7099	M
Nasalis larvatus	MCZ 37325	M
Nasalis larvatus	MCZ 37326	M
Nasalis larvatus	MCZ 37327	M
Nasalis larvatus	MCZ 37330	M
Nasalis larvatus	MCZ 37341	F
Nasalis larvatus	MCZ 37343	F
Nasalis larvatus	MCZ 41554	F
Nasalis larvatus	MCZ 41555	F
Nasalis larvatus	MCZ 41557	M
Nasalis larvatus	MCZ 41559	F
Nasalis larvatus	MCZ 41560	F
Nasalis larvatus	MCZ 41561	M
Nasalis larvatus	MCZ 41563	M
Pan troglodytes	AMNH 51376	F
Pan troglodytes	AMNH 51393	M
Pan troglodytes	AMNH 53330	M
Pan troglodytes	AMNH 89351	F
Pan troglodytes	AMNH 89354	F
Pan troglodytes	AMNH 90292	F
Pan troglodytes	AMNH 167342	M
Pan troglodytes	AMNH 167343	F
Pan troglodytes	AMNH 167344	M
Pan troglodytes	AMNH 167346	M
Pan troglodytes	AMNH 174860	F
Pan troglodytes	AMNH 174861	M
Papio anubis	NMNH 162899	M
Papio anubis	NMNH 236976	M
Papio anubis	NMNH 354984	F
Papio anubis	NMNH 354989	M
Papio anubis	NMNH 354992	F
Papio anubis	NMNH 384223	M
Papio anubis	NMNH 384227	F
Papio anubis	NMNH 384228	F
Papio anubis	NMNH 384229	M
Papio anubis	NMNH 384234	M
Papio anubis	NMNH 384235	F
Papio anubis	NMNH 395441	F
Papio anubis	AMNH 51380	M
Papio cynocephalus	UTA P25	M
Papio cynocephalus	UTA P26	M
Papio cynocephalus	UTA P27	F
Papio cynocephalus	UTA P33a	F
Papio cynocephalus	UTA P34	F
Papio cynocephalus	UTA P35	M
Papio cynocephalus	UTA P4	F
Papio cynocephalus	UTA P40	F
Papio cynocephalus	UTA P47	M
Papio cynocephalus	UTA P48	M
Papio cynocephalus	UTA P5	F
Papio cynocephalus	UTA P50	M
Piliocolobus badius	PCM M178	M
Piliocolobus badius	PCM M206	F
Piliocolobus badius	PCM M215	F
Piliocolobus badius	PCM M222	F
Piliocolobus badius	PCM M223	M
Piliocolobus badius	PCM M230	M
Piliocolobus badius	PCM M232	M
Piliocolobus badius	PCM M236	F
Piliocolobus badius	PCM M246	M
Piliocolobus badius	PCM M260	M
Piliocolobus badius	PCM M261	F
Piliocolobus badius	PCM M286	F
Piliocolobus badius	PCM M290	M
Piliocolobus foai	RMCA 1802	M
Piliocolobus foai	RMCA 2117	U
Piliocolobus foai	RMCA 5988	M
Piliocolobus foai	RMCA 18042	F
Piliocolobus foai	RMCA 26624	F
Piliocolobus foai	RMCA 29112	F
Piliocolobus foai	RMCA 36975	F
Piliocolobus foai	RMCA 37643	F
Piliocolobus foai	RMCA 37646	M
Piliocolobus kirkii	RMCA 33090	M
Piliocolobus kirkii	RMCA 33099	F
Piliocolobus kirkii	RMCA 33101	F
Pongo pygmaeus	AMNH 140426	M
Pongo pygmaeus	NMNH 49768	F
Pongo pygmaeus	NMNH 49769	F
Pongo pygmaeus	NMNH 49957	F
Pongo pygmaeus	NMNH 49958	M
Pongo pygmaeus	NMNH 49959	F
Pongo pygmaeus	NMNH 49961	M

Species	Catalogue	Sex
Pongo pygmaeus	NMNH 49962	M
Pongo pygmaeus	NMNH 49963	F
Pongo pygmaeus	NMNH 49965	F
Pongo pygmaeus	NMNH 49967	M
Pongo pygmaeus	NMNH 153823	M
Presbytis melalophos	BMNH 1164.a	F
Presbytis melalophos	BMNH 1879.8.30.6	M
Presbytis melalophos	BMNH 1879.8.30.7	F
Presbytis melalophos	NMNH 49749	M
Presbytis rubicunda	MCZ 35564	M
Presbytis rubicunda	MCZ 35566	M
Presbytis rubicunda	MCZ 35570	F
Presbytis rubicunda	MCZ 35596	M
Presbytis rubicunda	MCZ 35599	F
Presbytis rubicunda	MCZ 35601	M
Presbytis rubicunda	MCZ 35609	F
Presbytis rubicunda	MCZ 35616	M
Presbytis rubicunda	MCZ 35702	F
Presbytis rubicunda	MCZ 35703	M
Presbytis rubicunda	MCZ 35704	F
Presbytis rubicunda	MCZ 35705	F
Presbytis rubicunda	MCZ 35707	F
Pygathrix nemaeus	AIM 10753	F
Pygathrix nemaeus	AIM 11036	M
Pygathrix nemaeus	AIM 12100	M
Pygathrix nemaeus	AMNH 87255	M
Pygathrix nemaeus	AMNH 87256	F
Pygathrix nemaeus	FM 46509	M
Pygathrix nemaeus	FM 46510	F
Pygathrix nemaeus	FM 46512	M
Pygathrix nemaeus	FM 46513	F
Pygathrix nemaeus	FM 46514	M
Pygathrix nemaeus	MCZ 36224	F
Pygathrix nemaeus	MCZ 36259	M
Pygathrix nemaeus	NMNH 356576	M
Pygathrix nemaeus	NMNH 356577	M
Pygathrix nemaeus	NMNH 356854	F
Pygathrix nemaeus	NMNH 357628	M
Rhinopithecus roxellana	AMNH 117413	U
Rhinopithecus roxellana	AMNH 119648	F
Rhinopithecus roxellana	BMNH 1908.10.9.1	M
Rhinopithecus roxellana	BMNH 1908.10.9.3	U
Rhinopithecus roxellana	FM 31143	M
Rhinopithecus roxellana	NMNH 258986	M
Rhinopithecus roxellana	NMNH 268886	F
Rhinopithecus roxellana	NMNH 268887	M
Rhinopithecus roxellana	NMNH 268888	M
Rhinopithecus roxellana	NMNH 268889	F
Rhinopithecus roxellana	NMNH 268890	U
Rhinopithecus roxellana	NMNH 268894	F
Rhinopithecus roxellana	NMNH 268895	F
Rhinopithecus roxellana	NMNH 268896	M
Rhinopithecus roxellana	NMNH 268897	F
Saguinus oedipus	NMNH 501082	F
Saguinus oedipus	NMNH 501084	F
Saguinus oedipus	NMNH 501092	F
Saguinus oedipus	NMNH 501093	M
Saguinus oedipus	NMNH 501094	M
Saguinus oedipus	NMNH 501095	M
Saguinus oedipus	NMNH 501100	F
Saguinus oedipus	NMNH 501102	F
Saguinus oedipus	NMNH 501103	M
Saguinus oedipus	NMNH 501105	M
Saimiri sciureus	NMNH 397758	M
Saimiri sciureus	NMNH 397842	M
Saimiri sciureus	NMNH 397844	M
Saimiri sciureus	NMNH 397845	M
Saimiri sciureus	NMNH 397905	F
Saimiri sciureus	NMNH 397907	F
Saimiri sciureus	NMNH 397909	F
Saimiri sciureus	NMNH 397910	F
Saimiri sciureus	NMNH 397914	F
Saimiri sciureus	NMNH 397915	M
Semnopithecus entellus	AIM AS-1823	F
Semnopithecus entellus	AIM PAL75	M
Semnopithecus entellus	BMNH 1910.10.13.1	M
Semnopithecus entellus	FM 44834	F
Semnopithecus entellus	FM 44835	F
Semnopithecus entellus	FM 53698	F
Semnopithecus entellus	FM 92867	F
Semnopithecus entellus	FM 92868	F
Semnopithecus entellus	FM 104168	M
Semnopithecus entellus	NMNH 49701	M
Theropithecus gelada	AIM 6980	M
Theropithecus gelada	AIM 7183	F
Theropithecus gelada	AIM 8555	F
Theropithecus gelada	AIM 9278	F
Theropithecus gelada	AIM 9300	F
Theropithecus gelada	AIM 9706	F
Theropithecus gelada	AIM 10126	F
Theropithecus gelada	AIM 10351	F
Theropithecus gelada	AIM 12102	M
Theropithecus gelada	AMNH 201008	U
Theropithecus gelada	FM 27040	M
Theropithecus gelada	NME MCA 443	F
Theropithecus gelada	NME MCA 444	F

Species	Catalogue	Sex
Theropithecus gelada	NMNH 240885	M
Theropithecus gelada	NMNH 305107	M
Theropithecus gelada	UCB 108	M
Theropithecus gelada	UCB 109	M
Theropithecus gelada	UCB 110	F
Theropithecus gelada	UCB 111	F
Theropithecus gelada	UCB 113	F
Trachypithecus cristatus	MCZ 35618	F
Trachypithecus cristatus	MCZ 35665	M
Trachypithecus cristatus	MCZ 35666	M
Trachypithecus cristatus	MCZ 35671	M
Trachypithecus cristatus	MCZ 35672	M
Trachypithecus cristatus	MCZ 35678	F
Trachypithecus cristatus	MCZ 35688	F
Trachypithecus cristatus	MCZ 35696	F
Trachypithecus cristatus	MCZ 35709	M
Trachypithecus cristatus	MCZ 35718	F
Trachypithecus cristatus	MCZ 37388	M
Trachypithecus cristatus	MCZ 37404	F
Trachypithecus obscurus	BMNH 71.703	F
Trachypithecus obscurus	BMNH 71.704	F
Trachypithecus obscurus	BMNH 71.707	F
Trachypithecus obscurus	BMNH 71.709	M
Trachypithecus obscurus	BMNH 71.711	F
Trachypithecus obscurus	BMNH 71.723	F
Trachypithecus obscurus	BMNH 71.724	F
Trachypithecus obscurus	BMNH 71.725	M
Trachypithecus obscurus	BMNH 71.727	F
Trachypithecus obscurus	BMNH 71.728	M
Trachypithecus obscurus	BMNH 71.732	U
Trachypithecus obscurus	BMNH 71.736	F
Trachypithecus obscurus	BMNH 71.738	M
Trachypithecus obscurus	FM 105652	M
Trachypithecus obscurus	FM 105684	M
Trachypithecus phayrei	MCZ 35922	M
Trachypithecus phayrei	MCZ 37714	F
Trachypithecus phayrei	MCZ 37716	M
Trachypithecus phayrei	MCZ 37717	F
Trachypithecus phayrei	MCZ 37718	M
Trachypithecus phayrei	MCZ 37720	M
Trachypithecus phayrei	MCZ 37722	F
Trachypithecus phayrei	MCZ 37729	F
Trachypithecus phayrei	MCZ 37733	F
Trachypithecus phayrei	MCZ 38631	F
Trachypithecus phrayei	FM 39379	M
Trachypithecus phrayei	FM 99697	F

Appendix D. Species means for all variables in the study (for abbreviations see Appendix B)

