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Form, function, and allometry of the cercopithecoid foot

Strasser, Elizabeth, Ph.D.

City University of New York, 1989

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FORM, FUNCTION, AND ALLOMETRY OF THE CERCOPITHECID FOOT

by

ELIZABETH STRASSER

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

1989

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This manuscript has been read and accepted for the Graduate Faculty in Anthropology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

FORM, FUNCTION, AND ALLOMETRY OF THE CERCOPITHECID FOOT

by

Elizabeth Strasser

Advisor: Professor Eric Delson

The goal of this dissertation was to determine the mechanical basis for some distinctive proportional differences in the hindlimb skeleton, especially the foot, of cercopithecoid monkeys. Proportional differences were the focus of study because they have occupied a central position in the description of the cercopithecoid hindlimb. Many proportions describe morphological, not mechanical, units. Consequently, interpreting their mechanical significance was difficult. In order to determine the mechanical significance of the dimensions comprising the proportions, biomechanical models were utilized. The choice of biomechanical models was dependent upon frequency data, culled from the literature, which documented positional activities of cercopithecoids in the wild. The major modes of locomotion utilized by cercopithecoids involved pronograde arboreal quadrupedalism, terrestrial cursorial quadrupedalism, leaping and climbing.

The fifty cercopithecoid species examined in this study range in

average body mass from 1.5 to 28.5 kg. Because the absolute size of an organism will affect the relative proportions of its musculoskeletal system, the scaling of the dimensions comprising hindlimb and pedal proportions were examined.

Four major conclusions were reached. 1) The hindlimb and foot segment dimensions scale with body mass to maintain mechanical similarity among locomotor groups. Therefore, indices which describe the relative lengths of the lever arms for muscle groups around the knee, talocrural and metatarsophalangeal joints all decrease with an increase in body mass. The majority of traditional indices which described the foot in cercopithecids revealed differences which were primarily a function of size. 2) The major adaptation of terrestrial cercopithecines in the features analysed was reduction in the length of the phalanges due to the assumption of digitigrady. Theropithecus and Erythrocebus also have a high crural index relative to their body mass. 3) Colobines have elongated the hindlimb, probably to enhance leaping. Colobines are also characterized by a distinctive pseudo-artiodactyl condition of the digits, as well as elongated phalanges. 4) Dramatically shortened limbs in Macaca fuscata and M. thibetana suggest that thermal conditions have as profound an effect on the lengths of the hindlimb segments, relative to body mass, as do adaptations to particular locomotor modes.

ACKNOWLEDGEMENTS

I thank the following people and institutions for access to specimens in their care: Dr. G. Musser and the staff of the Mammalogy Dept., American Museum of Natural History; Dr. R. Thorington, jr., and the staff of the Division of Mammals, National Museum of Natural History; Ms. P. Jenkins and the staff of the Dept. of Zoology (Mammals) and Dr. P. Andrews, Dept. of Paleontology, the British Museum (Natural History); Mr. D. Howlett and staff of the Powell Cotton Museum; Dr. T. van den Audenaerde and staff of the Dept. of Mammalogy, Koninklijk Museum voor Midden Afrika; Dr. K. Smeenk of the Rijksmuseum van Natuurlijke Histoire, Leyden; Dr. H. Baagoe and staff of the Zoologigisk Museum at the University of Copenhagen; Dr. H.-J. Kuhn, Dr. U. Zeller and the staff at the Zentrum Anatomie des Fachbereiches Medizin, Abteilung Morphologie, Georg-August Universität; Dr. H. Felten of the Natur-Museum Senckenberg; Dr. W. Maier and staff at the Zentrum der Morphologie der Klinik der Johann Wolfgang Goethe Universität; Dr. B. Engesser and Dr. J. Hürzeler of the Naturhistorisches Museum Basel; Dr. P. Schmid of the Anthropologisches Institut und Museum der Universität Zürich-Irchel; Dr. F.-K. Jouffroy, Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle; Mr. R. Leakey, Director, and Mrs. N. Mudida, Head of Osteology Dept., National Museums of Kenya; Dr. N. Tappen, University of Wisconsin-Milwaukee; Dr. J.F. Oates, Hunter College, C.U.N.Y.; Dr. R. Honeycutt, Museum of Comparative Zoology, Harvard University; and Dr. R. Timm, Field Museum of Natural History.

I thank the curators and staff of the Dept. of Vertebrate Paleon-

tology, American Museum of Natural History, for providing me with an office, materials and access to casting and illustrative equipment, as well as the collections, for my tenure in New York. Equally important was the access to collections granted to me by Dr. G. Musser of the Dept. of Mammalogy, American Museum of Natural History, who has always been generous in his support of my research. My year as a predoctoral fellow, with Dr. R. Thorington, jr. and the staff of the Division of Mammals, National Museum of Natural History, was a joy that I wish on all graduate students in mammalian studies.

I thank the National Science Foundation for their support of my research (BNS-8407911), the Smithsonian Institution for my tenure as a predoctoral fellow, the Wenner-Gren Foundation for Anthropological Research for their grant-in-aid, and the Graduate School of C.U.N.Y. for the Mina-Reese Award in the Sciences. Without their financial support, this dissertation could not have been undertaken.

Mr. C. Tarka and Ms. L. Meeker, of the Dept. of Vertebrate Paleontology, American Museum of Natural History, deserve special mention for their tutelage in the visual arts, their patience, and their wonderful generosity, without which my publications and presentations to date would have been inadequate.

My education has greatly benefited from the bi-monthly Physical Anthropology Seminars, which brought together the students and faculties from the many campuses that comprise the amalgamation called C.U.N.Y.. Often intimidating, but always stimulating, the seminars were perhaps the most critical of my courses in training me for a professional

career.

I thank Dr. J.F. Oates, for his clarity in thinking and honesty as a scientist, which has been an outstanding example for me, and for being a friend.

I thank my fellow students and predecessors as students in the program for their support and many discussions, for which I am indebted. Among those students are Drs. M. Dagosto and D. Dykyj, Ms. A. Muskin, S. Sawitzke and S. Walker. Dr. A. Rosenberger, who fills that same role, is also acknowledged for the pleasure of co-authoring two papers with him and for his sympathetic support and advice during my years at C.U.N.Y.. Ms. L. Brown was a great help with the illustrations.

I thank Drs. S. Blum and L. Marcus who provided statistical advice and much assistance on the use of the Statistical Analysis System, and Dr. W. Jungers for his generosity with his time to discuss problems in allometry with me.

Dr. M. Novacek kindly allowed me to use his Apple MacIntosh to generate the bivariate plots presented in Chapters 6 and 7 while Drs. E. Delson and L. Marcus generously provided me access to their computer with which to generate the summary statistics and statistical tests given in Chapters 6 and 7.

My aunt, brothers and their families have been wonderful throughout this experience, but I am particularly grateful to Peter, Cassandra and Zachary Strasser for their emotional and financial support, without which I could have never survived in New York. Furthermore, their welcoming me into their home enabled me to finish this dissertation in an

atmosphere of loving support. In a similar, albeit different role, I would like to acknowledge Ms. L. Dahransoff.

My parents deserve special acknowledgement, for their love, support, and the intellectual climate which they have always provided.

I thank Dr. W. Kinzey for his insightful advice on Figures 2 and 4.

I thank Dr. E. Sarmiento. It would be an understatement to say that I could not have produced this dissertation without his help. His generosity in time, his pedagogical abilities in conveying the intricacies of biomechanics, and his critical reading of most pages of this dissertation go beyond the limits of friendship.

I am especially grateful to my dissertation committee, Drs. T. Olson, M. Rose, F.S. Szalay, and especially my advisor Dr. E. Delson, for their patience and forbearance throughout this process. Dr. T. Olson is gratefully acknowledged for his direction in how to use the English language, as well as his instructions in gait analysis and biomechanics. Dr. Olson's thoroughness and pedagogical skills have been an inspiration for me. Dr. M. Rose has been most generous of his time, to discuss with me not only my dissertation, but a variety of topics in primatological research. His calm and friendly nature has been a balm to me throughout this process. Dr. F.S. Szalay has consistently been supportive of me throughout my graduate career. His conviction for the manner in which evolutionary biology should proceed has had a profound influence on me, and this dissertation, for which I am most grateful.

Dr. E. Delson has been a paragon in the role of an advisor. His absolute and total belief in my abilities carried me through when my own

belief failed. Without his support I could never have accomplished this dissertation, as well as my other achievements as a graduate student at C.U.N.Y.. Indeed, there would have been no achievements without his guidance. Special thanks, therefore, go to Dr. E. Delson.

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Chapter 1. INTRODUCTION

Goal of Dissertation

The goal of this dissertation is to determine the mechanical basis for some distinctive differences in the hindlimb proportions, especially the feet, of cercopithecoid monkeys. The lengths of the lever arms for muscle groups that move the foot around their major joints (talocrural and metatarsophalangeal), the relative lengths of the hindlimb long bones (femur and tibia), and digital length and robusticity formulas, form the basis of this study. However, these lever arms, long bone lengths and digit formulas are only one aspect of form which affects the movements of the hindlimb during the positional behaviors of cercopithecoids. Another important determinant is the configuration of the articular surfaces at the joints themselves, since the configuration determines the range of motion at the joints and therefore the hindlimb segments. Furthermore, the relative size of muscles and more important, the distance of their attachment to bones from the joints they are moving, determines the amount of power which is available to generate momentum in moving the body through space. All of these mechanical aspects of the hindlimb only indicate the possible range and types of movements of which the hindlimb is capable. Without direct observation of the actual movements of animals and their parts in natural settings, it is impossible to determine what part of their potential is utilized and more importantly, the adaptive significance of the form-function units in the lives of the animals (Bock, 1963, 1977, 1980, 1981; Bock

and Miller, 1959; Bock and von Wahlert, 1965). Only when the mechanical constraints and utilized aspects of a form-function complex are documented, is it possible to speculate on the taxonomic value of particular morphologies for unravelling the phylogenetic histories of animals (Bock, 1977, 1981). Some examples of such complete studies of primate locomotor systems are the work of Cartmill (1974) on the significance of claws and digital pads in climbing and especially Sarmiento (1988) on the biomechanics of the whole body, and especially the forearm and wrist, in climbing. The analysis presented here provides the groundwork for understanding the potential limits of a few aspects of movement of the hindlimb in cercopithecids. A complete study of the hindlimb in cercopithecids, and particularly the foot, requires the sort of documentation discussed above, some of which is in progress.