Appendix D.1. Species mean for variables from the humerus

Species	**HL**	**MLHH**	**SIHH**	**MGT**	**MLT**	**BGW**	**MLOF**	**PDOF**	**PDC**	**MLC**	**PDT**	**MLTR**	**MLCT**	**BB**	**GTH**	**HHL**	**DL**	**EL**	**GTI**	**MEI**	**HHI**	**AME**
Allenopithecus nigroviridis	112.500	12.895	11.520	12.110	8.680	3.530	7.790	7.055	7.745	5.820	9.305	7.930	14.045	21.390	14.936	12.747	10.906	4.282	1.169	0.398	1.118	0.666
Allochrocebus lhoesti	133.286	14.576	12.941	13.581	9.540	3.813	9.324	7.149	9.961	7.114	10.896	8.550	15.391	22.691	16.832	14.181	12.406	3.848	1.187	0.310	1.127	0.727
Alouatta palliata	149.667	14.750	16.571	15.456	10.216	5.198	10.398	7.113	10.157	8.491	11.039	9.227	17.508	28.272	18.267	17.764	7.847	7.718	1.028	1.012	0.894	0.399
Aotus azarai	80.250	8.707	8.628	7.956	4.758	2.765	5.110	3.022	5.388	4.006	6.204	6.209	9.695	14.878	9.951	9.548	5.611	3.748	1.042	0.684	1.012	0.476
Cebus apella	104.000	11.583	11.369	10.647	6.843	3.555	9.159	8.403	6.712	5.627	6.918	7.239	12.519	19.734	13.468	12.798	8.509	4.463	1.052	0.531	1.019	0.558
Cercocebus torquatus	162.231	17.475	16.292	16.876	12.442	5.723	11.448	9.134	11.905	8.386	14.682	11.583	20.277	28.347	22.279	18.187	15.479	3.562	1.224	0.233	1.074	0.735
Cercopithecus ascanius	117.615	12.833	11.803	11.661	8.559	3.867	8.237	6.239	8.422	6.198	9.625	8.387	14.107	19.947	15.294	13.194	9.956	3.405	1.159	0.347	1.091	0.644
Cercopithecus cephus	115.300	13.120	11.920	11.960	8.750	4.290	8.450	6.050	8.480	5.780	10.270	8.490	14.230	20.560	15.475	13.032	10.491	3.166	1.187	0.307	1.102	0.670
Cercopithecus diana	129.333	13.395	12.253	12.258	9.622	4.462	8.755	7.172	8.898	6.167	10.258	8.760	15.282	21.273	16.332	13.486	11.270	2.742	1.213	0.245	1.096	0.705
Cercopithecus hamlyni	139.000	15.307	13.553	14.297	10.263	4.563	8.853	7.607	9.410	7.670	11.443	9.793	16.657	23.690	18.112	15.090	12.066	3.583	1.199	0.316	1.132	0.649
Cercopithecus mitis	131.231	14.991	13.522	13.387	9.952	4.938	9.435	6.638	9.896	6.998	11.565	9.738	16.842	23.272	18.239	15.622	11.958	3.287	1.171	0.272	1.113	0.663
Cercopithecus mona	124.091	13.573	12.648	12.783	9.288	4.665	9.062	6.115	8.627	6.275	10.403	8.793	15.343	21.615	16.750	14.133	11.513	3.305	1.184	0.294	1.076	0.664
Cercopithecus neglectus	131.900	14.729	13.134	13.733	10.033	4.796	9.872	6.942	9.477	6.276	11.141	9.367	15.626	23.282	18.162	15.052	12.519	3.831	1.208	0.311	1.120	0.696
Cercopithecus nictitans	131.250	14.549	13.765	13.667	9.998	4.518	9.582	6.792	9.348	6.973	11.181	9.433	16.390	22.307	17.595	15.013	11.918	3.492	1.173	0.297	1.059	0.670
Cercopithecus pogonias	117.455	12.700	11.882	11.736	8.936	4.509	8.682	6.809	8.427	5.909	9.809	8.191	14.673	20.236	15.545	12.932	10.084	3.334	1.203	0.328	1.068	0.646
Chlorocebus aethiops	120.000	13.408	11.874	12.401	8.923	4.325	8.694	6.459	8.704	5.574	10.345	8.583	14.228	20.840	16.580	13.550	11.638	2.814	1.223	0.245	1.137	0.718
Chlorocebus pygerythrus	118.214	12.945	11.476	11.842	8.920	3.930	8.844	6.198	8.601	5.888	9.760	8.243	14.194	20.049	16.053	13.032	11.100	2.545	1.232	0.229	1.130	0.713
Colobus guereza	151.143	17.229	15.211	17.214	10.845	4.732	12.359	7.710	11.376	8.822	12.411	11.881	20.364	28.373	19.930	17.020	11.985	4.886	1.172	0.411	1.136	0.563
Erythrocebus patas	169.917	16.958	14.764	16.493	12.813	5.389	10.953	7.429	12.136	8.995	14.285	10.493	19.631	27.367	22.595	17.336	15.875	2.733	1.303	0.173	1.146	0.768
Hylobates lar	233.333	18.190	17.211	12.975	6.117	2.935	8.837	7.504	11.508	8.447	11.346	12.018	20.082	27.550	19.217	17.929	7.040	6.352	1.072	0.917	1.058	0.336
Lophocebus albigena	153.750	16.291	15.394	15.028	11.226	5.604	11.443	9.458	11.186	8.598	12.331	10.945	19.397	27.051	21.148	16.913	14.074	3.639	1.251	0.258	1.059	0.712
Macaca arctoides	151.636	18.115	16.224	17.440	11.410	6.151	11.861	9.607	11.584	8.952	13.682	11.906	21.094	30.410	22.283	18.040	16.116	3.916	1.234	0.245	1.118	0.714
Macaca assamensis	154.400	17.770	16.182	16.646	11.462	5.584	12.340	9.154	11.162	8.878	13.824	12.038	20.868	28.954	22.051	17.636	14.496	4.437	1.250	0.311	1.098	0.648
Macaca fascicularis	120.750	12.619	11.840	12.265	8.365	4.933	9.029	7.173	8.883	6.960	10.121	8.582	15.426	21.133	16.385	12.806	11.594	2.962	1.279	0.262	1.068	0.687
Macaca mulatta	150.667	17.530	15.277	17.048	11.631	6.170	11.368	8.195	11.435	8.881	14.126	11.299	20.650	28.908	21.217	16.808	15.485	3.677	1.262	0.237	1.147	0.694
Macaca nemestrina	156.692	16.144	14.818	15.082	10.465	6.117	10.748	9.337	11.204	8.066	11.808	11.002	19.150	26.111	20.413	16.315	14.855	3.126	1.253	0.211	1.091	0.740
Macaca nigra	149.900	17.587	14.924	15.727	11.463	5.468	10.725	8.350	11.507	9.222	13.507	10.854	20.012	27.694	20.791	16.897	15.459	3.509	1.228	0.227	1.178	0.723
Macaca sinica	139.000	15.667	13.350	14.683	10.133	5.281	9.697	7.824	9.501	7.433	12.126	10.231	17.340	24.873	18.486	14.728	14.537	2.812	1.255	0.196	1.173	0.743
Macaca sylvanus	163.833	20.288	18.112	18.368	12.777	6.573	12.635	9.583	13.613	9.648	15.403	13.282	23.145	33.625	25.313	20.330	19.819	3.904	1.243	0.200	1.120	0.744
Macaca thibetana	161.750	21.205	18.023	19.556	13.706	6.055	13.749	9.360	13.709	9.389	15.266	13.768	23.661	34.610	25.500	19.825	18.946	4.616	1.289	0.251	1.177	0.715

Macaca tonkeana	155.500	19.483	16.635	17.090	12.450	6.170	11.618	9.993	12.243	9.350	14.160	12.325	21.975	30.915	23.583	18.220	18.197	3.911	1.293	0.214	1.168	0.781
Mandrillus sphinx	229.900	25.569	21.701	22.175	16.666	8.502	13.912	11.404	15.614	12.581	18.901	15.033	27.521	39.507	30.958	24.630	24.045	4.429	1.256	0.181	1.188	0.813
Miopithecus talapoin	77.938	8.927	8.031	8.043	4.981	2.709	5.508	4.974	5.422	3.918	6.641	5.646	9.241	12.825	10.216	9.083	6.599	1.855	1.125	0.284	1.113	0.656
Nasalis larvatus	197.750	20.440	19.049	18.423	13.016	4.699	13.379	11.850	14.010	11.685	13.748	14.041	25.388	33.293	24.837	22.071	14.020	4.037	1.125	0.287	1.073	0.554
Pan troglodytes	296.167	38.731	35.689	33.182	14.643	6.313	22.298	17.153	20.977	18.092	25.752	26.249	44.538	60.369	41.263	38.194	24.785	11.022	1.081	0.453	1.086	0.516
Papio anubis	211.545	23.854	21.188	21.814	16.728	7.768	15.167	10.641	17.043	12.621	18.197	15.205	28.238	38.382	32.475	24.248	23.227	2.814	1.338	0.125	1.128	0.821
Papio cynocephalus	206.083	22.763	20.595	21.208	16.994	8.327	14.310	9.894	16.292	11.848	18.296	15.108	26.723	35.334	31.063	23.325	22.968	2.315	1.331	0.099	1.105	0.879
Piliocolobus badius	157.500	16.800	15.758	16.350	11.683	4.175	10.225	6.917	11.542	9.175	12.933	12.775	21.550	29.575	21.184	17.933	13.212	4.452	1.181	0.343	1.066	0.582
Piliocolobus foai	153.125	16.831	14.770	15.098	10.350	4.108	10.365	8.326	10.505	7.844	11.460	11.124	18.885	27.630	19.568	16.651	11.434	4.981	1.175	0.443	1.140	0.541
Piliocolobus kirkii	138.333	16.087	14.017	14.187	9.653	4.633	9.530	7.150	9.987	7.757	11.107	10.080	17.670	25.950	18.605	15.739	12.016	4.389	1.183	0.390	1.148	0.620
Pongo pygmaeus	349.417	41.543	40.263	34.195	16.945	8.342	23.997	18.006	25.158	17.789	29.795	29.879	47.757	67.618	45.308	43.529	25.366	13.126	1.042	0.532	1.034	0.509
Presbytis comata	131.917	13.983	12.648	13.094	8.169	3.464	9.231	7.674	9.105	7.316	10.046	9.617	17.070	23.513	16.011	13.592	9.710	4.360	1.178	0.452	1.106	0.528
Presbytis melalophos	136.250	14.370	13.208	12.538	8.288	3.775	9.220	6.703	9.583	7.370	10.105	9.985	17.250	23.818	17.334	14.867	10.803	3.418	1.167	0.317	1.089	0.606
Pygathrix nemaeus	192.833	18.240	16.907	16.017	11.190	4.827	11.574	10.402	12.339	9.693	12.693	11.754	21.308	30.534	20.881	17.032	13.075	5.573	1.498	0.432	1.081	0.561
Rhinopithecus roxellana	175.333	18.938	18.240	16.580	11.401	4.837	13.377	10.228	12.302	9.862	13.273	13.197	23.537	30.429	24.302	20.770	14.212	4.087	1.171	0.293	1.040	0.588
Saguinus oedipus	49.900	6.079	6.039	5.781	3.390	2.621	4.352	2.522	3.715	2.784	3.923	4.528	7.389	10.990	7.270	6.842	3.759	2.449	1.063	0.676	1.008	0.443
Saimiri sciureus	69.100	7.475	7.622	6.985	4.765	2.273	5.626	4.059	4.911	3.825	4.877	4.784	8.564	12.522	9.021	8.510	5.042	2.455	1.061	0.495	0.982	0.523
Semnopithecus entellus	144.433	17.434	16.187	16.018	10.754	5.563	11.947	8.619	12.241	8.627	14.277	11.879	20.701	28.642	22.137	18.404	15.827	3.798	1.199	0.237	1.098	0.734
Theropithecus gelada	180.000	20.429	19.179	19.736	15.104	6.857	12.391	9.740	14.753	10.418	14.977	13.038	23.187	32.448	28.701	21.555	21.062	2.710	1.332	0.130	1.063	0.876
Trachypithecus cristata	138.500	14.132	12.678	13.086	8.830	4.257	9.626	8.644	9.609	7.504	10.396	9.549	17.002	23.921	16.688	14.594	11.029	4.132	1.143	0.383	1.115	0.602
Trachypithecus obscurus	138.273	14.541	13.761	13.607	9.742	4.126	9.634	8.630	9.841	7.516	11.031	10.506	18.406	25.421	18.013	15.512	11.726	4.108	1.162	0.353	1.057	0.629
Trachypithecus phrayei	140.000	14.825	14.138	13.914	9.839	4.433	10.419	7.983	10.186	8.453	11.022	10.764	19.398	26.584	18.366	16.106	10.699	4.565	1.140	0.429	1.050	0.542

Appendix D.2. Species mean for variables from the femur

Species	FL	APFH	PDFH	PDLT	APMC	PDMC	MLMC	APLC	PDLC	MLLC	BCB	PH	PW	API	PDI	MLI	FNA	ACON
Allenopithecus nigroviridis	136.500	11.800	11.125	8.515	16.855	11.505	7.030	17.095	12.440	6.205	20.335	11.475	9.065	1.718	1.544	0.988	0.924	1.136
Allochrocebus lhoesti	160.429	12.756	12.269	8.206	19.829	14.620	8.116	20.703	15.989	6.741	23.624	14.413	10.913	1.725	1.539	0.959	0.919	1.211
Alouatta palliata	153.556	13.977	13.559	8.093	19.268	14.866	8.106	17.111	13.659	6.574	24.018	13.646	12.397	1.883	1.461	1.126	1.090	1.236
Aotus azarai	102.167	7.856	7.438	6.696	12.129	8.323	4.305	11.938	8.699	4.588	14.256	9.166	6.700	1.841	1.481	1.017	0.957	0.939
Cebus apella	124.200	9.917	9.519	5.763	13.894	10.596	6.110	13.688	10.685	5.714	18.417	9.519	8.337	1.848	1.491	1.015	0.992	1.072
Cercocebus torquatus	207.231	17.304	16.792	10.643	24.869	18.357	10.253	24.747	18.822	8.489	28.622	17.595	14.907	1.758	1.500	1.006	0.976	1.216
Cercopithecus ascanius	149.286	11.868	11.566	7.898	17.902	13.001	7.067	17.844	13.632	6.087	21.034	12.364	9.651	1.743	1.541	1.003	0.954	1.163
Cercopithecus cephus	147.100	12.080	12.000	7.470	17.800	13.270	7.230	18.160	13.720	5.590	21.080	12.660	9.960	1.749	1.547	0.980	0.969	1.293
Cercopithecus diana	161.000	12.748	12.557	7.998	18.273	13.767	7.770	18.542	14.173	6.412	23.088	12.425	10.718	1.763	1.511	0.984	0.969	1.218
Cercopithecus hamlyni	168.667	12.910	12.747	8.630	20.317	15.220	8.510	20.843	15.793	7.410	23.867	14.790	10.930	1.713	1.509	0.972	0.963	1.158
Cercopithecus mitis	160.769	13.907	13.372	8.522	20.952	15.384	8.242	20.846	15.775	7.189	24.398	14.575	11.516	1.756	1.543	1.005	0.976	1.149
Cercopithecus mona	151.846	12.253	11.830	7.975	18.470	13.545	7.597	18.995	14.288	6.625	21.868	13.667	10.785	1.787	1.521	0.972	0.948	1.152
Cercopithecus neglectus	162.091	13.465	13.085	8.636	19.936	14.611	7.735	19.995	15.226	7.138	23.951	14.842	11.651	1.778	1.518	0.999	0.963	1.084
Cercopithecus nictitans	159.545	13.199	13.069	8.483	19.626	14.268	7.757	19.541	14.721	6.535	23.574	13.762	11.153	1.761	1.513	1.004	0.972	1.187
Cercopithecus pogonias	144.364	11.791	11.500	7.618	17.255	12.418	6.700	15.782	12.727	5.691	20.491	12.127	9.809	1.778	1.524	1.895	0.977	1.187
Chlorocebus aethiops	151.000	12.193	11.857	7.407	18.059	13.221	7.180	18.392	13.834	6.018	21.858	13.180	10.777	1.759	1.539	0.982	0.960	1.197
Chlorocebus pygerythrus	142.857	11.784	11.196	6.851	17.704	12.893	6.810	17.924	13.469	5.973	20.546	12.601	9.718	1.754	1.539	0.989	0.966	1.142
Colobus guereza	199.533	16.719	15.992	9.567	24.299	18.183	10.705	24.478	19.520	9.609	29.841	17.392	14.834	1.782	1.588	0.994	0.932	1.120
Erythrocebus patas	190.333	15.837	15.289	9.262	24.878	17.057	10.039	25.956	17.762	8.266	28.863	15.799	13.498	1.776	1.514	0.958	0.964	1.214
Hylobates lar	202.750	15.863	15.368	9.383	19.303	15.263	8.887	17.951	14.832	6.553	24.868	15.654	15.277	1.930	1.432	1.076	1.029	1.363
Lophocebus albigena	199.083	15.976	15.612	9.942	21.628	16.191	9.118	21.475	16.558	7.847	26.371	14.948	14.013	1.781	1.540	1.009	0.977	1.166
Macaca arctoides	164.917	16.488	15.701	10.164	23.533	16.489	9.558	21.952	16.691	7.475	28.376	15.672	12.687	1.778	1.526	1.073	0.989	1.285
Macaca assamensis	165.200	16.282	15.258	10.272	22.750	16.608	9.120	21.510	16.468	7.302	27.944	15.184	11.912	1.821	1.488	1.058	1.008	1.252
Macaca fascicularis	134.083	11.854	11.393	8.095	16.478	12.773	6.991	15.904	12.595	5.948	20.204	12.671	9.685	1.805	1.528	1.036	1.014	1.180
Macaca mulatta	181.417	16.209	15.542	10.550	22.812	17.236	11.135	22.912	17.864	8.481	29.163	16.561	13.825	1.776	1.577	0.995	0.964	1.313
Macaca nemestrina	177.769	15.438	14.575	9.399	21.585	16.138	9.059	20.725	16.110	7.559	26.391	14.805	12.758	1.831	1.515	1.042	1.001	1.203
Macaca nigra	174.556	16.074	15.542	9.627	23.442	17.629	10.258	22.781	17.474	8.762	29.129	15.048	13.816	1.810	1.529	1.026	1.010	1.180
Macaca sinica	160.429	13.861	13.337	9.324	20.750	15.121	9.603	20.230	16.026	7.259	24.453	15.431	11.686	1.764	1.554	1.027	0.943	1.326
Macaca sylvanus	199.333	18.247	17.537	11.303	26.597	19.205	11.802	26.453	21.277	9.902	31.542	18.268	15.633	1.772	1.559	1.006	0.901	1.196
Macaca thibetana	174.778	19.103	18.122	11.854	26.291	19.606	11.176	24.403	19.118	8.430	32.873	16.631	14.253	1.808	1.477	1.076	1.026	1.326
Macaca tonkeana	174.333	17.797	16.700	10.083	23.607	17.880	10.510	21.717	17.457	8.893	29.903	15.377	13.607	1.762	1.470	1.089	1.024	1.180
Mandrillus sphinx	262.400	22.920	21.612	13.585	31.994	24.185	14.289	32.035	24.828	11.690	37.986	22.263	18.896	1.770	1.498	1.000	0.973	1.222