Proportionate differences in the skeleton of the foot and hindlimb of cercopithecids were chosen as the focus of this study because, historically, they have occupied a central position in the description of the cercopithecoid foot. The reason for this is that proportionate differences are immediately apparent when examining the skeleton of the foot and are also correlated with either distinctive locomotor differences among cercopithecids or with taxonomic groups. However, many of the distinctive proportions identified by earlier workers on the cercopithecoid foot quantify morphological units, not mechanical units. For instance, the length of the tarsus relative to the length of the whole foot does not directly relate to the lever arms of any muscle group. Consequently, interpreting the significant differences identified by

earlier workers, in mechanical terms, is difficult. Furthermore, it is well documented that proportions or indices are difficult to interpret because it is not possible to tell why an index may be changing in value given only that value. Because of these attendant difficulties, interpreting the well-documented proportionate differences in the cercopithecoid foot was chosen as a problem which required resolution.

Plan of Dissertation

The next chapter provides a review of the various indices constructed by earlier workers to describe the form of the foot and hindlimb in cercopithecids and the interpretation and conclusions which these authors offered about the importance of the indices for understanding the cercopithecoid foot. The variety of proportions in the cercopithecoid hindlimb and foot are best organized according to their anatomical relationships. Thus, four different groups of proportions can be identified. The first group involves those proportions describing the relative development of the segments of the hindlimb. The second group involves those proportions that describe the development of the non-hallucal segments of the foot. The third group involves those proportions that describe the development of the hallux and the fourth group involves the proportions that describe the relative development of the lateral digits to each other, i.e., digital length and robusticity formulas.

It is important that any mechanical explanation for the proportions of isolated bones is based in the larger context of the biomechanics of

the hindlimb and whole body during locomotion. Biomechanical models are requisite not only for interpreting differences associated with major adaptive shifts, but also for interpreting those which are simply consequent to a change in size. In order to choose and utilize biomechanical models, it is obviously necessary to have some idea of how the relevant animals are moving in the wild. The logical relationship of these factors determined the sequence for the organization of the rest of this dissertation.

Chapter 3 is a synthesis of two types of data. The first type relates to locomotor and postural profiles of particular cercopithecoid species. By culling frequency data from the literature on the actual locomotor and postural behaviors for eight cercopithecine and colobine species, it was possible to identify some distinctive differences in the ways colobines and cercopithecines move in the trees and on the ground. While the locomotor behavior of only eight cercopithecoid species has been studied in detail, there does appear to be a clear correlation between the level (i.e., lower, middle, or upper) of the canopy occupied by a cercopithecoid species and the type of locomotion in which it engages, given its phylogenetic history. This correlation is important, because it provides the basis for predicting the likely locomotor behaviors in animals for which we only have information about the level of the canopy which they occupy. Thus, the second type of data synthesized in Chapter 3 concerns where the remaining cercopithecoid species of this study are found in their environment and, if arboreal, how often they descend to the ground to move between trees or to raid crops. A clear

pattern emerged from these data, showing that middle-canopy dwellers descended more often to the ground than did species at any other level of the canopy. That middle-canopy dwellers often descended to the ground is certainly a consequence of the structural discontinuity of the middle-canopy. Thus, middle-canopy dwellers are not only acrobatic enough to deal with discontinuities, but this agility in the trees apparently translates into an ability to negotiate passage on the ground. The material presented in Chapter 3 shows that the major modes of locomotion utilized by cercopithecids are in part a function of the habitat. The major modes involve differential use of pronograde arboreal quadrupedalism, terrestrial cursorial quadrupedalism, leaping and climbing.

Chapter 4 presents descriptions of the movements of the hindlimb, including the relative displacement of the major segments and the muscles responsible for bone motion, during quadrupedal walking, leaping and climbing. This description is followed by a summary of biomechanical models that predict which aspects of locomotion are likely to be enhanced for cursoriality and leaping. Chapter 4 is concluded with a summary of previous works which have related particular morphological features in the hindlimbs of cercopithecoid species to their optimizing aspects of cursoriality, leaping and climbing.

As in all biomechanical (or engineering) studies, it is clear that the absolute size of an organism will affect the relative proportions of its organs. Since cercopithecoid species range in average body mass from approximately 1.5 kg to 28.5 kg it was necessary to consider the effect

of body mass on the relative proportions of the segments under study, specifically the lever arms for muscle groups. Therefore, a part of this study (Chapter 5) involved examining two of the available models for interpreting the effect of changing body mass, or scaling, on the dimensions of the analysed segments. This summary is followed by a brief review of the application and demonstrated utility of allometric methods, when coupled with biomechanical models, for clarifying the meaning of changes in the values of the inter- and intramembral indices.

Chapter 6 is a presentation of the materials examined in this study and the statistical methods used to analyze them. The statistical methods were used to identify both significantly different proportions among groups, as well as to determine the effect of size on the measurements used in calculating the proportions. Chapter 7 presents the results of this analysis, organized according to the four groups identified above.

Chapter 8 is a discussion of the results presented in Chapter 7. The strongly documented differences between colobines and cercopithecines in the proportions of the hindlimb, and particularly the feet, are considered in terms of the biomechanical models presented in chapter 4. Specifically, four groups of lever arms were examined for differences among cercopithecids. In addition, the robusticity of the digits, the relative size of the hallux, and the digital formulas were examined. It was clear from the analysis presented in Chapter 7 that colobines show a distinct elongation of the hindlimb which is argued to be related to their propensity for leaping. Furthermore, colobines have a unique digit

length and robusticity formula which, given current descriptions of locomotion and grasping postures, is difficult to interpret. The terrestrial cercopithecines all share shortening of the digits associated with digitigrady. Theropithecus and E. patas also have high values for the crural index which are interpreted as adaptations to cursoriality. Finally, several species differ strongly from their subfamilial proportionate and allometric patterns in several regards. These differences are interpreted as adaptations to particular thermal conditions.

Taxonomy of Cercopithecids

The taxonomic nomenclature used in this study (Table 1) is an amalgamation from a number of sources. The assignment of cercopithecine genera to tribes (Table 1a) follows Strasser and Delson (1987), which is based on Szalay and Delson (1979) and Jolly (1965, 1970). The division of colobine and cercopithecine genera into the subtribes given by Strasser and Delson was not relevant to this study, therefore these categories were not employed here. The subgenera recognized by Strasser and Delson are also utilized in this study. The species which were studied are listed in Table 1b. It should be noted that the specimens of Miopithecus sampled in this study represent the northern populations of Miopithecus and thus represent a new species, which has yet to be named (Napier, 1981; Thorington and Groves, 1970). Because there has not been any resolution to the question of the validity of two species within Miopithecus, and because the species name talapoin has traditionally been used for these populations, that usage is continued here. Table 1c

presents a list of informal species groups, following Fooden (1976, 1980) and Napier (1981). These species groups are only relevant to understanding the grouping of species in Chapter 3 and in the tables of Chapter 7.

Table 1a. Classification of cercopithecoid genera.

Order Primates
 Semiorder Euprimates
 Suborder Haplorhini
 Parvorder Anthropoidea
 Infraorder Catarrhini
 Hyporder Eucatarrhini
 Family Cercopithecidae
 Subfamily Cercopithecinae
 Tribe Cercopithecini
 Subtribe Cercopithecina
 Cercopithecus
 Miopithecus
 Erythrocebus
 Subtribe Allenopithecina
 Allenopithecus
 Tribe Papionini
 Subtribe Macacina
 Macaca
 Subtribe Papionina
 Cercocobus
 Papio
 (Mandrillus)
 Theropithecus
 Subfamily Colobinae
 Colobus
 Procolobus
 (Piliocolobus)
 Sennopithecus
 (Trachypithecus)
 Presbytis
 Pygathrix
 (Rhinopithecus)
 Nasalis
 (Simias)

Table 1b. Taxonomy of cercopithecoid species used in this study.

<u>Cercopithecus</u>	<u>Macaca</u>	<u>Colobus</u>
<u>pygerythrus</u>	<u>arctoides</u>	<u>angolensis</u>
<u>ascanius</u>	<u>thibetana</u>	<u>guereza</u>
<u>cephus</u>	<u>assamensis</u>	<u>pelykomos</u>
<u>petaurista</u>	<u>sylvanus</u>	<u>vellerosus</u>
<u>campbelli</u>	<u>nemestrina</u>	<u>satana</u>
<u>mona</u>	<u>nigra</u>	<u>Procolobus</u>
<u>pogonias</u>	<u>tonkeana</u>	<u>verus</u>
<u>albogularis</u>	<u>fascicularis</u>	<u>P. (Piliocolobus)</u>
<u>mitis</u>	<u>fuscata</u>	<u>badius</u>
<u>nictitans</u>	<u>mulatta</u>	<u>Semnopithecus</u>
<u>Miopithecus</u>	<u>Cercocebus</u>	<u>entellus</u>
<u>talapoin</u>	<u>albigena</u>	<u>S. (Trachypithecus)</u>
<u>Erythrocebus</u>	<u>galeritus</u>	<u>cristata</u>
<u>patas</u>	<u>torquatus</u>	<u>obscura</u>
	<u>Papio</u>	<u>Presbytis</u>
	<u>anubis</u>	<u>aygula</u>
	<u>cynocephalus</u>	<u>frontata</u>
	<u>hamadryas</u>	<u>hosei</u>
	<u>ursinus</u>	<u>melalophos</u>
	<u>P. (Handrillus)</u>	<u>rubicunda</u>
	<u>leucophaeus</u>	<u>Pygathrix</u>
	<u>sphinx</u>	<u>nemaeus</u>
	<u>Theropithecus</u>	<u>P. (Rhinopithecus)</u>
	<u>gelada</u>	<u>roxellanae</u>
		<u>Nasalis</u>
		<u>larvatus</u>

Table 1c. Informal species groups recognized in this study.