Miopithecus talapoin	93.250	7.873	7.803	5.012	11.291	8.437	4.332	11.296	8.352	3.584	13.686	8.520	6.168	1.761	1.510	1.000	1.013	1.212
Nasalis larvatus	228.000	20.408	19.620	11.778	27.246	20.908	12.309	26.160	21.817	10.359	33.072	21.000	17.138	1.801	1.511	1.043	0.958	1.191
Pan troglodytes	292.333	33.071	31.523	19.623	44.111	34.393	21.766	38.263	30.585	17.257	61.411	27.733	29.063	1.946	1.470	1.155	1.126	1.262
Papio anubis	242.364	23.251	22.336	14.485	32.690	23.544	13.357	31.459	23.975	11.493	38.073	19.336	18.459	1.744	1.528	1.042	0.984	1.162
Papio cynocephalus	242.667	21.546	21.073	13.146	30.310	22.028	12.768	30.210	23.262	10.863	36.445	20.068	17.692	1.757	1.525	1.005	0.948	1.176
Piliocolobus badius	185.000	16.350	15.642	10.425	24.042	17.908	10.542	23.233	18.508	8.708	28.583	17.317	14.125	1.815	1.553	1.035	0.968	1.211
Piliocolobus foai	183.625	15.774	15.141	8.884	22.164	16.094	8.868	22.094	16.710	8.998	27.333	16.744	12.994	1.814	1.533	1.004	0.964	0.992
Piliocolobus kirkii	175.000	15.373	14.530	7.873	22.627	16.367	8.490	22.153	17.143	8.310	26.447	16.677	12.670	1.764	1.561	1.024	0.962	1.024
Pongo pygmaeus	269.833	35.060	33.119	17.663	43.822	34.646	20.723	37.824	30.667	17.893	58.801	25.676	28.411	2.132	1.458	1.161	1.128	1.165
Presbytis comata	195.167	14.577	14.033	7.616	20.298	15.535	8.949	20.272	16.531	7.778	25.687	15.438	12.320	1.797	1.538	1.002	0.941	1.155
Presbytis melalophos	186.250	15.045	14.970	8.623	21.560	16.538	8.378	21.803	17.038	8.415	25.985	16.280	12.360	1.745	1.583	0.988	0.969	0.998
Pygathrix nemaeus	225.909	18.602	17.759	9.473	26.560	20.073	11.250	25.945	20.753	10.142	31.285	19.525	15.949	1.797	1.527	1.024	0.967	1.113
Rhinopithecus roxellana	201.500	18.723	18.014	10.388	25.905	19.621	11.526	25.669	20.427	10.242	32.184	19.395	15.740	1.833	1.542	1.010	0.962	1.131
Saguinus oedipus	63.500	5.908	5.627	3.169	8.193	6.141	3.131	8.234	6.020	2.729	10.067	6.862	4.138	1.803	1.577	0.995	1.020	1.155
Saimiri sciureus	84.800	6.545	6.285	4.466	10.138	7.121	3.854	9.832	7.236	3.498	11.922	8.405	4.994	1.804	1.543	1.032	0.985	1.105
Semnopithecus entellus	210.900	17.638	16.846	9.132	24.662	18.909	10.598	24.962	20.048	9.232	30.270	17.990	14.419	1.770	1.515	0.991	0.950	1.152
Theropithecus gelada	199.941	19.624	18.987	13.778	28.238	20.800	11.921	26.787	20.898	9.561	34.356	18.455	17.469	1.825	1.551	1.053	0.999	1.256
Trachypithecus cristatus	174.083	14.211	13.643	7.469	19.438	14.431	75.392	20.055	15.444	7.012	24.838	14.379	11.280	1.791	1.561	0.969	0.934	10.662
Trachypithecus obscurus	174.636	14.985	14.527	7.794	20.847	16.145	8.580	20.523	16.480	7.285	25.937	15.872	12.160	1.837	1.565	1.016	0.980	1.181
Trachypithecus phayrei	178.167	15.280	14.727	8.888	20.548	15.754	8.853	20.820	16.783	7.404	25.969	15.851	12.492	1.801	1.558	0.987	0.938	1.202

Appendix D.3. Species mean for variables from the astragalus

Species	**AL**	**BPD**	**HNPD**	**DHTF**	**TW**	**HMR**	**HLR**	**DHFF**	**PDFF**	**EW**	**EL**	**WTH**	**PT**	**DT**	**ASM**	**WED**	**ATH**	**TAS**
Allenopithecus nigroviridis	18.280	10.910	9.535	6.830	8.265	8.710	9.135	8.290	10.755	5.440	7.940	7.685	6.635	8.705	1.052	1.317	2.256	1.681
Allochrocebus lhoesti	21.760	12.292	11.846	7.482	10.316	10.060	10.720	9.072	12.374	6.444	9.638	8.854	9.066	10.248	1.066	1.136	2.112	1.623
Alouatta palliata	23.145	13.134	13.009	6.968	8.965	8.538	9.376	8.990	11.708	5.678	11.531	8.820	8.725	10.183	1.102	1.171	1.481	1.336
Aotus azarai	14.832	7.773	8.564	4.437	5.801	6.678	6.585	6.033	7.270	3.803	6.914	5.583	4.853	6.221	0.990	1.287	1.789	1.480
Cebus apella	18.463	9.887	10.343	5.840	8.097	8.102	8.117	7.574	9.764	5.374	8.162	7.238	6.722	8.208	1.002	1.221	1.766	1.486
Cercocebus torquatus	26.066	15.348	14.607	10.342	11.649	12.921	13.518	11.794	15.147	7.837	11.848	11.532	10.360	12.122	1.046	1.177	2.354	1.671
Cercopithecus ascanius	19.836	11.368	10.922	7.109	9.314	9.569	9.971	8.805	10.702	6.053	9.305	8.176	7.710	9.474	1.042	1.231	2.082	1.644
Cercopithecus cephus	20.630	11.680	11.330	7.490	9.320	9.490	9.840	8.390	11.480	5.990	9.100	8.600	7.950	9.590	1.038	1.208	1.956	1.695
Cercopithecus diana	21.240	12.067	11.573	8.290	8.953	9.667	10.107	8.917	11.643	5.950	8.967	8.573	8.727	9.723	1.046	1.115	2.155	1.633
Cercopithecus hamlyni	23.636	13.880	12.970	8.498	10.950	11.816	12.152	10.194	13.106	6.912	11.088	10.712	9.500	10.782	1.029	1.143	2.030	1.519
Cercopithecus mitis	22.780	13.085	11.977	8.699	10.013	11.063	11.393	9.741	12.784	6.569	10.592	9.504	9.301	10.723	1.030	1.157	2.118	1.653
Cercopithecus mona	20.417	11.938	10.734	7.672	8.831	9.659	10.330	9.136	11.701	6.251	9.654	8.649	8.211	9.405	1.070	1.147	2.092	1.699
Cercopithecus neglectus	21.739	12.847	11.909	7.760	10.075	10.294	10.961	9.652	12.375	6.455	10.059	8.822	8.624	10.325	1.064	1.197	1.911	1.716
Cercopithecus nictitans	22.276	12.822	11.900	8.384	10.061	10.382	10.920	9.849	12.598	6.338	10.361	9.242	8.648	10.417	1.054	1.211	2.125	1.717
Cercopithecus pogonias	19.917	11.617	11.100	6.925	8.617	8.933	9.533	8.567	11.225	5.692	9.117	8.017	7.558	8.817	1.067	1.169	1.951	1.643
Chlorocebus aethiops	21.346	11.994	11.109	7.287	9.360	9.867	10.576	8.991	11.803	6.310	9.547	8.586	7.410	9.733	1.073	1.321	2.061	1.650
Chlorocebus pygerythrus	20.071	11.308	11.136	7.146	8.909	9.180	9.686	8.661	11.125	5.824	8.675	8.303	7.586	9.021	1.055	1.195	2.123	1.713
Colobus guereza	27.837	15.312	15.738	9.637	12.647	13.447	13.668	11.456	15.094	8.485	13.172	12.364	11.239	13.011	1.019	1.163	2.107	1.615
Erythrocebus patas	26.855	15.398	14.898	9.999	11.542	12.644	13.143	10.654	14.418	7.915	11.511	11.632	10.972	12.361	1.042	1.132	2.249	1.736
Hylobates lar	20.913	13.127	10.128	8.084	7.922	10.289	10.675	10.153	12.634	6.478	10.763	9.876	7.969	8.885	1.040	1.117	1.551	1.447
Lophocebus albigena	25.796	14.344	13.853	9.516	11.596	12.036	12.886	11.075	14.158	7.704	11.046	10.716	9.570	12.149	1.071	1.271	2.141	1.681
Macaca arctoides	24.749	15.296	13.861	9.005	10.865	11.577	12.906	10.783	13.700	7.323	11.739	10.319	9.773	11.425	1.118	1.174	1.913	1.692
Macaca assamensis	24.320	14.620	13.022	8.746	10.067	11.145	12.444	11.136	13.964	7.065	11.417	9.836	9.569	11.012	1.118	1.152	1.794	1.675
Macaca fascicularis	19.401	11.249	10.745	7.209	7.879	8.857	9.732	8.347	10.963	5.730	8.736	7.887	7.465	8.772	1.101	1.178	1.918	1.671
Macaca mulatta	26.258	15.429	14.543	10.137	10.690	12.719	13.231	10.903	15.210	8.162	11.493	11.161	10.209	12.158	1.041	1.197	1.875	1.660
Macaca nemestrina	23.727	13.504	13.278	8.856	10.051	11.128	12.075	10.683	13.237	7.224	10.842	10.175	9.242	10.621	1.086	1.157	1.938	1.672
Macaca nigra	25.925	15.249	15.006	9.244	11.735	12.383	13.617	12.079	14.776	7.948	11.653	11.414	11.093	12.628	1.101	1.140	1.832	1.688
Macaca sinica	22.022	13.210	11.914	7.368	10.082	10.488	11.288	10.376	12.730	6.600	10.554	9.590	8.858	9.950	1.076	1.124	1.874	1.626
Macaca sylvanus	27.508	17.217	15.273	9.645	11.730	12.898	14.487	12.923	16.573	8.707	12.692	11.813	10.488	12.957	1.128	1.238	1.745	1.644
Macaca thibetana	27.266	15.803	15.043	8.399	12.416	12.910	13.984	12.601	15.324	8.234	13.051	11.583	11.394	13.797	1.083	1.212	1.709	1.671
Macaca tonkeana	26.323	14.483	15.380	10.143	12.138	13.180	14.190	12.078	14.708	7.920	11.865	11.425	10.055	12.835	1.079	1.277	1.459	1.659
Mandrillus sphinx	31.982	19.238	17.834	12.163	14.393	16.301	17.386	14.663	18.963	10.278	13.973	15.375	12.681	15.577	1.068	1.236	1.582	1.605