Cercopithecus aethiops group: pygerythrus

Cercopithecus cephus group: cephus, ascanius, petaurista

Cercopithecus mona group: mona, campbelli, pogonias

Cercopithecus mitis group: mitis, albobularis, nictitans

Cercocebus albigena group: albigena

Cercocebus torquatus group: torquatus, galeritus

Macaca silenus-sylvanus group: sylvanus, nemestrina, nigra, tonkeana

Macaca sinica group: thibetana, assamensis

Macaca fascicularis group: fascicularis, fuscata, mulatta

Macaca arctoides group: arctoides

Chapter 2. HISTORICAL BACKGROUND

Introduction

Historically, most descriptive or functional studies on the hindlimb have included only a few cercopithecoid species as part of broader comparative studies (e.g., Forster, 1922, 1923, 1924, 1929; Langdon, 1986; LeMinor, 1987; Lewis, 1972, 1980a,b,c, 1981; Manners-Smith, 1907, 1908; Moriyama, 1981; Rose, 1986; Szalay, 1975; Szalay and Dagosto, 1988; Szalay and Langdon, 1986; Volkov, 1905). However, on occasion, cercopithecoids themselves have been the focus of studies, which have resulted in excellent descriptive and/or functional assessments of individual bones in the hindlimb (e.g., Jolly, 1965; Olivier and Fenart, 1956; Olivier and Fontaine, 1957; Olivier and Piganiol, 1957). The use of proportions in describing the shape of the hindlimb or its segments has been a particularly popular vehicle for research in physical anthropology (e.g., Gabis, 1960; Jouffroy and Lessertisseur, 1976, 1978; Lessertisseur and Jouffroy, 1973; Midlo, 1934; Mollison, 1910; Schultz, 1930, 1963a,b; Washburn, 1942) and is of special interest in this study, for the reasons given in the previous chapter. The work of five authors is relevant to this study, since their focus (if not wholly, then in great part) is on the proportions of the hindlimb, and especially the foot, in cercopithecoids. These authors are Midlo (1934), Washburn (1942), Gabis (1960), Schultz (1963a,b) and Jolly (1965). The work of each will be surveyed in turn.

Previous Work on the Cercopithecoid Foot

Midlo

Midlo (1934) described the external form of the foot in a wide variety of primates, focusing on the proportions of the sole, the distal extent and attachment of the digits and the topographic relations of the digits to certain skeletal structures. His purpose for this study was to provide an accurate documentation of the external form of the foot (and hand). He studied one hundred six specimens including all the major groups of primates. Thirty-one specimens represented the family Cercopithecidae, distributed over the genera and subgenera Macaca, Cercocebus, Papio, Erythrocebus, Cercopithecus, S. (Trachypithecus) and Nasalis. Midlo also analysed the records collected by Schultz on the digit length formulas of the feet. Schultz's records for cercopithecids included seventy-one specimens distributed over the above-named genera as well as Colobus.

Midlo found that cercopithecids as a whole were characterized by elongated, well-padded soles, with better delineated interdigital pads than seen in platyrrhine monkeys. He noted that cercopithecids had an extremely slender sole compared to papionins, and that within the latter group, Papio had the proximally broadest sole. Midlo also found that interdigital webbing was the rule in cercopithecoid monkeys. The interdigital webs typically extended beyond the plantarodigital line and sometimes to the proximal interphalangeal joints. Midlo reported that interdigital webbing was best developed in Macaca.

Midlo described the cercopithecoid hallux as usually more robust

than the other digits, opposable to a limited degree, and able to be widely abducted. However, the free length of the hallux in cercopithecids was shorter than in New World monkeys, excluding the tamarins and marmosets. In cercopithecids, the free length of the hallux had a range of values from 24 to 35 (Table 2), whereas in the above-mentioned platyrrhines the values ranged from 32 to 44. Midlo described the lateral, non-hallucal, toes as relatively long in most cercopithecids. This was true for the length of the third digit (taken as representative of the lateral digits) relative to the sole, whether measured by its free length or by the length of the phalanges themselves (Table 2). Midlo noted that among cercopithecids, Erythrocebus and Papio had the relatively shortest lateral toes. The lateral toes of Erythrocebus and Papio were not only the shortest in their family, but the shortest of all primates but for humans.

Midlo considered the pedal digit length formula in the sample which he described as practically invariably 3>4>2>5>1 (Table 2). Midlo described the fourth digit as only slightly shorter than the third. He also noted that the second digit extended only as far as the distal interphalangeal joint of the third digit, and therefore was much shorter than the fourth digit. Within colobines, Midlo found that the second digit was especially markedly reduced in length: in Trachypithecus and Nasalis it was equal in length to the fifth digit whereas in Colobus the second digit was shorter than the fifth. (Midlo [1934] stated in text that in Colobus the second digit was equal to the fifth and in Nasalis the second digit was shorter than the fifth. However, the data which he

presented in his Table 3 indicated the opposite. Since the data were more extensive and specific in his table, I followed that rather than his written description in text.) Midlo documented that the reduction in length of the colobine second digit was accompanied by the proximal migration of its metatarsophalangeal joint. Therefore, certainly the second metatarsal, and possibly the phalanges of the second digit, was reduced in length.

Midlo (1934) considered the only notable features in the foot of cercopithecids to be: (1) the uniformity of species in the digit length formula, which he considered the primitive one for primates; (2) the relatively small size of the hallux; (3) the strong tendency to interdigital webbing between the toes; and (4) the prominent volar pads in cercopithecids. Midlo concluded that the feet of Old World monkeys, compared to those of other primates, were externally rather generalized.

Washburn

Washburn (1942) reported on the skeletal proportions of adult Macaca fascicularis, Semnopithecus (Trachypithecus) cristata and Presbytis rubicunda. His reason for focusing on langurs, and comparing them to Macaca fascicularis, was that many conceptions of Old World monkeys were based on Macaca only. This was due to M. fascicularis being a common laboratory animal, the then recent publications by Schultz (1937) on the fetal growth of rhesus macaques, and the compendium edited by Hartman and Straus (1933) on the anatomy of the rhesus macaque. Furthermore, Hollison's (1910) observations of cercopithecids, in his treatise

on primate proportions, was based primarily on cercopithecines. As a consequence, Washburn's aim in his study was to determine to what extent the then current generalizations about Old World monkeys, which were based on cercopithecines and their comparison to apes, would be changed if they were based on langurs.

Washburn studied ninety-eight complete skeletons of adult specimens which were relatively evenly divided among the three species and between the two sexes. Washburn discussed at length the difficulties associated with interpreting the values of proportions or indices without considering the actual measurements themselves. In order to determine which limb measurements were changing the most, the measurements had to be compared to some independent measurement. As a consequence, Washburn used trunk height, as measured from suprasternale to symphysis, as the comparative basis for determining the source of differences in index values. Because of great differences in sexual dimorphism in body weight (macaques were the most dimorphic with males 60% larger than females and Presbytis was the least sexually dimorphic with males 3% larger than females), Washburn suggested that indiscriminate averaging of sexes for a species concealed more information than it revealed.

Washburn reported that the values of the internembral index clearly distinguished the three species of monkeys (Table 3). The crab-eating macaque had the highest indices because, relative to trunk height, the forelimb bones were long and the hindlimb bones short (Table 3). Semnopithecus (Trachypithecus) had intermediate values for the internembral index, because relative to trunk height, the forelimb bones were

slightly shorter and the hindlimb bones slightly longer than in macaques (Table 3). Presbytis had the lowest values for the intermembral index because, despite having long forelimb bones relative to trunk height, its hindlimb bones were extremely long (Table 3). Washburn noted that the intermembral index in Presbytis was lower than that reported by Mollison (1910) for S. entellus (78-79) or for C. guereza (77-79).

The brachial index also distinguished the macaque and two langurs studied by Washburn (Table 3). Semnopithecus (Trachypithecus) had the lowest mean brachial index, M. fascicularis had an intermediate mean value and Presbytis had the highest mean value. Washburn noted that there was a great deal of overlap in values between Macaca and S. (Trachypithecus), but that Presbytis was clearly separated from them. Furthermore, in the two langurs, the length of the humerus, relative to trunk length, was the same, so that the differences in their values for the brachial index could be attributed solely to differences in the lengths of the radius. Washburn compared his results to those obtained by Mollison (1910) and concluded that there was the same range of values for the brachial index in the two subfamilies of Old World monkeys.

There were no major differences between langurs and macaques in their values for the crural index (Table 3). Washburn suggested that it was possible that langurs had, on average, slightly lower indices than did cercopithecines, but that the difference was slight and could only be justified using statistical analysis on a larger series of animals than he had at his disposal.

Washburn (1942) compared the length of the foot to trunk height and

to the summed length of the femur and tibia (Table 3). He reported that relative to trunk height, macaques had the shortest feet and Presbytis the longest. The opposite pattern prevailed when the length of the foot was compared to the length of the long bones of the hindlimb: macaques had the relatively longest feet and Presbytis the shortest.

Washburn (1942) found that the langurs differed from macaques in having relatively longer lateral digits, and in particular longer lateral metapodials (Table 3). Clark (1934) and Wood Jones (1929) had reported that the typical digit formula in cercopithecids was $3 > 4 > 2 > 5 > 1$. Washburn found this was characteristic of all the macaque specimens, but that only 1 out of 34 S. (Trachypithecus) and 6 of the 36 Presbytis specimens had the typical formula. Washburn reported that the easiest way to distinguish the hands and feet of langurs from macaques was by examining the relative proportions of the fifth and second digits, because in langurs the great length of the fifth digit relative to the second was profound. Washburn pointed out how the digital formula in colobines approached that of certain lemurs, in which the lateral digits are also longer than the medial. This is also true for many platyrrhines, in which the fourth digit is longer than the third (see also Schultz, 1969).