Miopithecus talapoin	13.245	6.995	7.487	4.540	5.631	6.031	6.204	5.565	6.916	3.842	5.994	5.221	4.754	5.705	1.028	1.204	1.789	1.645
Nasalis larvatus	31.218	18.122	17.088	11.622	13.223	15.283	16.216	13.047	17.568	9.943	15.121	13.356	12.742	14.148	1.064	1.113	2.238	1.629
Pan troglodytes	43.468	27.993	23.096	15.980	18.816	22.943	24.151	22.854	26.131	16.867	25.506	23.068	18.450	21.028	1.054	1.142	1.907	1.511
Papio anubis	33.436	20.435	17.580	12.954	15.197	16.790	17.794	15.012	20.153	11.053	15.971	16.363	13.757	16.566	1.061	1.209	1.934	1.711
Papio cynocephalus	32.191	19.066	17.348	11.742	14.325	15.609	16.364	14.459	18.849	9.823	14.824	14.768	12.462	14.799	1.050	1.190	1.987	1.718
Piliocolobus badius	26.392	14.575	13.283	9.292	11.408	12.200	12.983	11.125	14.383	8.450	12.792	12.183	10.158	12.325	1.065	1.214	1.909	1.593
Piliocolobus foai	25.980	13.706	14.500	8.406	11.820	12.720	12.886	11.382	13.320	7.994	11.900	11.054	9.700	12.152	1.012	1.254	1.945	1.512
Pongo pygmaeus	47.989	26.039	23.998	14.690	21.911	18.792	23.233	21.027	24.750	15.569	24.545	20.959	20.737	23.168	1.234	1.124	1.365	1.544
Presbytis comata	23.133	13.023	13.292	9.046	10.511	10.913	11.704	9.424	12.255	6.748	10.833	10.168	9.943	11.028	1.071	1.109	2.385	1.631
Presbytis melalophos	24.943	14.130	13.757	9.543	10.517	11.827	12.280	10.927	12.340	9.527	10.523	10.613	10.160	11.153	1.046	1.102	2.318	1.666
Pygathrix nemaeus	28.834	15.884	15.355	11.099	12.325	14.735	14.401	12.138	15.052	9.722	13.296	12.889	11.315	13.418	0.981	1.191	2.003	1.569
Rhinopithecus roxellana	28.766	15.548	15.206	9.423	13.381	14.154	14.527	12.246	15.071	9.565	12.936	13.076	11.504	14.161	1.027	1.243	1.981	1.650
Saguinus oedipus	10.297	5.225	5.799	3.323	3.669	4.200	3.741	3.895	5.195	2.532	4.550	3.644	3.746	4.232	0.891	1.132	1.768	1.447
Saimiri sciureus	12.455	6.881	7.023	4.231	4.477	5.491	5.200	4.878	6.701	3.094	5.936	4.459	4.457	5.103	0.946	1.145	1.720	1.456
Semnopithecus entellus	27.294	15.567	15.143	10.620	12.741	13.984	14.383	10.940	14.299	8.973	13.010	12.500	11.791	13.464	1.028	1.139	2.326	1.650
Theropithecus gelada	28.181	16.352	16.342	11.364	13.253	14.321	14.859	12.719	15.876	8.898	13.622	13.345	11.865	13.964	1.037	1.179	1.918	1.597
Trachypithecus cristatus	22.216	12.152	13.027	8.972	9.352	10.807	11.488	9.353	11.475	7.290	10.361	9.529	8.990	9.948	1.063	1.107	1.840	1.579
Trachypithecus obscurus	22.676	12.624	12.979	8.450	10.013	11.263	11.822	9.480	12.050	7.177	11.244	10.248	9.392	10.542	1.052	1.123	2.227	1.633
Trachypithecus phrayei	24.296	13.948	13.790	9.142	10.704	11.871	12.748	10.024	12.976	7.183	11.228	10.343	9.960	11.239	1.075	1.130	2.221	1.702

Appendix D.4 Species mean for variables from the calcaneus

Species	**CL**	**PDA**	**CTL**	**PDF**	**MLF**	**MLS**	**HCF**	**CTW**
Allenopithecus nigroviridis	22.000	15.040	5.000	6.310	5.540	3.950	6.950	6.600
Allochrocebus lhoesti	29.200	20.072	7.150	8.678	7.046	5.294	8.644	8.784
Alouatta palliata	28.500	19.326	6.268	11.046	6.775	5.361	9.076	8.039
Aotus azarai	20.091	14.955	3.679	6.543	4.219	4.040	5.983	4.862
Cebus apella	24.333	16.800	5.944	7.190	5.555	5.153	7.347	7.473
Cercocebus torquatus	36.833	19.958	10.285	10.280	9.834	6.510	10.683	10.044
Cercopithecus ascanius	27.091	17.993	6.829	8.087	6.543	4.815	8.122	7.763
Cercopithecus cephus	27.600	18.240	6.720	7.940	7.360	5.360	7.810	8.100
Cercopithecus diana	29.000	18.343	7.667	7.523	6.740	5.213	8.150	8.087
Cercopithecus hamlyni	31.500	19.773	8.318	8.775	8.348	5.520	9.025	9.830
Cercopithecus mitis	30.583	19.668	8.390	8.918	8.117	5.543	8.888	8.587
Cercopithecus mona	29.071	18.356	7.266	8.501	7.253	5.091	8.404	8.452
Cercopithecus neglectus	29.100	19.338	8.289	8.894	7.589	5.620	8.423	8.869
Cercopithecus nictitans	30.615	19.609	7.134	8.938	7.741	5.972	8.941	8.698
Cercopithecus pogonias	26.667	18.233	5.883	7.725	6.742	5.225	7.850	7.900
Chlorocebus aethiops	29.833	19.032	8.308	8.552	6.952	5.825	8.613	8.915
Chlorocebus pygerythrus	27.100	17.798	7.321	7.451	6.314	5.136	7.857	8.227
Colobus guereza	37.071	22.955	10.529	11.206	10.257	6.599	11.184	10.516
Erythrocebus patas	37.833	24.403	11.647	10.443	8.872	6.002	11.110	11.405
Hylobates lar	24.500	16.971	5.240	9.492	8.234	5.790	7.690	7.588
Lophocebus albigena	33.786	22.086	8.886	9.217	8.555	7.261	10.375	10.052
Macaca arctoides	34.000	22.281	9.071	10.873	8.445	5.965	10.716	9.322
Macaca assamensis	31.429	20.517	8.186	9.914	8.233	5.910	9.403	8.871
Macaca fascicularis	25.417	16.400	6.558	7.114	6.633	4.725	7.448	7.471
Macaca mulatta	35.250	21.538	9.580	10.278	9.376	6.423	11.343	10.815
Macaca nemestrina	32.917	20.896	8.681	9.443	8.073	5.878	10.286	9.622
Macaca nigra	35.455	22.567	9.294	10.789	9.327	6.346	11.816	10.965
Macaca sinica	29.500	18.223	8.750	8.775	7.540	4.970	9.158	9.668
Macaca sylvanus	38.500	23.382	10.792	11.720	9.958	6.018	12.858	12.345
Macaca thibetana	37.714	24.219	9.780	12.231	9.761	6.257	12.071	11.546
Macaca tonkeana	35.000	22.023	9.500	10.528	9.158	7.258	12.368	11.088
Mandrillus sphinx	47.545	27.366	14.882	13.776	12.862	9.219	15.642	13.750

Miopithecus talapoin	17.357	12.158	3.689	5.124	4.193	3.139	5.476	5.491
Nasalis larvatus	40.900	25.953	10.190	12.127	11.710	8.341	11.351	11.051
Pan troglodytes	53.833	35.097	14.038	22.931	18.638	13.515	18.306	19.413
Papio anubis	47.333	28.918	14.144	14.544	13.233	9.712	15.502	16.070
Papio cynocephalus	45.750	26.826	13.253	12.982	12.378	8.644	14.883	14.588
Piliocolobus badius	35.167	22.150	9.100	11.133	10.250	6.825	10.775	10.325
Piliocolobus foai	33.600	22.670	8.646	10.254	9.214	6.000	9.808	9.332
Pongo pygmeaus	56.182	36.264	12.493	22.194	17.175	13.525	19.956	15.578
Presbytis comata	31.364	20.609	8.088	9.262	8.866	6.458	8.074	8.730
Presbytis melalophos	32.000	21.110	6.605	9.985	9.690	6.325	9.765	9.730
Pygathrix nemaeus	37.154	23.802	9.098	11.086	11.169	7.279	11.183	10.866
Rhinopithecus roxellana	37.200	24.617	8.725	11.056	10.980	9.210	12.596	11.236
Saguinus oedipus	12.400	9.357	2.718	4.454	2.940	2.615	3.682	3.439
Saimiri sciureus	15.900	12.148	2.766	5.280	3.490	2.987	4.264	4.712
Semnopithecus entellus	37.000	23.080	10.463	11.829	11.311	6.871	11.160	11.247
Theropithecus gelada	41.125	23.841	12.336	12.113	10.298	6.759	13.389	12.649
Trachypithecus cristatus	31.091	19.650	6.848	9.137	7.657	5.560	8.228	8.408
Trachypithecus obscurus	31.125	20.045	6.255	9.729	8.656	5.814	9.191	8.590
Trachypithecus phrayei	32.000	21.075	6.954	9.947	8.494	5.898	8.815	9.422

Appendix E. Terrestriality Assessment Survey sent to primatologists and referred to in Appendix A

Terrestriality Assessment

Thank you for filling out this assessment. If you are assessing more than one species please fill out the assessment separately for each species. This form can be e-mailed back to agosselinildari@gmail.com

Information provided in this Terrestriality Assessment will be summarized in a table in my dissertation and all respondents will be appropriately cited. Citations in my dissertation and future publications will be referenced as pers. comm.

Name of Investigator:

Species you are assessing:

Do you have percentage data for the amount of time your species spends on the ground relative to observation time?

- ☐No
- ☐Yes; the percentage is

If yes, please indicate the sampling method here:

If yes, does this percentage have a seasonality component?

- ☐No, this percentage accurately reflects my species' time on ground throughout the year.
- ☐Yes, and this percentage reflects the amount of time my species spends on the ground during the season that it is most terrestrial.
- ☐Yes, and this percentage reflects the amount of time my species spends on the ground averaged throughout the entire year. If you have a percentage for the amount of time your species spends on the ground during its most terrestrial season please enter it here:

For the following questions please score your species based on your personal observations even if you entered percentage data above.

My species (please check more than one box if applicable):

- ☐Rarely or never comes to the ground
- ☐Spends most of its time in trees but comes to the ground regularly for brief periods of time
- ☐Spends equal amounts of time in the trees and on the ground
- ☐Spends most of its time on the ground but will enter trees regularly for brief periods of time

☐Rarely or never enters the trees
☐Spends a substantial amount of time on the ground for a few months of the year
☐Spends a substantial amount of time on the ground for half the year

When on the ground my species is primarily (please check more than on box if applicable):

☐Not applicable
☐Travelling
☐Feeding
☐Drinking
☐Resting
☐Other:

If you study more than one species or if your study site is inhabited by more than one primate species please rank the species with which you are familiar according to their degree of terrestriality (1 = most terrestrial). You may list more than 1 species in the same place if their degree of terrestriality is equal.

☐ Not applicable

1.

2.

3.

4.

5.

If you have any anecdotal evidence you would like to add please use this space:

If you have a preference for how I reference this information please enter it here:

Appendix F. Phylogenies used to run analyses in the dissertation: a) Cercopithecoid phylogeny downloaded from 10KTrees, b) Anthropoid phylogeny downloaded from 10KTrees, c) modified Springer et al. (2012) phylogeny, d) Anthropoid phylogeny from 10KTrees with 2 added fossils, e) Anthropoid phylogeny from 10KTrees with 8 added fossils, f) modified Springer et al. (2012) phylogeny with 2 added fossils, g) modified Springer et al. (2012) phylogeny with 8 added fossils

A) Cercopithecoid only tree

```
#NEXUS
[created by the 10kTree Website - http://10kTrees.fas.harvard.edu]
BEGIN TREES;
translate
1 Allenopithecus_nigroviridis,
2 Cercocebus_torquatus,
3 Cercopithecus_ascanius,
4 Cercopithecus_cephus,
5 Cercopithecus_diana,
6 Cercopithecus_hamlyni,
7 Cercopithecus_lhoesti,
8 Cercopithecus_mitis,
9 Cercopithecus_mona,
10 Cercopithecus_neglectus,
11 Cercopithecus_nictitans,
12 Cercopithecus_pogonias,
13 Chlorocebus_aethiops,
14 Chlorocebus_pygerythrus,
15 Colobus_guereza,
16 Erythrocebus_patas,
17 Lophocebus_albigena,
18 Macaca_arctoides,
19 Macaca_assamensis,
20 Macaca_fascicularis,
21 Macaca_mulatta,
22 Macaca_nemestrina,
23 Macaca_nigra,
24 Macaca_sinica,
25 Macaca_sylvanus,
26 Macaca_thibetana,
27 Macaca_tonkeana,
28 Mandrillus_sphinx,
29 Miopithecus_talapoin,
30 Nasalis_larvatus,
31 Papio_anubis,
32 Papio_cynocephalus,
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33 Piliocolobus_badius,
34 Piliocolobus_foai,
35 Piliocolobus_kirkii,
36 Presbytis_comata,
37 Presbytis_melalophos,
38 Pygathrix_nemaeus,
39 Rhinopithecus_roxellana,
40 Semnopithecus_entellus,
41 Theropithecus_gelada,
42 Trachypithecus_cristatus,
43 Trachypithecus_obscurus,
44 Trachypithecus_phayrei;
tree consensus_44species =
(((1:11.894902,(((((8:3.762640,11:3.762640):2.666569,(3:2.018943,4:2.018944):4.410266):1.46
1009,(((9:3.167176,12:3.167176):2.820105,(5:5.588511,10:5.588511):0.398770):1.355876,6:7.3
43158):0.547060):1.957908,((7:7.939800,16:7.939800):0.687445,(13:1.880772,14:1.880772):6.
746472):1.220881):1.644988,29:11.493113):0.401789):2.980276,(((2:5.304298,28:5.304297):6.
046166,((17:4.896861,41:4.896862):0.872302,(31:2.058446,32:2.058446):3.710717):5.581300):
1.502062,((((18:4.705214,(19:3.228863,24:3.228863):1.476351):1.331851,((27:3.501040,23:3.5
01041):0.766095,22:4.267135):1.769930):0.840931,((20:5.045978,21:5.045978):1.475126,26:6.
521104):0.356891):1.782804,25:8.660800):4.191726):2.022653):6.535196,((15:12.537452,(33:5
.435125,(34:4.764087,35:4.764086):0.671038):7.102327):2.897705,((((30:9.634813,38:9.63481
3):0.839771,39:10.474584):2.310063,(40:11.461377,((42:4.015007,43:4.015007):1.237980,44:5.
252987):6.208391):1.323270):0.523455,(36:5.778211,37:5.778211):7.529891):2.127056):5.975
217);
END;
```

B) Anthropoid tree

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#NEXUS
[created by the 10kTree Website - http://10kTrees.fas.harvard.edu]
BEGIN TREES;
translate
1 Allenopithecus_nigroviridis,
2 Alouatta_palliata,
3 Aotus_azarai,
4 Cebus_apella,
5 Cercocebus_torquatus,
6 Cercopithecus_ascanius,
7 Cercopithecus_cephus,
8 Cercopithecus_diana,
9 Cercopithecus_hamlyni,
10 Cercopithecus_lhoesti,
11 Cercopithecus_mitis,
12 Cercopithecus_mona,
13 Cercopithecus_neglectus,
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14 Cercopithecus_nictitans,
15 Cercopithecus_pogonias,
16 Chlorocebus_aethiops,
17 Chlorocebus_pygerythrus,
18 Colobus_guereza,
19 Erythrocebus_patas,
20 Hylobates_lar,
21 Lophocebus_albigena,
22 Macaca_arctoides,
23 Macaca_assamensis,
24 Macaca_fascicularis,
25 Macaca_mulatta,
26 Macaca_nemestrina,
27 Macaca_nigra,
28 Macaca_sinica,
29 Macaca_sylvanus,
30 Macaca_thibetana,
31 Macaca_tonkeana,
32 Mandrillus_sphinx,
33 Miopithecus_talapoin,
34 Nasalis_larvatus,
35 Pan_troglodytes_schweinfurthii,
36 Papio_anubis,
37 Papio_cynocephalus,
38 Piliocolobus_badius,
39 Piliocolobus_foai,
40 Piliocolobus_kirkii,
41 Pongo_pygmaeus,
42 Presbytis_comata,
43 Presbytis_melalophos,
44 Pygathrix_nemaeus,
45 Rhinopithecus_roxellana,
46 Saguinus_oedipus,
47 Saimiri_sciureus,
48 Semnopithecus_entellus,
49 Theropithecus_gelada,
50 Trachypithecus_cristatus,
51 Trachypithecus_obscurus,
52 Trachypithecus_phayrei;
tree consensus_52species =
(((((1:11.894902,(((((11:3.762640,14:3.762640):2.666569,(6:2.018943,7:2.018944):4.410266):1.
461009,(((12:3.167176,15:3.167176):2.820105,(8:5.588511,13:5.588511):0.398770):1.355876,9
:7.343158):0.547060):1.957908,((10:7.939800,19:7.939800):0.687445,(16:1.880772,17:1.88077
2):6.746472):1.220881):1.644988,33:11.493113):0.401789):2.980276,(((5:5.304298,32:5.30429
7):6.046166,((21:4.896861,49:4.896862):0.872302,(36:2.058446,37:2.058446):3.710717):5.581
300):1.502062,((((22:4.705214,(23:3.228863,28:3.228863):1.476351):1.331851,((31:3.501040,2
```

```
7:3.501041):0.766095,26:4.267135):1.769930):0.840931,((24:5.045978,25:5.045978):1.475126,
30:6.521104):0.356891):1.782804,29:8.660800):4.191726):2.022653):6.535196,((18:12.537452,
(38:5.435125,(39:4.764087,40:4.764086):0.671038):7.102327):2.897705,((((34:9.634813,44:9.6
34813):0.839771,45:10.474584):2.310063,(48:11.461377,((50:4.015007,51:4.015007):1.237980,
52:5.252987):6.208391):1.323270):0.523455,(42:5.778211,43:5.778211):7.529891):2.127056):5
.975217):8.589626,(20:19.605945,(35:15.132454,41:15.132455):4.473491):10.394055):16.8118
21,(2:21.321301,((3:19.487522,46:19.487522):0.605006,(4:18.569905,47:18.569905):1.522623)
:1.228773):25.490521);
END;
```

C) modified Springer et al. (2012) phylogeny

```
#NEXUS
[written Sat Oct 12 15:20:12 EDT 2013 by Mesquite  version 2.74 (build 550) at Ashley-
Gosselin-Ildaris-MacBook-Pro-2.local/10.0.1.3]

BEGIN TREES;
        Title 'Trees from "springer_autocorrelated_hardbounds.nex"';
        LINK Taxa = Taxa;
        TRANSLATE
                1 Alouatta_palliata,
                2 Saimiri_sciureus,
                3 Cebus_apella,
                4 Saguinus_oedipus,
                5 Aotus_azarae,
                6 Pongo_pygmaeus,
                7 Pan_troglodytes,
                8 Hylobates_lar,
                9 Macaca_sylvanus,
                10 Macaca_nemestrina,
                11 Macaca_tonkeana,
                12 Macaca_nigra,
                13 Macaca_arctoides,
                14 Macaca_thibetana,
                15 Macaca_assamensis,
                16 Macaca_sinica,
                17 Macaca_mulatta,
                18 Macaca_fascicularis,
                19 Theropithecus_gelada,
                20 Papio_cynocephalus,
                21 Papio_anubis,
                22 Lophocebus_albigena,
                23 Mandrillus_sphinx,
                24 Cercocebus_torquatus,
                25 Chlorocebus_pygerythrus,
                26 Chlorocebus_aethiops,
```

```
		27 Cercopithecus_lhoesti,
		28 Erythrocebus_patas,
		29 Cercopithecus_hamlyni,
		30 Cercopithecus_neglectus,
		31 Cercopithecus_mona,
		32 Cercopithecus_pogonias,
		33 Cercopithecus_diana,
		34 Cercopithecus_nictitans,
		35 Cercopithecus_mitis,
		36 Cercopithecus_ascanius,
		37 Cercopithecus_cephus,
		38 Allenopithecus_nigroviridis,
		39 Miopithecus_talapoin,
		40 Semnopithecus_entellus,
		41 Trachypithecus_cristatus,
		42 Trachypithecus_obscurus,
		43 Trachypithecus_phayrei,
		44 Rhinopithecus_roxellana,
		45 Nasalis_larvatus,
		46 Pygathrix_nemaeus,
		47 Presbytis_rubicunda,
		48 Presbytis_melalophos,
		49 Piliocolobus_foai,
		50 Piliocolobus_badius,
		51 Colobus_guereza;
	TREE 'tree 1++' =
((1:0.228153,((2:0.18033600000000002,3:0.180334):0.025303,(4:0.20162599999999997,5:0.20
1625):0.004012):0.022515):0.199843,(((6:0.173188,7:0.17318699999999998):0.029005,8:0.202
192):0.07507,((((9:0.046727,((10:0.030189,(11:0.014559,12:0.014559):0.015629999999999998)
:0.008426,((13:0.029671,((14:0.005585,15:0.005585):0.013789,16:0.019374):0.010296):0.0019
78,(17:0.027619,18:0.027619):0.004029):0.006966):0.008113):0.032155,((19:0.0399,((20:0.011
159,21:0.011159):0.021663,22:0.032822):0.007077):0.028336,(23:0.046519000000000005,24:0
.046518000000000004):0.021718):0.010646):0.020377,((((25:0.011984,26:0.011982999999999
999):0.044950000000000004,(27:0.052286,28:0.052286):0.004647):0.014201,(29:0.06248,((30:
0.056258,(31:0.023077,32:0.023077):0.033181):0.002642,(33:0.054136,((34:0.028582,35:0.028
582):0.012001,(36:0.020192,37:0.020191):0.020391):0.013553):0.004765):0.00358):0.008654):
0.005261,(38:0.072431,39:0.072431):0.003965):0.022864):0.056418,((((40:0.057492,(41:0.0210
81,(42:0.019956,43:0.019956):0.001124):0.036412):0.018561,(44:0.062778,(45:0.05894399999
9999996,46:0.058943999999999996):0.003835):0.013274):0.002503,(47:0.00814099999999999
9,48:0.008142):0.070414):0.023016,((49:0.036507,50:0.036507):0.043019,51:0.079526):0.0220
46):0.054105):0.121586):0.150733):0.24552;

END;
```

D) Anthropoid phylogeny from 10KTrees with 2 added fossils

```
#NEXUS
[written Mon Oct 28 12:33:29 EDT 2013 by Mesquite  version 2.74 (build 550) at Ashley-
Gosselin-Ildaris-MacBook-Pro-2.local/10.0.1.3]

BEGIN TREES;
        Title 'Trees from "tree_wo_piliocolobuskirkii.txt"';
        LINK Taxa = Taxa;
        TRANSLATE
                1 Allenopithecus_nigroviridis,
                2 Alouatta_palliata,
                3 Aotus_azarai,
                4 Cebus_apella,
                5 Cercocebus_torquatus,
                6 Cercopithecus_ascanius,
                7 Cercopithecus_cephus,
                8 Cercopithecus_diana,
                9 Cercopithecus_hamlyni,
                10 Cercopithecus_lhoesti,
                11 Cercopithecus_mitis,
                12 Cercopithecus_mona,
                13 Cercopithecus_neglectus,
                14 Cercopithecus_nictitans,
                15 Cercopithecus_pogonias,
                16 Chlorocebus_aethiops,
                17 Chlorocebus_pygerythrus,
                18 Colobus_guereza,
                19 Erythrocebus_patas,
                20 Hylobates_lar,
                21 Lophocebus_albigena,
                22 Macaca_arctoides,
                23 Macaca_assamensis,
                24 Macaca_fascicularis,
                25 Macaca_mulatta,
                26 Macaca_nemestrina,
                27 Macaca_nigra,
                28 Macaca_sinica,
                29 Macaca_sylvanus,
                30 Macaca_thibetana,
                31 Macaca_tonkeana,
                32 Mandrillus_sphinx,
                33 Miopithecus_talapoin,
                34 Nasalis_larvatus,
                35 Pan_troglodytes_schweinfurthii,
                36 Papio_anubis,
                37 Papio_cynocephalus,
                38 Piliocolobus_badius,
```

```
                39 Piliocolobus_foai,
                40 Pongo_pygmaeus,
                41 Presbytis_comata,
                42 Presbytis_melalophos,
                43 Pygathrix_nemaeus,
                44 Rhinopithecus_roxellana,
                45 Saguinus_oedipus,
                46 Saimiri_sciureus,
                47 Semnopithecus_entellus,
                48 Theropithecus_gelada,
                49 Trachypithecus_cristatus,
                50 Trachypithecus_obscurus,
                51 Trachypithecus_phayrei,
                52 Victoriapithecus_macinnesi,
                53 Parapapio_lothagamensis;
        TREE 'UNTITLED+' =
((((((1:11.894902,(((((11:3.76264,14:3.76264):2.666569,(6:2.018943,7:2.018944):4.410266):1.4
61009,(((12:3.167176,15:3.167176):2.820105,(8:5.588511,13:5.588511):0.39877):1.355876,9:7.
343158):0.54706):1.957908,((10:7.9398,19:7.9398):0.687445,(16:1.880772,17:1.880772):6.746
472):1.220881):1.644988,33:11.493113):0.401789):2.980276,(53:7.3125,(((5:5.304298,32:5.304
297):6.046166,((21:4.896861,48:4.896862):0.872302,(36:2.058446,37:2.058446):3.710717):5.5
813):1.502062,((((22:4.705214,(23:3.228863,28:3.228863):1.476351):1.331851,((31:3.50104,27
:3.501041):0.766095,26:4.267135):1.76993):0.840931,((24:5.045978,25:5.045978):1.475126,30:
6.521104):0.356891):1.782804,29:8.6608):4.191726):1.0):1.022653):6.535196,((18:12.537452,(
38:5.435125,39:5.435125):7.102327):2.897705,((((34:9.634813,43:9.634813):0.839771,44:10.4
74584):2.310063,(47:11.461377,((49:4.015007,50:4.015007):1.23798,51:5.252987):6.208391):1
.32327):0.523455,(41:5.778211,42:5.778211):7.529891):2.127056):5.975217):1.0,52:7.704):7.5
89626,(20:19.605945,(35:15.132454,40:15.132455):4.473491):10.394055):16.81182100000000
2,(2:21.321301,((3:19.487522,45:19.487522):0.605006,(4:18.569905,46:18.569905):1.522623):
1.228773):25.490521);

END;
```

E) Anthropoid phylogeny from 10KTrees with 8 added fossils

```
#NEXUS
[written Mon Oct 28 11:07:30 EDT 2013 by Mesquite  version 2.74 (build 550) at Ashley-
Gosselin-Ildaris-MacBook-Pro-2.local/10.0.1.3]