As stated above, Washburn's goal in undertaking his description of the langur skeleton was to see how the type of monkey used in comparisons of "lower" and "higher" catarrhines would affect identifying discriminating differences. He demonstrated that if Presbytis, rather than Macaca, were used as the basis of comparison with Hylobates, the

conclusions reached would be profoundly different. Indeed, many of the differences between lower and higher catarrhines would disappear.

One of the most significant conclusions reached by Washburn was that if the measurements which underlie proportions were considered, it was possible to identify those measurements which distinguished taxa. As a result, subsequent investigations need only focus on those few measurements. Furthermore, Washburn found that the measurements which were responsible for the greatest differences among groups were those associated with differences in locomotion.

Gabis

Gabis (1960) examined the proportions of the fore- and hindlimbs in a wide variety of cercopithecids for two reasons. First, the cercopithecids had never been the sole focus of any broadly comparative study on the postcranium, and yet cercopithecids represented a major radiation of primates. Second, the exact affinities of Mesopithecus were open to question, with it appearing more similar to macaques in some regards and closer to colobines in others. In order to clarify the phylogenetic position of Mesopithecus, as well as its mode of locomotion, Gabis undertook a comparative study within Cercopithecidae, based on 23 colobine, 49 cercopithecine, and 29 papionin specimens. On the basis of published descriptions of cercopithecoid species locomotion, Gabis considered Cercocebus, Cercopithecus and the colobines as arboreal species in contrast to the more terrestrial Erythrocebus, Papio and Theropithecus. The macaques were considered by Gabis to represent inter-

mediate forms.

Gabis found that the intermembral index clearly distinguished highly arboreal from terrestrial forms (Table 4). The colobines and arboreal cercopithecines had low values for the intermembral index while Papio and Theropithecus had higher values. The macaques were intermediate between the extremely arboreal and terrestrial forms. Thus, in terrestrial cercopithecids the forelimb approached the length of the hindlimb while in the highly arboreal forms the forelimb was extremely short relative to the hindlimb.

Gabis found a similar distinction, albeit not so strong, between arboreal and terrestrial forms in their values for the brachial index. In Cercopithecus and Cercocebus the average value for the brachial index was below 100, indicating a radius shorter than the humerus. Papio and Theropithecus, on the other hand, had an average value for the brachial index of over 100, indicating a longer radius than humerus. The colobines and macaques had average values intermediate between these two extremes. However, as Gabis' figures and table of species values indicated (summarized here in Table 2.3), there was a great deal of variation for this index, with many "arboreal" species having average values of over 100.

Gabis reported that Schultz had noted that cercopithecids tended to have a crural index above 100, whereas hominoids had a crural index below 100. Gabis found, however, that only Theropithecus had a crural index of 100 and that all other cercopithecids had lower values (Table 4). This was probably a function of differences in their sample composi-

tion and sample sizes. Furthermore, with the exception of Theropithecus, the most extreme values for this index characterized the arboreal species (colobines and cercopithecins) while intermediate values characterized the terrestrial species (Table 4). Gabis concluded, therefore, that the crural index did not permit a distinction between arboreal and terrestrial forms.

Gabis reported the lengths of the three principal segments of the foot (tarsus, metatarsal 3, phalanges 3) as functions of the total length of the foot. Gabis found that the relative length of the third metatarsal was practically invariant in cercopithecids and had a narrow range of mean values (Table 4). Therefore, the metatarsal3/foot index allowed no separation of arboreal from terrestrial forms. In contrast, the length of the tarsus relative to the rest of the foot showed some separation among arboreal and terrestrial forms (Table 4). The most arboreal and agile forms, the colobines, were characterized by a very short tarsus while the most terrestrial genera, Papio, Theropithecus and Erythrocebus, had the relatively longest tarsus. Between these two extremes there was less separation of locomotor groups, since the macaques, reportedly more terrestrial than Cercopithecus and Cercocebus, had a shorter tarsus. Gabis noted that Schultz (1930) also found a similar pattern in tarsal length, from the more to less arboreal apes. Not surprisingly, a similar pattern obtained for the index expressing the length of the third digit relative to total foot length (Table 4). The arboreal colobines had the longest phalanges while the terrestrial Papio and Theropithecus had the shortest. Given the inverse relationship

between the lengths of the phalanges and the length of the tarsus, an index comprising these two lengths (phalanges 3 length/tarsus length) accentuated the differences between the arboreal and terrestrial forms (Gabis, 1960) (Table 4).

Gabis also constructed two indices which described the relative development of the hallux (Table 4). Gabis found that the length of the hallux, either relative to the length of the third digit (metatarsal plus phalanges) or relative to the length of the invariant third metatarsal alone, clearly distinguished colobines from cercopithecines. Colobines tended to have a very short hallux and macaques the longest, with the other genera scattered in between. Gabis did not discuss the fact that Erythrocebus was also noteworthy for having a relatively short hallux (Table 4).

On the basis of the above-summarized indices, as well as others not reported here, Gabis concluded that the forelimb of Mesopithecus was more specialized than the hindlimb, since the forelimb had more adaptations to terrestriality, similar to those seen in mixed-habitat macaques. The hindlimb was clearly similar to that of the highly arboreal colobines and therefore, according to Gabis, less advanced.

Schultz

Schultz (1963a,b) reported on nine indices which described the relative proportions of the foot in primates (Table 5). He examined these proportions in 238 primate specimens distributed over 37 genera, in order to identify proportions which characterized particular

phylogenetic and locomotor assemblages of primates. Of the 37 genera which Schultz studied, 9 were cercopithecoid, 6 of which were cercopithecine. Fifty-one specimens made up the cercopithecoid sample. Schultz pooled the sexes because he found no evidence for sexual dimorphism. He also pooled several species within Papio, Cercopithecus and Presbytis. However, he reported that when more than one species made up a generic sample, the data for one species did not fall out of the range of variation for the other species.

Schultz reported that high values for the ratio of the power arm to the load arm of the foot (which he considered to function as a first class lever during the propulsive stage of the stride, with the fulcrum at the talocrural joint) distinguished Old World monkeys from other primates, with the exception of Gorilla and Homo (Table 5). Schultz (1963b) suggested that the proportionate lengths of the lever arms in primates must reflect a complicated assortment of factors, since the distribution of lever arm ratios did not correlate simply with either body size or locomotion within primates.

Like Gabis (1960), who in part based his measurements on Schultz (1930), Schultz (1963a,b) reported on the proportions of the main segments of the foot relative to total foot length. Schultz also found that colobines were distinguished from cercopithecines by the relatively short length of their tarsus (Table 5). Schultz noted that within cercopithecines, the terrestrial forms had a relatively longer tarsus than did the arboreal genera. Schultz also found, as did Gabis (1960), that the relative length of the metatarsus was invariant in cercopithecids

(and anthropoids generally). Schultz considered the relative length of the phalanges to be more interesting than the previous two indices, because there was more apparent variation in it. Within cercopithecids, Schultz noted that the terrestrial forms had comparatively shorter phalanges than the arboreal forms. In order to highlight differences in phalangeal length, Schultz constructed an index that compared the length of the phalanges to the relatively invariant metatarsal length (Table 5). He noted that only Erythrocebus and Theropithecus had indices below 100, and that colobines had relatively longer phalanges than did cercopithecines.

Schultz constructed four indices to describe the relative development of the hallux and its parts (Table 5). He discussed how colobines had a shorter hallux relative to the third ray than did cercopithecines. Furthermore, compared to other primates, cercopithecids were surprisingly uniform in the narrow range of values for the index comparing the first metatarsal to the third metatarsal. Schultz pointed out that colobines, especially Colobus, had a relatively shorter hallux than did cercopithecines because of the relative length of the phalangeal component (Table 5). Finally, Schultz noted that cercopithecids had a relatively shorter phalangeal component to hallucal length than did platyrrhine monkeys (Table 5). However, he did not comment on the fact that Theropithecus had a noticeably much shorter hallucal phalanx than did other cercopithecids (Table 5).

Jolly

Jolly (1965) analysed fifteen body proportions, constructed by Mollison (1910), in order to identify features associated with arboreality and terrestriality in cercopithecines. Jolly had classified cercopithecine species along an arboreal-terrestrial cline, which he had constructed on the basis of data in the literature. Within Cercopithecini and Papionini, Jolly recognized three groups of species, classified as arboreal, semiterrestrial or terrestrial. For each group in both tribes, Jolly calculated descriptive statistics (mean and standard deviation) for the indices Mollison (1910) had published. He then examined the indices for the groups of species within each tribe to see whether any were statistically significantly different (using Student's t-tests). Jolly argued that if there were any body- and limb-proportions associated with increasing terrestriality, they should be revealed by their independent and parallel evolution in the two phyletic groups.

The data in Table 6 (taken from Jolly's Tables 5-8) are grouped by body region (forelimb indices, hindlimb indices and intermembral index). The species are arranged according to Jolly's classification, from most arboreal to most terrestrial. Thus, within Cercopithecini, Cercopithecus spp. represents the most arboreal species (C. mona, C. cephus, C. diana), C. aethiops represents an intermediate grade and E. patas the most terrestrial species. Within Papionini, Cercocebus represents the most arboreal species, Macaca is an assortment of species intermediate in grade, and Papio has the most terrestrial species. The number of specimens upon which Mollison's (1910) indices were based totaled 140.

Jolly found that with increased terrestriality both the pelvis and

shoulder became broader (Table 6). He argued that a narrower pelvis (and presumably shoulder) in arboreal forms could be interpreted as adaptive to above-branch walking, in which the transverse breadth of the substrate is narrow. He suggested that it would be advantageous to minimize the effect of momentary displacement of the weight-line beyond the support maintained by the feet in an arboreal setting. The fact that C. aethiops had a broader pelvis than did the similarly-sized arboreal Cercopithecus suggested to Jolly that a broad pelvis was not simply a size-related phenomenon.

Jolly found that both the fore- and hindlimbs become longer with increased terrestriality (Table 6). He argued that relative elongation of the limbs was an adaptation to terrestrial cursorial life, since elongated limbs increased the length of the stride. In addition, Jolly interpreted the relatively short limbs of arboreal forms as adaptive to climbing, since the amount of strain exerted on the anchoring forelimbs was in proportion to their length. More recent analyses of climbing suggest that this particular adaptive explanation is unlikely, and that, in fact, long forelimbs would be expected in climbing forms (see Cartmill, 1974; Sarmiento, 1985, 1989). However, Jolly also argued that short limbs would be advantageous to above-branch walking, since short limbs would lower the center of gravity, thus increasing stability.

Jolly found that the internembral index increased with increased terrestriality because the length of the forelimb, relative to trunk length, increased more than that of the hindlimb (Table 6). He suggested that in an arboreal milieu the fore- and hindlimbs have different func-

tions and therefore have different lengths. In terrestrial forms, however, Jolly suggested that the equality in the lengths of the limbs may be related to their similarity in function.

Jolly reported that with increased terrestriality there was an increase in the length of the forearm relative to the arm (Table 6). Jolly interpreted this increase in the brachial index in terms of the use of the forelimb in locomotion. He argued that the distance through which the body is propelled forward and upward for a given amount of elbow extension during a stride is proportionate to the length of the limb distal to the elbow. Therefore, by lengthening the forearm, an advantage is gained in terms of speed as well as in lengthening the stride.

Jolly found that there was no change in the length of the hand relative to trunk length with increased terrestriality (Table 6). However, because the lower arm increased in length with terrestriality, the index of hand length to lower arm length showed a decrease with increasing terrestriality (Table 6).

Jolly found that the increase in hindlimb length took a different form in the two tribes (Table 6). In papionins, both the upper and lower leg increased in length relative to trunk length, but the upper increased more rapidly, so that there was a decrease in the crural index. In cercopithecins, this trend also characterized the transition from the arboreal to semiterrestrial groups but not the transition from the semiterrestrial to terrestrial forms. Indeed, in E. patas, the tibia was relatively longer than the femur, so that its crural index was more

similar to arboreal forms than to other terrestrial forms.

Jolly reported that there were no differences between arboreal and terrestrial forms in the length of the foot relative to the trunk (Table 6). However, he did find that in both tribes the length of the foot decreased relative to the length of the lower leg with an increase in terrestriality.

Jolly had plotted out the values of the indices against the values he had assigned to the species groups for their position along the arboreal-terrestrial cline. The more terrestrial the species, the higher their value along the X-axis of the plot. Jolly discovered that for those indices in which the value of the index increased with increasing terrestrial adaptation, the line connecting the cercopithecine species lay below that connecting the papionin species. In other words, for comparable values of the arboreal-terrestrial index, cercopithecines had a lower value for particular indices than did papionins. While this could have indicated that Jolly incorrectly classified species, he pointed out that for all of those indices, trunk length was the denominator. In the indices expressing the relationships between segments of the limbs or between the limbs, no such consistent pattern was apparent. As a result, Jolly concluded that the trunk was longer in cercopithecines than papionins, relative to the overall size of the animal, and no matter what the value of the arboreal-terrestrial index. Jolly suggested that if his conclusion were true, then the adaptational significance of a long trunk in cercopithecines remained to be clarified. Jolly (1965) did suggest, however, that a long trunk may be related to

the tendency of cercopithecins to use a bounding gallop, which may involve a propulsive use of the vertebral column.

Jolly re-analysed Midlo's (1934) and Gabis' (1960) data in light of his assignment of species to an arboreal-terrestrial index. Jolly discussed how Pocock (1925b) assumed that terrestrial life favored reduction in the length of the phalanges and in the length and robusticity of the hallux. Midlo's (1934) and Gabis' (1960) data confirmed Pocock's assumption that the phalanges were reduced in length in terrestrial forms (see Tables 2 and 4). Jolly pointed out that it was more relevant to paleontological studies, where isolated bones are more common than complete pedal specimens, that the phalanges of terrestrial forms were reduced in length relative to their breadths. His analysis of the length and breadth of the proximal phalanx of the third digit clearly indicated that Theropithecus showed an extreme reduction in the length of the phalanges relative to their breadth.

Midlo's (1934) data also supported Pocock's (1925b) assumption that the hallux was reduced in length in terrestrial forms. However, Midlo's (1934) data indicated that cercopithecins had a relatively shorter hallux than did papionins, for comparable values of the arboreal-terrestrial index. Jolly attributed this difference between the tribes to the fact that the length of the sole was used as the denominator in Midlo's (1934) indices. Jolly suggested that, as was the case with Hollison's (1910) data where trunk length was used as the denominator, the long sole of cercopithecins biased the results.

As was seen above, Gabis (1960) concluded that a reduction in the

length of the hallux was associated with arboreality, not terrestriality. Jolly pointed out, however, that Gabis' (1960) conclusion was based on a sample wherein colobines represented the arboreal specialists while the cercopithecines, Papio and Theropithecus, represented the terrestrial specialists. Jolly argued that the phylogenetic heterogeneity of Gabis' (1960) sample precluded firm conclusions about reduction of the hallux. Jolly's (1965) re-analysis of Gabis' (1960) data for cercopithecines supported Pocock's (1925) assumption about reduction in the length of the hallux. Jolly (1965) noted that Gabis' (1960) data, like Midlo's (1934), indicated that cercopithecins had a shorter hallux than did papionins. Again, Jolly related this result to the variable used as the denominator in Gabis' (1960) indices, the length of the third ray or metatarsal, which Jolly (1965) interpreted as elongated in cercopithecins.

Jolly (1965) examined the order of robusticity in the metatarsals, as measured by their breadth at mid-shaft, in P. (Mandrillus), P. (Papio) and Theropithecus, a series of animals which he reported as similar in size but differing in degree of specialization to terrestrial life. In P. (Mandrillus), the robusticity formula was $1 > 3 \ 2 \ 4 > 5$. In P. (Papio), the robusticity formula was either $3 > 4 > 1 \ 2 > 5$, $3 > 1 > 4 \ 2 > 5$, or $3 = 1 > 4 \ 2 > 5$. In Theropithecus, the robusticity formula was $3 > 4 = 2 > 1 = 5$. Thus, it can be seen that in the more arboreal forms [other arboreal genera had the same formula as P. (Mandrillus)] the hallucal metatarsal was the most robust. With an increase in terrestrial behavior, the robusticity of the hallucal metatarsal was diminished.

Jolly (1965) also examined the relative robusticity and lengths of the proximal phalanges in the same series of animals for which he calculated metatarsal robusticity formulas. Jolly found the same length formula, $3 > 4 > 2 > 5 > 1$, in all the specimens that he examined. However, Jolly found that the genera did differ in their phalangeal robusticity formulas. In P. (Mandrillus) the formula was $1 > 3 > 4 > 5 > 2$. Papio (Papio) had the same formula as P. (Mandrillus) but the hallucal phalanx was not as robustly developed, relative to the third phalanx, as in P. (Mandrillus). Theropithecus had a formula of $3 > 4 > 5 > 2 = 1$, indicating the diminution of the hallucal phalanx. Thus, Jolly (1965) concluded that terrestrial life indeed led to a reduction in the length, and robusticity, of the hallux, as Pocock (1925b) assumed.

Summary

Two conclusions emerge from the results of previous studies presented above. The first is that there were distinct differences in the values of indices describing the postcranium in species of different phylogenetic groups. The second conclusion is that terrestriality had a profound effect on the proportions of the postcranium.

Colobines were distinguished from cercopithecines in the relative length of the tarsus and phalanges (Gabis, 1960; Schultz, 1963a,b), in the relative length of the hallux (Midlo, 1934; Schultz, 1963a,b) and in their digital length formula (Midlo, 1934; Washburn, 1942). Presbytis was distinguished from S. (Trachypithecus) in its intermembral index, brachial index and relative length of its foot (Washburn, 1942). Cerco-

pitheciines were distinguished from papionins in their lower values for indices in which either the length of the trunk, or the length of the sole of the foot, was the denominator (Jolly, 1965).

Terrestrial cercopitheciines were distinguished from arboreal cercopitheciines in having relatively wider limb girdles (Jolly 1965), relatively longer limbs and higher brachial indices (Jolly, 1965), a relatively longer tarsus (Gabis, 1960; Schultz, 1963a,b), relatively shorter phalanges (Gabis, 1960; Jolly, 1965; Midlo, 1934; Schultz, 1963a,b) and a relatively shorter and less robust hallux (Jolly, 1965).

It was also apparent from the review presented above that, with the exception of Jolly (1965), and in one case Schultz (1963a,b), none of the authors considered the biomechanical basis for the differences that they documented. For instance, aside from stating a correlation between short toes and terrestriality, no mechanical explanation for why short toes should be adaptive to terrestrial locomotion was proffered by Midlo (1934), Gabis (1960), Schultz (1963a,b) or Jolly (1965). Perhaps such explanations were obvious and implicitly understood by these authors, but unless stated explicitly, in biomechanical terms, it is difficult for others to appreciate the implication of short toes for a terrestrial life.

Another example of where it would be useful to invoke a biomechanical model to explain changes in the shapes of bones involves the proportions of the tarsus. Why should terrestrial cercopitheciids have a relatively longer tarsus than do arboreal forms? The tarsus, in and of itself, is not a functional unit distinct from the rest of the foot.