BEGIN TREES;
        Title 'Trees from "tree_wo_piliocolobuskirkii.txt"';
        LINK Taxa = Taxa;
        TRANSLATE
                1 Allenopithecus_nigroviridis,
                2 Alouatta_palliata,
```

3 Aotus_azarai,
4 Cebus_apella,
5 Cercocebus_torquatus,
6 Cercopithecus_ascanius,
7 Cercopithecus_cephus,
8 Cercopithecus_diana,
9 Cercopithecus_hamlyni,
10 Cercopithecus_lhoesti,
11 Cercopithecus_mitis,
12 Cercopithecus_mona,
13 Cercopithecus_neglectus,
14 Cercopithecus_nictitans,
15 Cercopithecus_pogonias,
16 Chlorocebus_aethiops,
17 Chlorocebus_pygerythrus,
18 Colobus_guereza,
19 Erythrocebus_patas,
20 Hylobates_lar,
21 Lophocebus_albigena,
22 Macaca_arctoides,
23 Macaca_assamensis,
24 Macaca_fascicularis,
25 Macaca_mulatta,
26 Macaca_nemestrina,
27 Macaca_nigra,
28 Macaca_sinica,
29 Macaca_sylvanus,
30 Macaca_thibetana,
31 Macaca_tonkeana,
32 Mandrillus_sphinx,
33 Miopithecus_talapoin,
34 Nasalis_larvatus,
35 Pan_troglodytes_schweinfurthii,
36 Papio_anubis,
37 Papio_cynocephalus,
38 Piliocolobus_badius,
39 Piliocolobus_foai,
40 Pongo_pygmaeus,
41 Presbytis_comata,
42 Presbytis_melalophos,
43 Pygathrix_nemaeus,
44 Rhinopithecus_roxellana,
45 Saguinus_oedipus,
46 Saimiri_sciureus,
47 Semnopithecus_entellus,
48 Theropithecus_gelada,

```
                49 Trachypithecus_cristatus,
                50 Trachypithecus_obscurus,
                51 Trachypithecus_phayrei,
                52 Aegyptopithecus_zeuxis,
                53 Victoriapithecus_macinnesi,
                54 Parapapio_lothagamensis,
                55 Proconsul_africanus,
                56 Microcolobus_sp,
                57 Theropithecus_brumpti,
                58 Theropithecus_oswaldi,
                59 Apidium_phiomense;
        TREE 'UNTITLED+' =
((((((((1:11.894902,(((((11:3.76264,14:3.76264):2.666569,(6:2.018943,7:2.018944):4.410266):1.
461009,(((12:3.167176,15:3.167176):2.820105,(8:5.588511,13:5.588511):0.39877):1.355876,9:
7.343158):0.54706):1.957908,((10:7.9398,19:7.9398):0.687445,(16:1.880772,17:1.880772):6.74
6472):1.220881):1.644988,33:11.493113):0.401789):2.980276,(54:7.3152,(((5:5.304298,32:5.30
4297):6.046166,((21:4.896861,(57:0.01,(58:0.01,48:2.21):1.1):1.58686):0.872302,(36:2.058446,
37:2.058446):3.710717):5.5813):1.502062,((((22:4.705214,(23:3.228863,28:3.228863):1.476351
):1.331851,((31:3.50104,27:3.501041):0.766095,26:4.267135):1.76993):0.840931,((24:5.045978
,25:5.045978):1.475126,30:6.521104):0.356891):1.782804,29:8.6608):4.191726):1.0):1.022653)
:6.535196,(56:6.6352,((18:12.537452,(38:5.435125,39:5.435125):7.102327):2.897705,((((34:9.6
34813,43:9.634813):0.839771,44:10.474584):2.310063,(47:11.461377,((49:4.015007,50:4.0150
07):1.23798,51:5.252987):6.208391):1.32327):0.523455,(41:5.778211,42:5.778211):7.529891):
2.127056):1.0):4.975217):1.0,53:7.704):7.589626,(55:3.6059,(20:19.605945,(35:15.132454,40:1
5.132455):4.473491):1.0):9.394055):1.0,52:0.8):15.811821,(2:21.321301,((3:19.487522,45:19.4
87522):0.605006,(4:18.569905,46:18.569905):1.522623):1.228773):25.490521):1.0,59:17.61182
2);

END;
```

F) modified Springer et al. (2012) phylogeny with 2 added fossils

```
#NEXUS
[written Tue Oct 29 08:06:51 EDT 2013 by Mesquite  version 2.74 (build 550) at Ashley-
Gosselin-Ildaris-MacBook-Pro-2.local/10.0.1.3]



BEGIN TREES;
        Title 'Trees from "springer_autocorrelated_hardbounds.nex"';
        LINK Taxa = Taxa;
        TRANSLATE
                1 Alouatta_palliata,
                2 Saimiri_sciureus,
                3 Cebus_apella,
                4 Saguinus_oedipus,
                5 Aotus_azarae,
```

6 Pongo_pygmaeus,
7 Pan_troglodytes,
8 Hylobates_lar,
9 Macaca_sylvanus,
10 Macaca_nemestrina,
11 Macaca_tonkeana,
12 Macaca_nigra,
13 Macaca_arctoides,
14 Macaca_thibetana,
15 Macaca_assamensis,
16 Macaca_sinica,
17 Macaca_mulatta,
18 Macaca_fascicularis,
19 Theropithecus_gelada,
20 Papio_cynocephalus,
21 Papio_anubis,
22 Lophocebus_albigena,
23 Mandrillus_sphinx,
24 Cercocebus_torquatus,
25 Chlorocebus_pygerythrus,
26 Chlorocebus_aethiops,
27 Cercopithecus_lhoesti,
28 Erythrocebus_patas,
29 Cercopithecus_hamlyni,
30 Cercopithecus_neglectus,
31 Cercopithecus_mona,
32 Cercopithecus_pogonias,
33 Cercopithecus_diana,
34 Cercopithecus_nictitans,
35 Cercopithecus_mitis,
36 Cercopithecus_ascanius,
37 Cercopithecus_cephus,
38 Allenopithecus_nigroviridis,
39 Miopithecus_talapoin,
40 Semnopithecus_entellus,
41 Trachypithecus_cristatus,
42 Trachypithecus_obscurus,
43 Trachypithecus_phayrei,
44 Rhinopithecus_roxellana,
45 Nasalis_larvatus,
46 Pygathrix_nemaeus,
47 Presbytis_rubicunda,
48 Presbytis_melalophos,
49 Piliocolobus_foai,
50 Piliocolobus_badius,
51 Colobus_guereza,

```
		52 Victoriapithecus_macinnesi,
		53 Parapapio_lothagamensis;
	TREE 'tree 1+++' =
((1:0.228153,((2:0.18033600000000002,3:0.180334):0.025303,(4:0.20162599999999997,5:0.20
1625):0.004012):0.022515):0.199843,(((6:0.173188,7:0.17318699999999998):0.029005,8:0.202
192):0.07507,(52:0.018677,(((((9:0.046727,((10:0.030189,(11:0.014559,12:0.014559):0.015629
999999999998):0.008426,((13:0.029671,((14:0.005585,15:0.005585):0.013789,16:0.019374):0.
010296):0.001978,(17:0.027619,18:0.027619):0.004029):0.006966):0.008113):0.032155,((19:0.
039900000000000005,((20:0.011159,21:0.011159):0.021663,22:0.032822):0.007077):0.028336,
(23:0.046519000000000005,24:0.046518000000000004):0.021718):0.010646):0.01,53:0.023482
):0.01037,((((25:0.011984,26:0.011982999999999999):0.044950000000000004,(27:0.052286,28
:0.052286):0.004647):0.014201,(29:0.06248,((30:0.056258,(31:0.023077,32:0.023077):0.03318
1):0.002642,(33:0.054136,((34:0.028582,35:0.028582):0.012001,(36:0.020192,37:0.020191):0.0
20391):0.013553):0.004765):0.00358):0.008654):0.005261,(38:0.072431,39:0.072431):0.00396
5):0.022864):0.056418,((((40:0.057492,(41:0.021081,(42:0.019956,43:0.019956):0.001124):0.0
36412):0.018561,(44:0.062778,(45:0.058943999999999996,46:0.058943999999999996):0.0038
35):0.013274):0.002503,(47:0.008140999999999999,48:0.008142):0.070414):0.023016,((49:0.0
36507,50:0.036507):0.043019,51:0.079526):0.022046):0.054105):0.01):0.111586):0.150733):0.
01;

END;
```

G) modified Springer et al. (2012) phylogeny with 8 added fossils

```
#NEXUS
[written Mon Oct 28 19:35:22 EDT 2013 by Mesquite  version 2.74 (build 550) at Ashley-
Gosselin-Ildaris-MacBook-Pro-2.local/10.0.1.3]


BEGIN TREES;
	Title 'Trees from "springer_autocorrelated_hardbounds.nex"';
	LINK Taxa = Taxa;
	TRANSLATE
		1 Alouatta_palliata,
		2 Saimiri_sciureus,
		3 Cebus_apella,
		4 Saguinus_oedipus,
		5 Aotus_azarae,
		6 Pongo_pygmaeus,
		7 Pan_troglodytes,
		8 Hylobates_lar,
		9 Macaca_sylvanus,
		10 Macaca_nemestrina,
		11 Macaca_tonkeana,
		12 Macaca_nigra,
		13 Macaca_arctoides,
```

14 Macaca_thibetana,
15 Macaca_assamensis,
16 Macaca_sinica,
17 Macaca_mulatta,
18 Macaca_fascicularis,
19 Theropithecus_gelada,
20 Papio_cynocephalus,
21 Papio_anubis,
22 Lophocebus_albigena,
23 Mandrillus_sphinx,
24 Cercocebus_torquatus,
25 Chlorocebus_pygerythrus,
26 Chlorocebus_aethiops,
27 Cercopithecus_lhoesti,
28 Erythrocebus_patas,
29 Cercopithecus_hamlyni,
30 Cercopithecus_neglectus,
31 Cercopithecus_mona,
32 Cercopithecus_pogonias,
33 Cercopithecus_diana,
34 Cercopithecus_nictitans,
35 Cercopithecus_mitis,
36 Cercopithecus_ascanius,
37 Cercopithecus_cephus,
38 Allenopithecus_nigroviridis,
39 Miopithecus_talapoin,
40 Semnopithecus_entellus,
41 Trachypithecus_cristatus,
42 Trachypithecus_obscurus,
43 Trachypithecus_phayrei,
44 Rhinopithecus_roxellana,
45 Nasalis_larvatus,
46 Pygathrix_nemaeus,
47 Presbytis_rubicunda,
48 Presbytis_melalophos,
49 Piliocolobus_foai,
50 Piliocolobus_badius,
51 Colobus_guereza,
52 Aegyptopithecus_zeuxis,
53 Victoriapithecus_macinnesi,
54 Microcolobus_sp,
55 Parapapio_lothagamensis,
56 Proconsul_africanus,
57 Theropithecus_brumpti,
58 Theropithecus_oswaldi,
59 Apidium_phiomense;

```
        TREE 'tree 1++' =
(((1:0.228153,((2:0.18033600000000002,3:0.180334):0.025303,(4:0.20162599999999997,5:0.20
1625):0.004012):0.022515):0.199843,(52:0.01,((((6:0.173188,7:0.17318699999999998):0.02900
5,8:0.202192):0.01,56:0.0422):0.06507,(53:0.018677,(((((9:0.046727,((10:0.030189,(11:0.01455
9,12:0.014559):0.015629999999999998):0.008426,((13:0.029671,((14:0.005585,15:0.005585):0
.013789,16:0.019374):0.010296):0.001978,(17:0.027619,18:0.027619):0.004029):0.006966):0.0
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Appendix G. Data from fossils used in Chapters 3 and 4. See Appendix B for measurement abbreviations; Blank cells indicate when a measurement was not taken due to breakage or distortion; Asterisks (*) indicate when a measurement was taken when a feature suffered from slight erosion; Units are in millimeters.