There are two major joint complexes within the tarsus (subtalar and transverse tarsal joints) as well as two major joint complexes between the tarsus and adjacent segments (talocrural and tarsometatarsal joints). Furthermore, elongation of the tarsus could be due to one bone elongating, several bones elongating or, indeed, only a portion of one bone elongating, such as the segments proximal or distal to the proximal articulation between the calcaneus and astragalus. Furthermore, given the nature of the indices, it is not certain that terrestrial cercopithecids indeed have a longer tarsus. It may be that the tarsus simply appears longer because of changes taking place elsewhere in the foot. Therefore, it needs to be demonstrated that terrestrial cercopithecids indeed do have a longer tarsus before addressing the even more complex question of explaining why this morphological, but not functional, unit should be elongated. The same argument applies to demonstrating, then explaining, why colobines have the pedal proportions reported above.

Aside from the fact that biomechanical models were rarely invoked to explain the proportions presented above, another drawback to interpreting those indices has to do with the fact that no author, with the exception of Washburn (1942), considered the effect of the differences in body size on the proportions that they described. For instance, Schultz (1963a,b) demonstrated that cercopithecids have a relatively high value among primates for the ratio of the power arm to the load arm in the foot. Furthermore, Schultz (1963a,b) explicitly provided the mechanical basis, albeit slightly flawed, for interpreting this ratio and discussed its relationship to both locomotor modes and body size.

However, because Schultz (1963a,b) was describing the relative proportions of the foot in all primates, he did not examine in any detail the relationship between the power arm/load arm ratio and body size. Schultz did caution that this ratio was not comparable across all primates, because of the conflicting patterns that cut across phylogenetic and locomotor groups (see also Langdon, 1976). However, given their relative uniformity (Schultz, 1970), cercopithecids provide an excellent group with which to examine in more detail the relationship between the values of the power arm/load arm ratio and body size. Such an analysis has yet to be performed.

Jolly's (1965) analysis provides another example of the necessity to consider body size when analyzing proportions. Jolly (1965) observed that the reason there were major differences between cercopithecins and papionins in their hindlimb and pedal proportions was because of the difference in length of the denominator used to calculate the proportions, the trunk and sole. Jolly (1965) considered the length differences between cercopithecins and papionins, in the trunk and sole, as due to fundamental adaptive shifts. Given Aiello's (1981) subsequent demonstration of a negative allometric relationship between trunk length and body mass in catarrhines, there is a distinct possibility that the difference in trunk length between cercopithecins and papionins is due to allometric scaling, to maintain mechanical similarity, rather than due to major adaptive differences between the two groups. However, it remains to be demonstrated that the difference in sole length between cercopithecins and papionins is also a function of size.

The above-summarized authors made only a few attempts at determining which component of a bivariate relationship was changing and giving rise to different values in the indices. Washburn (1942) and Jolly (1965) were able to determine the basis for differences in the intermembral, brachial and crural indices among their groups. Similarly, Schultz (1963a,b) concluded that the hallux was shorter in specific cercopithecoid groups because of changes in phalangeal, not metatarsal, length. Furthermore, Jolly (1965) suggested that it was a change in length, and not breadth, that gave rise to robust phalanges in terrestrial forms. However, the basis for changes in the relative lengths of the segments of the foot was not assessed by Gabis (1960) or Schultz (1963a,b).

Finally, it has yet to be demonstrated if the differences in digit length formulas identified for a few colobine and cercopithecine species (Hidlo, 1934; Washburn, 1942) in fact characterize the two subfamilies. Similarly, Jolly (1965) documented differences in the digital length and robusticity formulas between some arboreal and terrestrial cercopithecines, but this should be examined in a broader spectrum of species. In addition, it has yet to be explained what the differences in digital formulas mean in terms of how these animals locomote.

Table 2. Mean values reported by Midlo (1934) for indices of the foot. Digit length formulas: left, most frequent permutation; right, less frequent permutation.

	Free Length Ray1/ Sole	Free Length Ray3/ Sole	Total Length Ph3/ Sole	Digit Length Formulas
Macaca	34	41	54	3>4>2>5>1
Cercocebus	34	36	50	3>4>3>5>1
Papio	29	32	44	3>4>2>5>1 3>2>4=5>1
Erythrocebus	24	29	39	3>4>2>5>1
Cercopithecus	29	38	51	3>4>2>5>1
S. (Trachypithecus)	35	45	56	3>4>2>5>1
Nasalis	31	38	52	3>4>2>5>1 3=4>5>2>1
Colobus	-	-	-	3>4>5>2>1 3>4>2>5>1

Table 3. Mean values reported by Washburn (1942) for indices.

	<i>Hacaca fascicularis</i>	<i>Sennopithecus cristata</i>	<i>Presbytis rubicunda</i>
forelimb/hindlimb	92	82	76
forelimb in % trunk height	82	76	83
hindlimb in % trunk height	89	92	109
radius/humerus	98	94	114
tibia/femur	92	90	91
foot length in % trunk height	43	44	49
foot length in % hindlimb length	48	47	46
digit length formulae	long medial	long lateral	long lateral

Table 4. Mean values reported by Gabis (1960) for indices.

	Forelimb	Radius	Tibia	Tarsus	Ht3	Ph3	Ph3	Ray1	Ray1
	Hindlimb	Humerus	Femur	Foot	Foot	Foot	Tarsus	Ray3	Ht3
<i>Macaca</i>	93	98	93	31	30	37	119	56	125
<i>Cercocebus</i>	84	99	94	32	30	35	109	55	130
<i>Papio</i>	93	104	91	35	32	32	91	55	112
<i>Theropithecus</i>	95	107	100	35	33	30	-	56	102
<i>Erythrocebus</i>	85	100	98	37	32	28	75	49	92
<i>Cercopithecus</i>	82	95	97	31	32	36	113	53	112
<i>S. (Senno.)</i>	76	104	90	29	33	37	128	47	100
<i>S. (Trachy.)</i>	81	95	91	29	31	39	136	52	119
<i>Presbytis</i>	79	99	93	29	31	38	132	46	102
<i>Nasalis</i>	91	101	88	29	30	38	123	53	109
<i>Pygathrix</i>	92	105	89	29	30	38	130	49	109
<i>Colobus</i>	76	94	93	28	32	39	142	45	104

Table 5. Mean values reported by Schultz (1963a,b) for indices of the foot.

	Power/ Load	Tarsus/ Foot	Ht3/ Foot	Ph3/ Foot	Ph3/ Ht3	Ray1/ Ray3	Ht1/ Ht3	Ph1/ Ph3	Ph1/ Ht1
Nacaca	22	32	33	36	110	55	66	46	77
Cercocebus	23	32	33	35	108	57	70	45	70
Papio	25	35	32	33	108	57	69	47	70
Theropithecus	25	36	35	29	83	54	60	46	65
Erythrocebus	23	37	33	30	89	53	59	45	69
Cercopithecus	22	32	33	35	108	55	65	45	76
Presbytis	24	30	32	38	122	50	65	38	72
Nasalis	25	29	32	39	122	52	65	42	79
Colobus	22	30	31	39	125	46	61	34	71

Table 6. Mean values reported by Jolly (1965) for indices calculated by Hollison (1910). *C. spp.* includes *C. capensis*, *C. nana* and *C. diana*. Sh.Br., shoulder breadth; Up.Arn, upper arm; Lv.Arn, lower arm; To.Arn, upper + lower arm;

	Sh.Br.	Up.Arn	Lv.Arn	Hand	Hand	To.Arn	Lv.Arn
	Trunk	Trunk	Trunk	Trunk	Lv.Arn	Trunk	Up.Arn
<i>C. spp.</i>	27	39	38	28	74	78	97
<i>C. aethiops</i>	29	41	39	27	70	80	97
<i>Erythrocebus</i>	28	42	45	27	60	87	107
<i>Cercocebus</i>	28	43	44	30	67	87	101
<i>Macaca</i>	33	46	46	34	75	93	99
<i>Papio</i>	34	51	55	35	65	106	109

Table 6. (cont.). Pl.Br., pelvic breadth; Up.Leg, upper leg; Lv.Leg, lower leg; To.Leg, upper + lower leg;

	Pl.Br.	Up.Leg	Lv.Leg	Foot	Foot	To.Leg	Lv.Leg	Forelimb
	Trunk	Trunk	Trunk	Trunk	Lv.Leg	Trunk	Up.Leg	Hindlimb
C. spp.	21	47	47	45	96	95	99	82
C. aethiops	23	49	47	45	95	95	96	83
Erythrocebus	25	50	50	44	88	100	101	88
Cercocebus	26	55	51	45	87	106	93	83
Nacaca	27	53	49	50	102	102	94	90
Papio	30	60	53	52	96	113	89	93

Chapter 3. OBSERVATIONS ON CERCOPITHECID POSITIONAL BEHAVIOR

Introduction

Much more is known about where to find a cercopithecoid than about how they move within their habitat. We know less about the latter because it is only in the last twenty years that attention has been directed specifically to studying primate positional behavior in natural habitats. In part, the impetus for such studies was the seminal paper by Prost (1965a), which enunciated the importance of careful description in documenting locomotor and postural behavior, as well as the importance of distinguishing between those behaviors. Prost (1965a:1200) defines locomotor behavior in a primate as the "set of locomotor actions...when its body mass (as opposed to limb mass) is grossly displaced relative to its physical surroundings" and he defines postural behavior as "...the alternative to locomotion...when the positional relations between a primate's body mass and environmental surroundings remain relatively stable. The alternative state to locomotion is posture". Thus, an animal can be engaged in either posture or locomotion, and both of these categories are included in the term 'positional behavior'. In that same paper, Prost described a research strategy which would give rigour to descriptions of positional activities. Prost elucidated the necessary correlation between positional behavior and substrate use, as well as the significance of large body size for the positional choices available to arboreal primates. The most obvious outcome of that paper is the now common usage of his terminology or definitions, coined to draw attention

to the differences between posture and locomotion, and between the behaviors an animal is capable of and those which are expressed.