Appendix G.1. Humerus measurements for fossils

Specimen	Number	Sex	Side	PDH	MLHH	SIHH	MGT	MLT	BGW	MLOF	PDOF	PDC	MLC	PDT	MLT	MLCT	BB	GTH	HHL	DL	EL	AME
Aegyptopithecus zeuxis	DPC 1275	U	L		13.57*	16.11	15.71	12.52	4.83	13.65	7.55	8.16*	8.49	9.89*	11.42*	19.49*	31.26	20.5	17.7	7.3	9.2	18.8
Cercopithecoides williamsi	KNM-ER 4420c	U	L	127*	26.9	24.4*	28.8	19.1	8.5		13.9*	17.8	12.2	21.2	19.4	33.2	44.3	33.9	25.6	23.5	4.7	40.9
Mesopithecus pentilicus	NMNH-P Pik355	U	R	149*	19.1	17.1	18.5	13.4	6.5	12.9	10.1	12.7	9.3	14.1	11.4	21.4	29.7	21.7	18.7	15.9	3.3	38.8
Mesopithecus pentilicus	NMNH-P Pik244	U	R	152*	14.8	13.7	12.6	11.3	4.8	10.5*	7.5*	10.9	7.6	11	9.8	17.5	25.3	17.6	15.2	11.4	2.6	34.3
Mesopithecus pentilicus	NMNH-P Pik1727	U	R	135*	14	12.6	14.4	10.1	5.4	9.3	9.4	10.4	7	10.5	9.3	17.1	24.2	19.5	16.1	14.1	2.4	41.9
Mesopithecus sp.	NMNH-S HD 1610	U	R	186*	20.6	17.06	19.04	13.61	6.35	12.15	10.77	13.14	9.78	15.46	14.88	24.48	30.79	23.5	19.1	18.9	2.6	44.5
Mesopithecus sp.	NMNH-S HD 1004/1450	U	R	155	16.79*	15.53	15.35	11.06	5.04	11.75	7.74	11.28	9.05*	11.62	11.31	19.58*		19.8	16.5	13	4.4	35.7
Mesopithecus sp.	NMNH-S HD 916/1467	U	R	155	15.14	14.68	14.82	10.6	5.26*	10.48*	9.1*	10.77	6.13*	11.49	12.27	18.64*	25.54	19.1	17.1	12.3	2.1	34
Paracolobus chemeroni	KNM-BC 3B S	U	L	261*	27*	27.4	23.7	18.9	6.2	19.8	16.5	19.5	12.8	21.8	20.3*	33.5*	46.5	34.3	28.9	27.6	4.3	44.5
Rhinocolobus turkanensis	KNM-ER 1542O/P	U	L		33.9*	29.5*	28.6	20.1	9.2	19.7	12.2	17.7	15.2	21.8*	21.7*	37.2*	51.9	37.7	31.4	22.3	10.6	33.1
Theropithecus brumpti	KNM-WT 38738	U	R	241*		24.5*	27.5	18.8*	19.2	12.6	13.3	19.3	13.1	20.6	20.3	34.5	46.4	36.1	29.6	24.6	6.8	41.3
Theropithecus oswaldi	KNM-ER 18917B	U	L	212*	25.5	22.9*	22.9	18.1	10.3	15.1	10.6	16.4	12.1	17.9	14.7	27.6	38.5	33.6	25.1	23.8	3.6	49.2
Theropithecus oswaldi	KNM-ER 5491 C/D	U	L		29.1*	26.4*	28.3	16.7	8.4	20.8	13.4	16.9	13	17.7*	20.4*	33.5*	44.1	40.9	31.8	27.8	3.3	46.5

Appendix G.2. Proximal humerus measurements for fossils

Specimen	Number	Sex	Side	MLHH	SIHH	MGT	MLT	BGW	GTH	HHL
Cercopithecoides kimeui	KNM-ER 176G	U	L	27.8*	23.9*	23.1	21.7		32.1	26.2
Cercopithecoides meavea	NME AL2-63	U	L?	20.2	19.8	21.9	15.5	9.3	28.9	24
Mesopithecus pentilicus	NMNH-P Pik298	U	R	18.1*	16.4	18.9	12.5	7.1	23.7	19.7
Mesopithecus sp.	NMNH-S HD 417	U	R	17.13	15.36	16.02	11.31	5.63	19	17
Parapapio lothagamensis	KNM-LT 28769	U	R	13.4*	12.9*	15.5	9.6	5.9	16.8	15.4
Theropithecus oswaldi	KNM-ER 567 E	U	L	30.9	26	31.2	20.8	10.6	36.1	30.2
Theropithecus oswaldi	KNM-ER 601 C	U	R	36.5*	29.2*	32.4		7.4	42.9	35.3
Theropithecus oswaldi	KNM-ER 13 A**	U	R	28.4	26.1	24.5*	21.2	10.5*	35.1	27.9
Victoriapithecus	KNM-MB 21809	U	R	12.7	12.5	14.2	10.4	4.2	17.3	14.6
Victoriapithecus	KNM-MB 12044	U	L	10.3	9.7	10.3	7.5	4.1	11.4	10.3

Appendix G.3. Distal humerus measurements for fossils

Specimen	Number	Sex	Side	MLOF	PDOF	PDC	MLC	PDT	MLT	MLCT	BB	DL	EL	AME
Aegyptopithecus zeuxis	DPC 6301	U	R	12.65	7.83	9.41	7.68	9.37	13.04*	21.5*	29.44	9.3	6.9	24.1
Aegyptopithecus zeuxis	DPC 8702	U	R	13.01	6.77	10.78	9.06*	10.97*	13.28*	22.38*	34.4	10.5	10	23.6
Apidium phiomense	DPC 1311	U	L	5.34	2.15	3.55	2.94	3.83	4.17	6.71	9.86	3.6	2.6	28.7
Apidium phiomense	DPC 2473	U	L	6.68	2.78	4.65*	3.69*	5.22	5.07	8.41*	13.14*	5.8	3.2	39
Apidium phiomense	DPC 6131	U	L	5.76	3.22	6.69	3.77	5.11*	4.93	8.09	13.29	6.8	3.6	38.1
Apidium phiomense	DPC 8710	U	R	5.52	2.65	4.9	3.99	5.59	5.1	9.15	14.38	5.6	3.9	29.7
Apidium phiomense	DPC 3831	U	R	6.27*	3.03*	4.91	3.97	5.65	6.06	10.28	15.12	5.9	4	31.1
Apidium phiomense	DPC 3101	U	L	6.28	3.26	4.58	3.11	4.94	5.31	8.97	13.53	5.5	3.5	30.1
Cercopithecoides meavea	NME AL2-64	U	L	17.8	10.5	15.5	10.6	16.6	14.7	25.3	35.9	21.1	6.7	47.5
Cercopithecoides williamsi	KNM-ER 4420D	U	R	21.1	15.5*	17.9	14	19.5*	19.3*	33.6*	44.4	23.6	4.8	41.1
Cercopithecoieds kimeui	NME AL577-1	U	L	18.9	14.4	16.8*	9.6*	18.1*	20.9*	30.4*	43.2*	22.7	10.9	38.3
Dolichopithecus ruscinensis	MNHN-L Per.010	U	L	16.6	11.5	18.4	12	16.6	15.9	27.9	41.9	21.7	7	37.4
Dolichopithecus ruscinensis	MNHN-L Per.011	U	L	14.2	11.1	17.1	11.9*	18.8	16.2	28.2*	37.2	21.1	2.6	44.7
Dolichopithecus ruscinensis	MNHN-L Per.012	U	L	14.3	10.9	14.5	11.2	15.3	16.8	29.6	38.1	18.5	3.3	36.3
Dolichopithecus ruscinensis	MNHN-L Pp23	U	R	14.3	10.8	13.6	*9.6	*14.4	*14.3	*24.2	33.4	21.4	3.6	47.5
Kuseracolobus hafu	NME ASI VP 2/59c	U	L	15.1	12.2	19.7	12.3	17.4	17.3	29.6	40.6	22.4	4.7	44.6
Mesopithecus pentilicus	NMNH-P Pik419	U	L	11.9	8.8	12.9*	8.9	13.1	10	19.4	30.1	20.5	3.8	51
Mesopithecus pentilicus	NMNH-P Pik356	U	R	9.2	6.3	11.1	10.4	17.4	22.3			13.3	1.2	43.4
Mesopithecus pentilicus	NMNH-P Pik245	U	L	9.8	7	9.1	6.8	10.1	9.9	17.1	24.4	12.6	3.5	39.7
Mesopithecus pentilicus	NMNH-P Pik1729	U	L	10.9	8.1	10	7.3	11.8	9.5	17.8	23.1			
Mesopithecus sp.	NMNH-S HD 1612	U	R	11.58	4.43	11.46	8.76*	11.31	11.77	19.86	25.97	10.9	4.5	30.5
Mesopithecus sp.	NMNH-S HD 1611	U	R	10.79	7.43	11.79	8.38*	10.73*	8.9*	17.31*	26.92	13.1	5.3	34.6
Mesopithecus sp.	NMNH-S HD 1624	U	L	10.25	5.15	10.73*	7.83*	11.74*	12.59*	20.11*				
Mesopithecus sp.	NMNH-S HD 1625	U	L	10.15*	8.08*	10.66	7.9	11.73	11.71*	19.7*	27.01*	15	4	41.1
Microcolobus sp.	KNM-NA 47916A	U	L	8.5	4.9	9.2	6.9	9.4	10.4	17	23.3	10	4.6	36.8
Paracolobus mutiwa	KNM-WT 16827J	U	L		20.9	15.5	13	19.1	20.6	33.6	50.9	25.9	6.4	34.3
Parapapio jonesi	NME AL363-12	U	R	15.2	13.3	16.4	10.4*	18.9	18.3	29.5*	42.3	24.4	4.2	42.1
Parapapio lothagamensis	KNM-LT 23074	U	L	11.4	9.3	11.3	8.5	14.2	12.9	21.4	30.9	20.5	2.6	51.4
Parapresbytis eohanuman†	PIN 3381-210	U	L	16.17	12.39	15.42	12.12	16.92	17.45	29.18	40.45	19.2	6.5	37.2
Proconsul africanus	KNM-RU 2036 AH	U	L	14.9	9.9	11.5	9.1	12.3*	16.8	26.3	32.9	12.9	4.1	29.9
Rhinocolobus turkanensis	NME AL300-1	U	L	19.5	14.5	16.3	11.2*	20.1	20.3	30.1*	46.8	17.4	11.6	28.3
Theropithecus brumpti	KNM-ER 3013 E	U	L	12.5	9.3	13.2	8.7	13.5	13.1	22.5	32.1	15.8	6.6	39.5
Theropithecus oswaldi	KNM-OG 1062	U	R	22.2	16.3	23.2	11.8	23.7*	25.7	38.8	52.9			
Theropithecus oswaldi	KNM-OG 1318	U	R			21.1	14.9	22.8*	27.1	42.5				
Theropithecus oswaldi	KNM-ER 3876 A	U	R	15.2*	13.4	16.7	17.1	30.3				21.2	5.4	39.9
Theropithecus oswaldi	KNM-ER 13 B	U	L	17.3	13.7	17.1*	12.8*	20.6*	20.9	36.1*	47.9	28.2	2.4	45.8
Victoriapithecus	KNM-MB 21207	U	R	7.1	5.3	7	4.9	7.5*	7.5*	12.3*	18	10.1	4.2	44.3
Victoriapithecus	KNM-MB 33513	U	L	7.1	6.1	9.1	6.9	9.6*	8.4*	15.4*	23			
Victoriapithecus	KNM-MB 34712	U	L			7.6	4.9*	8.3	7.1	12.2*	18.1	10.2	3.1	42.2
Victoriapithecus	KNM-MB 21818	U	L	8.6	4.6	8.4	6.2	9.5	7.2	14.3	22	12	4.6	42.2
Victoriapithecus	KNM-MB 21822	U	L	6.7	6.3	6.7	4.8	7.2	6.3	11.7	15.9	9.8	1.8	45.7

Victoriapithecus	KNM-MB 19	U	L	6.7	3.8	7.3	6.4	8.2	6.4	13.3	18.1	11.6	3.1	47.6
Victoriapithecus	KNM-MB 3	U	L	7.6	6.4	6.2	4.7	6.4	5.5	10.6	16.8	8.5	5.6	36.6

† *Parapresbytis* distal humerus measured from cast collection of Eric Delson (CUNY).

Appendix G.4. Femur measurements for fossils

Specimen	Number	Sex	Side	PDF	APFH	PDFH	PDLT	APMC	PDMC	MLMC	APLC	PDLC	MLLC	BCB	PH	PW	FNA	ACON
Dolichopithecus ruscinensis	MNHN-L Per.008	U	L	224*	24.5	22.2		32.9	26	13.7	31.2	25.9	12.8	38.8	22.4	20.2	100.6	97.1
Dolichopithecus ruscinensis	MNHN-L Pp24	U	R	214*	22.2	20.7		29.9*	23.4	13.4	*29.6	23.8	11.7	38.4	23.5	/	97.5	91.6
Mesopithecus pentilicus	NMNH-P Pik024	U	L	169*	15.3	14.3	8.9*	22.2	17.5	7.8*	22.4	18.9	8.8*	24.9	16.4	13.1	98.6	87.2
Mesopithecus pentilicus	NMNH-P Pik1731	U	L	190*	17.6	16.4	10.6	25.6	21.3	11.7	22.9*	17*	8.1*	28.5*	19.9	15.2	100.2	85.7
Mesopithecus sp. (left - less complete)	NMNH-S HD 1014/1430	U	L	182*	16.46	15.22		22.31	18.89	9.03	21.92	18.04						
Mesopithecus sp. (right)	NMNH-S HD 1010/1415	U	R	175*	16.3*	15.16*	10.08	23.05*	18.6*	7.7*		20.16*		26.64	12.51	17.6	94.6	84.5
Paracolobus chemeroni	KNM-BC 3B AR	U	L	283*	27.5	25.5	20.3	37.8	29.2	16.6	37.6	28.2	14.1	47.4	28.6	23.6	101.3	85.8
Theropithecus brumpti	KNM-TH 46700	U	R	216	24.6	22.7	15.2	36.2	23.8	13.6	33.3	25.7	12.3	41.9	23.9	18.5	100.2	95.3

Appendix G.5. Proximal femur measurements for fossils

Specimen	Number	Sex	Side	APFH	PDFH	PDLT	FNA
Apidium phiomense	DPC 3092	U	L	6.37	5.94	5.73*	104.9
Apidium phiomense	DPC 2463	U	L	6.44*	5.47*	6.49	107.6
Cercopithecoides kimeui	KNM-ER 176I	U	L	27.8	25.9	12.7	104.2
Cercopithecoides meavea	NME AL2-80	U	R	22.6	21.5	13.3	
Cercopithecoides meavea	NME AL2-72	U	L		22.3	12.6	
Cercopithecoides williamsi	KNM-ER 4420T	U	R	26.6	25.5	15.4	96.7
Dolichopithecus ruscinensis	NMNH-P Pp24'	U	L	19.2	17.6	10.5	104.7
Mesopithecus pentilicus	NMNH-P Pik1732	U	L	18.5	17.2	10.4	103.1
Mesopithecus pentilicus	NMNH-P Pik1736	U	R	18.4	17	10.5	100.6
Mesopithecus pentilicus	NMNH-P Pik1738	U	R	14.6	13.3	8.8	97.2
Mesopithecus pentilicus	NMNH-P Pik1737	U	R	14.5	13.5	9.2	99.7
Mesopithecus pentilicus	NMNH-P Pik1734	U	R	15.2	14.3	8.2	113.6
Mesopithecus sp.	NMNH-S HD 912/1489	U	L	16.59*	15.48*		100.3
Mesopithecus sp. (left - less complete)	NMNH-S HD 402	U	L			8.72	
Mesopithecus sp. (right)	NMNH-S HD 403	U	R	16.43*	16.19*	7.85*	103
Microcolobus sp.	KNM-NA 47915G	U	R	13.4	12.8	7.6	
Parapapio jonesi	NME AL366-1c	U	R	20.8	18.3	12.8	94.7
Parapapio lothagamensis	KNM-LT 28724	U	R	16.8	15.6	8.6	100.4
Parapapio lothagamensis	KNM-LT 26403	U	L	16.5	15.2	9.2	96.1
Parapapio lothagamensis	KNM-LT 22974	U	R	16.8	15.8	8.7	104.5
Theropithecus brumpti	KNM-ER 3119 C		L	28.5	24.4*	16.4	
Theropithecus oswaldi	KNM-OG 1090	U	L	31.3*	31.7	22.9	96.1
Theropithecus oswaldi	KNM-ER 3876 D	U	L	25	22.7	14.6	
Theropithecus oswaldi	KNM-ER 13 E	U	L	28.3	25.4	18.9	97.8
Victoriapithecus	KNM-MB 20230	U	R	12.2	10.8	6.8	96.4
Victoriapithecus	KNM-MB 35518	U	R	11.9	11.2	6.6	105.1
Victoriapithecus	KNM-MB 35572	U	L	10.5	9.9*	6.2	97.8

Appendix G.6. Distal femur measurements for fossils

Specimen	Number	Sex	Side	APMC	PDMC	MLMC	APLC	PDLC	MLLC	BCB	PH	PW	ACON
Cercopithecoides meavea	NME AL2-74	U	R	29.8	25.9	10.8	30.3	23.8	11.9	36.4	23.2	20.7	92.5
Mesopithecus pentilicus	NMNH-P Pik287	U	L	17.8	14.5	8.2	17.8	16	8.2	23	15.6	12.5	86.2
Mesopithecus pentilicus	NMNH-P Pik1735	U	R	21.6	16.4	9.4	22.4	18	10	25.1	14.8	13.3	87.4
Mesopithecus pentilicus	NMNH-P Pik1733	U	R	25.4	19	10.8	26	21	11.3	29.1	17.7	15.9	89.1
Mesopithecus sp.	NMNH-S HD 1622	U	R	23.59	18.39	9.07		17.39*	13.31*				
Parapapio jonesi	NME AL366-1d	U	R	32.2*	23.2	13.6	31.5	23.9	11.2	37.6	21.8	18.7*	85.1

Appendix G.7. Astragalar measurements for fossils

Specimen	Number	Sex	Side	MPD	BPD	HNPD	DHTF	TW	HMR	HLR	DHFF	PDFF	EW	EL	MLH	PT	DT	ATH	TAS
Aegyptopithecus zeuxis	DPC 3052	U	R	21.41*	12.23	11.02*	7.05	8.42	8.68	9.39	8.07	10.64	5.43*	11.27*	8.29*	8.46	9.28	92.5	69.7
Aegyptopithecus zeuxis	DPC 1301	U	L	22.75*	12.68*	11.15*	6.85	8.93	10.02*	10.71	10.23	12.31	5.84	10.62	9.18*	9.5	9.87*	105.6	79.1
Apidium phiomense	DPC 5027	U		11.6	6.63	6.74	4.58	4.35	5.35	4.93	4.6	5.12	2.75	5.52	4.02	3.92	5.15	89.4	87.6
Apidium phiomense	DPC 3054	U		12.93	7.15	7.5	4.88	4.46	6.19	5.3	6.17	4.4	3.31	6.32	4.66	4.73	5.69	87.3	82.1
Dolichopithecus ruscinensis	MHNL Pp20a	U	R	32.5	21.1	17.7	11.6	14.6	15.5	17.4	14.3	19.1	10.4	15.8	13.2	14.5	16.8	106.9	99.3
Dolichopithecus ruscinensis	MHNL Pp20b	U	L	32.1	20.5	17.2	9.1	15.5	15.2	16.1	13.5	*16.4	9.5	17.3	13.6	*14.5	16.8	103.6	102
Dolichopithecus ruscinensis	MHNL Pp20c	U	L	30.3	*18.3	16.2	9.4	12.7	15.2	*16.6	*11.7	*17.7	10	15.2	*13.4	12.4	15.6	104.6	97.1
Mesopithecus pentilicus	NMNH-P Pik237	U	R	24.8	11.5*	14.1	10.7	11.7	12.6	13.2	11.7	11.4*	7.9	11.2	11.1*	11.6	12.5	104.7	100.1
Mesopithecus pentilicus	NMNH-P Pik368	U	L	26.5	14.3	13.1	9.2	12	12.6	13.4	11.9	14	8.4	11.8	11.4	10.6	12.7	131.3	95.4
Mesopithecus pentilicus	NMNH-P Pik256	U	L	23.1	12.7	12.3	8.5	10.8	11.4	12.3	10.8	12.9	7.4	10.8	10.8	8.5	11.5	91.3	
Mesopithecus pentilicus	NMNH-P Pik238	U	R	27.8	16.3	15.3	11*	10.4*	12.9*	14.5	12.8	15.9	8.6	13	12.6	9.2*	13.3	93.4	91.7
Mesopithecus sp.	NMNH-S HD 1460/929	U	L		13.43*		7.54	10	10.2*	12.75	11.09	13.16*	8.12	10.37		10.08	11.52*		
Mesopithecus sp.	NMNH-S HD 1025/1493	U	L	24.5	14.41	13.19	9.56*	10.41*	11.96*	12.32	13.99*	11.16	8.18	10.75	11.46	9.97*	11.05	114.2	98.1
Microcolobus sp.	KNM-NA 47915K	U	R	22.8	14	12.7	7.8	11.3	9.6*	9.9	8.8	13.6	6.6	11.2	10	10.5	11	112.8	95.1
Paracolobus chemeroni	KNM-BC 3 AQ	U	L	43.1	24.4	23.4	12.7	18.2	22.1	21.9	16.2	22.6	13.8	20.2	19.4	17.5	21.2	98.8	93.3
Parapapio lothagamensis	KNM-LT 23081	U	R	25.1	15.9	14.5	10.6*	11.1*	11.9*	13.2	11	14.1	7.2	11.3	10.8	9.2*	12.1	118	99.6
Proconsul africanus	KNM-RU 2036 BF	U	L	29.5*	16.6*	16.1*	9.4	10.4	13.3	14.5	12.8	14.4	8.7	14.2	12.9	10.5	12.1*	90.3	85.7
Theropithecus brumpti	KNM-WT 17544 D	U	R	33.1	19.9	17.5	12.7	15.4	15.3	17.1	14.6	18.3	10.3	14.6	14.4	14.2	16.9	106.5	
Theropithecus brumpti	NME L865-1t	U	R	37.2	22.8	20.5	15.3	16.1	17.8	18.6	16.5	22.6	12.7	12.8	17.3	15.7	18	101.5	97.7
Theropithecus oswaldi	KNM-ER 3876 G	U	R	37.5	23.4	20.1	14.2	15.8	18.1	20.8	16.8	21.9	11.1	17.4	17.1	13.9	16.8	136.6	
Theropithecus oswaldi	KNM-OG 950	U	R	44.1	27.2	23.6	14.4	18.3*	19.7*	21.8	17.7	23.1	12*	22.3*		16.9	19.8	132	101.9
Theropithecus oswaldi	KNM-OG 1580	U	R	45.3	29.5	24.9	16.8	20.1	21.3	24.2	19.5	24.4	17.1	23.7	20.5	17.5	21.2	116.7	102.7
Theropithecus oswaldi	KNM-OG 1188	U	R	39.4	24.8	22.3	15.4	17	20.3	21.5	19.3	22.8	14.2	21		16.1	18.1	137	100.9
Theropithecus oswaldi	KNM-OG 948	U	R	45.9*	30.3	24.5*	18.3	20.4	24	25	22.8	26.4	16.9	25.1*	20.1	18.5	21.1	138.6	99.4
Victoriapithecus	KNM-MB 34814	U	R	18.2	10.4	10.2	6.7	8	8.5	8.8	7.5	9.3*	5.3	7.9	7.8	8	8.4	123.4	97.4
Victoriapithecus	KNM-MB 34810	U	R	19.8	11.4	10.6	8.4	8.3	9.2	9.1	7.3	10.7	6	8.9	8.7	8.5	8.7	122.9	95.9
Victoriapithecus	KNM-MB 34364	U	L	19.6	10.5*	12.4	6.9	8.5*	9.1	9.5*	8.6*	9.4*	5.8	8.9	8.9	8.4	9.5	98	86.7
Victoriapithecus	KNM-MB 34812	U	L	20.1	10.7	11.7	6.6	6.3*	9.3*	9.7	8	10.7	6.4	9.2	7.7	7.1*	9.3	98.4	91.6
Victoriapithecus	KNM-MB 34816	U	R	17	10.6	9.9	6.5*	8.1	8.6	9	7.4	9.7	4.7	7.6	7.8	7.7	8.6*	121.7	95.2
Victoriapithecus	KNM-MB 34809	U	R	19	10.8	11.1	7.5	7.7	8.9	9.4	7.8	10.3	5.7	8.1	8.8	6.8*	8.5	121.7	93.4
Victoriapithecus	KNM-MB 12013	U	R	20.1	11.3	11.5	7.9	6.9*	8.7*	10.2	8.8	10.9	5.8	8.5	8.2	7*	9.2*	106.9	98.5
Victoriapithecus	KNM-MB 9422	U	R		11.6		7.5	8,1	8.2*	9.3	8.5	11.1	5.6	9.1		7.9	8.5		

Appendix G.8. Calcaneal measurements for fossils

Specimen	Number	Sex	Side	PDC	PDA	PDT	PDF	MLF	MLS	DNF	MLT
Aegyptopithecus zeuxis	DPC 3051	U	L		19.79		9.29	6.76	7.02	7.39*	
Apidium phiomense	DPC 3050	U	R		11.22		5.18	3.29	3.07	4.33*	
Apidium phiomense	DPC 8810	U	R	22	13.68	5.89	6.57	5.36	3.46	5.37	6.08
Mesopithecus pentilicus	NMNH-P Pik240	U	L	31	17.6	9.8	7.9	7.8	6	9.7	9.1
Mesopithecus pentilicus	NMNH-P Pik266	U	L	37	21.8	8.2	9.9	9.7	7.4	9.3	11.3
Mesopithecus pentilicus	NMNH-P Pik1746	U	R	37	22.7	10.6	11.3	9.6	7.3	10.7	10.5*
Mesopithecus pentilicus	NMNH-P Pik239	U	R	38	22.4	10.8	10.5	11.1	6.8	10.9*	12
Mesopithecus sp.	NMNH-S HD 1569	U	L	30*	21.06*	7.68*	9.24	7.83	3.83*	10.11	9.53
Mesopithecus sp.	NMNH-S HD 408	U	R	32*	20.54	9.31	9.71	9.06	6.49	8.67*	9.52
Mesopithecus sp.	NMNH-S HD 1023/1492	U	R	33*	20.04*	9.67	9.79*	9.89*	6.68	8.83*	8.85*
Mesopithecus sp.	NMNH-S HD 410	U	L	31	19.87	9.56	9.33*	8.49*		9.22	9.74*
Paracolobus chemeroni	KNM-BC 3 R	U	L	59	34.7	20.4	16.6	15.9	10.7	16.1	16
Parapapio lothagamensis	KNM-LT 28575	U	L	36	23.1	10.6	10.9	8.4	6.7	10.2	11.3
Parapapio lothagamensis	KNM-LT 24125		R	36	22.3	11.2	9.9	8.2	6.8	9.6	10.6*
Proconsul africanus	KNM-RU 2036 CP	U	R		24.6*		11.7	9.8	5.7		
Theropithecus brumpti	NME L865-1r	U	R	51	32.1	17.2	18.5	13.6	9.8	16.1	16.2
Theropithecus oswaldi	KNM-ER 3878 C		L		32.6		16.7	12.5	10.2	18.2	
Theropithecus oswaldi	KNM-OG 475	U	L	68*	38.3	22.1*	23.2	18.6	15.1	20.1*	20.5
Theropithecus oswaldi	KNM-OG 1192	U	R	60*	36.9	17*	22.9	16.8	14.6	16.5	17.5*
Theropithecus oswaldi	KNM-OG 1138	U	R		37.6		22.2	15.6	13.5	17.2	
Theropithecus oswaldi	KNM-OG 958	U	L	67*	38.3	22.4*	22.3	18.8	13.2	21.1	17.7*
Theropithecus oswaldi	KNM-OG 472	U	L		40.4		22.8	16.9	9.9*	19.2	
Theropithecus oswaldi	KNM-OG 484	U	R	58*	37.2	18.8*	21.1	16.3	13.8	18.4	15.3*
Victoriapithecus	KNM-MB 21208	U	R			6.1	6.3	5.6	5.8		5.3
Victoriapithecus	KNM-MB 21209	U	R			7	7.7	6.7	6.6		8.4
Victoriapithecus	KNM-MB 21211	U	L		18.1		7.4	6.1	6.8	7.4	
Victoriapithecus	KNM-MB 35573	U	R	22	14.6	5.6	6.9	5.7	5.1	7.3	6.6
Victoriapithecus	KNM-MB 35571	U	L	28*	19.6	6	8.6*	7.2	5.6		
Victoriapithecus	KNM-MB 46664	U	L		15.3		6.5	4.5	5.3	6.9	
Victoriapithecus	KNM-MB 34821	U	L		17.8		8.7	5.7*	6.3	9.2	
Victoriapithecus	KNM-MB 34820	U	R	22	14.2	7.5	6.7	5.4	4.8	6.5	6.3
Victoriapithecus	KNM-MB 12006	U	L	18*	12.7	4.8*	5.7	4.2	3.5	5.1	5.5*
Victoriapithecus	KNM-MB 14375	U	L			9*	7.4	6.3	3.9		8.2*