Prost's work has stimulated a number of researchers to put into operation the approach he defined (e.g., Morbeck, 1976, 1977, 1979; Rose, 1977, 1978, 1979). But problems remain - the foremost of which, at least for this study, is agreement upon a common methodology of data gathering and presentation. Until data are gathered and presented in a uniformly systematic manner the results of studies on different species will not be comparable. For instance, Morbeck (1976, 1977) presents positional activities as a percentage of observations while Rose (1977, 1979) reports them in terms of the percentage of total time budgets. Fleagle (1978) reports his data as percentages of distance travelled while Cant (1988) uses both the percentages of distance moved as well as percentages of observations, depending upon the comparison. These three types of percentages are not comparable. A similar problem plagues dietary studies wherein the importance of food items can be calculated by the time spent in their foraging and harvesting or by the percentage weight each item contributes to the diet. As discussed by Richard (1985), given the first method, Alouatta is classified as a folivore whereas according to the second it is a frugivore. Because of the differences in data presentation for cercopithecoid positional behavior, it is not possible in this study to directly compare most of the available data for the colobines and cercopithecines whose positional behaviors have been documented in the last 15 years. Nevertheless, some distinctions do emerge from studies on the locomotor patterns of arboreal

colobines and cercopithecines as well as for those between arboreal and terrestrial animals (e.g., Table 7).

Since attention was directed to the importance of defining the substrate used by an animal (Napier, 1967; Prost, 1965a; Ripley, 1967) all studies provide some classification of the substrate. Not surprisingly, each classification differs in details and number of categories but all descriptions of branch size can be grouped into the following three categories, taken from Rose (1978): (1) slender branches which deform under the weight of an animal; (2) medium-sized branches which do not deform under an animal's weight but which require an animal to place its hands and feet in line with each other during progression; and (3) large-sized branches which are effectively similar to the ground in providing a wide base of support.

In the following pages, a summary of postural and locomotor activities is presented for eight cercopithecoid species (S. entellus, C. quereza, P. melalophos, P. rubicunda, S. obscura, C. aethiops, M. fascicularis, and P. anubis), since these were the only ones for which such data were available. This summary highlights some characteristic differences between cercopithecines and colobines, as well as between closely related species within each subfamily. Following this is a summary of the literature on habitat utilization by all the species considered in this study. It will be seen that it is possible to predict the likely positional behaviors for cercopithecoid species, given the micro-habitat that they occupy.

Postural Activities

Ripley (1967) discussed the fact that monkeys utilize a variety of postures during the course of a day. For instance, when S. entellus eats, sleeps or scans the surroundings it tends to sit in the leafy periphery of the crowns. When resting or grooming S. entellus will lie on the ground or branches and when drinking crouch on the ground. Quadrupedal standing is generally used during activities such as copulation or grooming, which require large supports such as thick branches or the ground. Bipedal standing is adopted when S. entellus is scanning its environment or eating from a bush. A similar catalogue of activities and associated postures would probably characterize all cercopithecids.

The age and sex of an individual will determine to a certain extent which postures are utilized more often (see also Rose, 1977). Infants engage in suspensory postures from their mother's ventrum more than any other posture. Juveniles, which practice positional and other behaviors during play, may find themselves clinging or hanging bimanually in precarious situations more often than would a cautious adult. Receptive females will not only have to bear their own weight in a quadrupedal stance but also that of an adult male. In some species certain individuals will act as the look-out and engage in bipedal standing more often than others. Presumably, over the course of an individual's lifetime many of these differences will be of little consequence for shaping the skeletal structure as might other species-specific behaviors. But even these latter may not always be expressed.

Probably the most important influence on an animal's positional

behavior is the nature of its particular habitat. An individual in a particular population may have occasion to utilize only a segment of the many species-specific behaviors available to it, because of the limits set by the habitat. Currently inhabited environments are contingent upon historical factors and may not represent the optimal habitat for the expression of behaviors shaped by natural selection in the past. Furthermore, if other similar species are occupying the same habitat, competition may determine to a certain extent which part of the available habitat is exploited. These influences may well account for the percentage differences of particular behaviors seen among the primates described below.

It is fairly well documented that arboreal species have well delineated periods of activity during the day, with several peaks of feeding and foraging interrupted by brief stretches of travel and longer ones of resting. Feeding peaks are not so marked in terrestrial species which tend to forage more continuously during the day (Rose, 1974). Resting, which by definition is a postural activity, accounts for 75% of C. guereza's diurnal activity budget, approximately 35% of the vervet's time and 20% of the olive baboons's (Rose, 1977, 1979). If these species were taken to represent discrete segments of the arboreal-terrestrial spectrum (C. guereza arboreal, C. aethiops semiterrestrial, P. anubis fully terrestrial), and if these figures were at all representative of the habitat categories, then postural activities seem to be especially important to arboreal forms. However, if postures associated with feeding are also considered, then even in terrestrial animals such as the

olive baboon, posture accounts for the majority of positional activities during the day (Rose, 1977). Thus, in both arboreal and terrestrial species postural behaviors can account for up to 75% of diurnal activity, and if nocturnal sleep is included, over 90% of all activity (Rose, 1974, 1977).

All researchers agree that the vast majority of postural activity is sitting, accounting for 67-99% of all postures (Cant, 1988; Davies, 1984; Fleagle, 1978; Rose, 1974, 1977, 1979). During sitting most support of a monkey's weight is taken by the callosities, but at times its balance is assisted or steadied with the hands or feet (Ripley, 1967; Rose, 1974). The only major variations in sitting behavior are first, that colobines tend to extend their hindlimbs along the surface of a branch or let them hang on either side of a branch whereas cercopithecines tend to keep their hindlimbs flexed at all the major joints (Morbeck, 1979; Ripley, 1967; Rose, 1974, 1979). Second, Rose (1977) describes the range of sitting postures in baboons as more limited than in arboreal primates. In an arboreal setting sitting postures are determined by the size and orientation of the substrate as well as the need to occasionally maintain balance by gripping nearby branches with the foot. On the ground, the support base poses no problems for maintaining stability so sitting is more stereotyped.

Standing is the second most important posture in most species. If it is associated with feeding then it is usually tripedal (Rose, 1974). In this posture in *P. anubis* the elbows and knees are maximally extended (Rose, 1977). When all four limbs are used for support the knees and

elbows are slightly more flexed. Balance during bipedal standing is often provided by the forelimbs holding on to nearby supports. Other postures utilized by monkeys are lying and suspension. Lying in a supine position is not uncommon among all species, but suspensory postures are reported for only a few colobines, such as P. melalophos, P. rubicunda and C. guereza (Davies, 1984; Fleagle, 1978; Morbeck, 1979).

Before proceeding to the summary of species-specific locomotor activities, it would be useful to review the types of gaits used by cercopithecids during locomotion.

Definitions of Cercopithecoid Gaits.

Recent years have witnessed an increase in attention given to the analysis of primate gaits, since Prost (1965b) and Hildebrand (1967) confirmed Muybridge's (1899) observation that primates utilized an atypical walking gait among mammals. Gaits are defined as the sequence in which limbs are regularly employed to propel the body during locomotion (Hildebrand, 1988). Different gaits are used, depending upon the speed of progression, maneuverability, stability, continuity of supports and size of animal. For cercopithecids on continuous supports, a walking gait is used at relatively slow speeds, a trotting gait is used at intermediate speeds and a galloping, bounding or hopping gait is used at high speeds (Morbeck, 1976; Rollinson and Martin, 1981). To cross discontinuities in substrates, leaping is used.

Gaits are described in terms of: 1) the sequence of footfalls; 2) the number and combination of limbs used in support; and, 3) the amount

of time spent by limbs in support of the body. At slow or intermediate speeds, there are two sequences of footfalls: lateral and diagonal. A lateral sequence is one in which the footfall of either hindlimb is followed by that of a forefoot on the same side of the body. A diagonal sequence indicates that the footfall of either hindlimb is followed by that of a forefoot on the opposite side of the body (Hildebrand, 1967; Iwamoto and Tomita, 1966). At higher speeds, there is more synchrony between footfalls and the pairs of limbs which move together are the forelimbs and hindlimbs (Morbeck, 1976). The number and combination of limbs used in support can vary from no limbs used in support (free flight) to one limb at a time supporting the body to all four limbs used in support. The number of limbs supporting the body at any one time can be indicated by a condensed support formula, such as 2.3.4.3.2, which indicates that support is by two limbs, followed by three limbs followed by four limbs etc. (Probst, 1965b). It is typical, however, for two limbs to move somewhat synchronously and therefore to support the body together. The term couplets refers to two limbs acting in synchrony. There are two types of couplets: lateral and diagonal. Lateral couplets involve two ipsilateral limbs whereas diagonal couplets involve diagonal limbs. Finally, if pairs of limbs spend an equal amount of time in support of the body the gait is referred to as symmetrical. If one pair of limbs spends more time than the other in supporting the body the gait is called asymmetrical (Hildebrand, 1968). The pairs of limbs used in asymmetrical gaits comprise the hindlimbs or forelimbs.

Primates use a diagonal sequence, diagonal couplet, symmetrical

gait when walking (Hildebrand, 1967; Prost, 1965b; Rollinson and Martin, 1981; Rose, 1973). It is typical in cercopithecines, however, for the number of supporting limbs to sequentially alternate in a pattern described by the condensed support formula 2.3.4.3.2.3.4.3 (Rollinson and Martin, 1981). When the center of gravity is propelled along a line connecting the two diagonally opposing supporting limbs there is a tendency for the body to yaw around a supero-inferior axis (Prost, 1965b). Unless resisted, this yawing torque could lead to falling. A third limb contacting the substrate after a couplet has begun propelling the center of gravity counteracts the yawing torque (Prost, 1965b). This additional support also provides stability since the center of gravity is then completely contained within a triangular base of support.

Rollinson and Martin (1981) described cercopithecines as using a form of trot at intermediate speeds. This trot is a symmetrical, diagonal sequence gait wherein the predominant support is by diagonal couplets which basically swing together, although the hindfoot typically contacts the substrate prior to the forefoot. Therefore, the condensed support formula of this trot is 2.1.2.1.

At high speeds cercopithecines, like other primates and mammals, gallop. The gallop in primates is an asymmetrical gait, wherein the hindlimbs spend more time in contact with the ground than do the forelimbs. The condensed support formula for the cercopithecine gallop is 2.1.2.3.2.1.0.1 (Rollinson and Martin, 1981). The zero in the formula indicates that there is a free-flight phase in this gait, during which no limb contacts the ground. An even greater speed can be achieved by

switching gaits to a full gallop, in which two unsupported intervals are included in the cycle (condensed support formula: 2.1.0.1.2.1.0.1) (Rollinson and Martin, 1981).

Bounding is described by Morbeck (1976) as an asymmetrical quadrupedal gait wherein the hindlimbs move in synchrony, as do the forelimbs. While Morbeck did not report the exact sequence of footfalls and support during bounding, her description suggested that the condensed support formula would be 2.0.2.2.0.2.

Hopping and leaping are bipedal gaits which are differentiated primarily by the position of the trunk. In hopping the trunk is held vertically and in leaping it is held horizontally (Morbeck, 1976).

Climbing and shinnying are quadrupedal modes of locomotion used when the supports are vertical (Rose, 1979). The determining factor in whether a cercopithecoid (or primate) climbs or shinny up a vertical support is the diameter of the trunk (Sarniento, pers. comm.). If the vertical supports are small enough in diameter to gain a hand or foot grip, climbing is used. If the vertical supports are too large in diameter for a hand or foot grip, then shinnying is used. Climbing and shinnying differ in the degree of abduction of the limb segments as well as in the motion of those segments. The relative placement of the limbs are similar to those described above for quadrupedal diagonal couplet, diagonal sequence walking. Shinnying has not been formally defined by Hildebrand (1988) or some of the authors which use the term or its equivalent "bear hug" (Hittermeier and Fleagle, 1976; Ripley, 1976). Sarniento (pers. comm.) defines shinnying (or bear climbing) on large-

diameter vertical supports as "hanging on for dear life" and states that usually there are at least three cheridia contacting the support. This form of locomotion occurs at slow speeds only.

Locomotor Activities

It is currently typical for researchers to quantify locomotor observations into categories associated with feeding and travelling between sites. In earlier years such discrete categories were not singled out. Instead, descriptions, rich in the subtle details and nuances which characterize the actions of individual social types in the pursuit of their success, are provided and positional behavior is contextualized in an ethological framework. An excellent example of this early work is Ripley's (1967) description of positional behavior in S. entellus. Ripley's work is the sole source of such detailed description of the positional behavior for this species, and one of the few of its kind for any cercopithecoid (see also Rose, 1977). The current classification of behaviors into discrete categories is certainly heuristic, since it allows comparison between otherwise disparate studies. Heurism does enhance simple summary, which is the aim of this section. But, in the process of standardizing the method of observation, many subtle, and possibly profound, differences in behavior can be obscured. As a consequence, the organization of the activities summarized below reflect the method of recording and reporting observations. Thus, Ripley's observations on S. entellus's locomotor behavior, which will be summarized first, do not fit many discrete categories. The more recent studies (on

C. guoreza, P. melalophos, P. rubicunda, S. obscura, C. aethiops, M. fascicularis and P. anubis), which consider the differences in locomotion associated with feeding or travelling, make observations in a somewhat more comparable manner because of their similarly defined categories. Thus, the data for these species are presented second, with the contrasts in locomotor behavior associated with feeding and travel made more apparent by being presented together.

Semnopithecus entellus.

Ripley (1967) suggested that the major locomotor adaptations seen in S. entellus are for speed on the ground and in climbing and for quadrupedalism in the canopy. While feeding on the ground, a slow quadrupedal walk was generally used when moving between bushes. Semnopithecus entellus's usual mode of locomotion on the ground, however, was an easy lope, the speed of which was situation dependent. Ripley (1967) did not define the term lope, but according to Hurov (1987) a lope is similar to a gallop but with no periods of suspension. When streams were crossed S. entellus took a leap in midstride, or more accurately, hopped bipedally. To ascend low-branching trees S. entellus relied on momentum from a run to get up to the branches. If the tree was a tall one which branched fairly high up then S. entellus climbed up using the forelimbs as pivot struts and the hindlimb for propulsion. In the trees S. entellus tended to run rather than walk. Ripley suggested that running assisted langurs in maintaining their balance on medium-sized supports. When a secure grasp was necessary, such as at the

periphery of crowns, then walking or climbing was used. When descending trees, S. entellus did so tail-first until near the bottom when entellus turned to run or drop down, usually landing on its hindlimbs which absorb the shock, as in all primates.

When gaps were met in the canopy these langurs leapt with ease. Ripley (1967) discussed leaping in terms of the supports used at take off and when landing. She recognized four categories of support combination: strong to strong, strong to flexible, flexible to flexible, flexible to strong. The first type of leap was used when an animal was escaping predators or attackers, engaged in dominance interactions or ascending or descending trees. These leaps were usually short and fast. They were generally taken from a running start and momentum was gained by not braking prior to the leap. Upon landing the shock of impact was usually absorbed by flexing the hind limbs. However, if this leap was used in a display, the forces were usually transferred to the branch itself so that it would shake or break. The second category (strong to flexible) were the longest and most spectacular type of leaps and were used in display or in escape. This type of leap had a high initial velocity, because the animals tended to run off the take-off support and generally landed on a much lower branch. The third type of leap (flexible to flexible) was used only when animals were moving between feeding spots and their attitude was calm. These leaps were very deliberate and it was essential that the branches have many twigs and leaves to increase the area for grasping. The langurs had to pump in place to achieve any momentum and such take-off supports were avoided

when langurs were in critical situations such as escaping predators. Therefore, when speed was critical firm supports were preferred for take-off but when speed was unimportant flexible ones were used. The last type of leap (flexible to strong) only occurred when a langur was dropping to the ground at the end of a descent.

Colobus guereza.

This species is perhaps the most lethargic of those for which the behaviors are summarized here. Morbeck (1977) reported that the C. guereza which she studied in a high altitude remnant montane forest near Limuru, Kenya, spent only 16% of their time locomoting and the rest (84%) in some sort of postural activity. Rose (1978, 1979) found comparable values in a C. guereza population near Lake Naivasha, which spent 70-75% of its activity budget resting and 25-30% in feeding or related activities. Quadrupedalism and leaping accounted for 77% of all locomotor activities at Lake Naivasha (Morbeck, 1976). When walking quadrupedally C. guereza, like all cercopithecids, employed a diagonal sequence, diagonal couplet gait pattern. This form of quadrupedalism was most common when speeds were slow. When speed increased they switched to a bounding pattern. This was most common on medium-sized, slightly sloping branches and accounted for 25% of quadrupedal locomotion (Morbeck, 1977). Leaping and hopping accounted for another 23% of all locomotor observations. At Limuru most leaps (75%) were short, less than 2 m in distance, and were primarily a large-branch activity (Morbeck, 1977). At Lake Naivasha, when C. guereza made major changes in its

location, it made use of medium-sized branches (Rose, 1979). While C. guereza characteristically followed trails with a minimum number of gaps that required leaping, leaps were frequent. Although small, deformable branches were used quite often, the preferred take-off and landing sites for these leaps were medium-sized branches. Furthermore, horizontal branches were used more often as a take-off or landing platform, although sloping ones did account for a significant proportion of the total (Rose, 1979). At Lake Naivasha, when C. guereza climbed they did so mostly in medium to large-sized branches. Furthermore, they spent nearly half of their locomotor time moving either within 4 meters of the ground or at the midcanopy levels 12-16 meters above the ground.

Rose (1978) reported that most of C. guereza's feeding time was spent sitting (98.6%). When they foraged (i.e., locomotion associated with feeding) they walked quadrupedally most of the time (48%) but also spent a great deal of time climbing (36%). Furthermore, they spent a not insignificant 15% of their time leaping. During these feeding bouts C. guereza spent almost 75% of their time on medium-sized branches and spent the clear majority of the remainder of time on small branches (24.4%) upon which they walked slowly and carefully (Rose, 1978). Finally, Rose (1973) reported that colobines have a tendency to gallop at all speeds.

Presbytis melalophos.

This species ranges throughout the canopy but is found most often in the understory (Curtin, 1976). As a consequence, leaping and hopping

are the most important locomotor modes used when travelling, accounting for 67% of the distance achieved (Fleagle, 1978). Presbytis melalophos engaged in much less quadrupedal walking and running (21%), even less climbing (8%) and employed only some armswinging (3.4%). In terms of time given to each activity, P. melalophos spent equal amounts of time in quadrupedal walking and running and leaping/hopping but much less time in climbing and armswinging (Fleagle, 1978). When travelling P. melalophos tended to move on or between branches. Presbytis melalophos tended to leap more on smaller supports and most leaps tended to be from a larger to smaller support. They engaged in quadrupedalism when on larger supports and climbing when among branches.

Not unexpectedly, P. melalophos switched to a different strategy when feeding than when travelling. Armswinging became negligible and quadrupedalism, leaping and climbing were about evenly utilized. Fleagle (1978) reported that they climb or walk when maneuvering around one small region of a tree, but when they move to another section they tend to hop more. In comparison to when they travel, P. melalophos utilized branches of small diameter when feeding. This substrate difference was reflected in the fact that they leapt much less often while feeding whereas the distance covered by climbing and quadrupedal walking/running increased substantially (Table 7).

Presbytis rubicunda.

When P. rubicunda traveled through the forest it frequently entered the understorey trees where larger branches were used as often as small

branches (Davies, 1984). Because of the discontinuity which characterizes this level of the forest, they frequently encountered major and small gaps between branches. As a consequence, they spent more time in leaping (45% of observations) than any other category of locomotion. However, walking and bounding accounted for a greater proportion of the distance covered during travel than did leaping (45% compared to 40%), which indicated to Davies (1984) that the animals selected large continuous branch supports.

When feeding, P. rubicunda utilized a very different pattern of locomotion. It generally was found on twigs and lianas and therefore tended to climb and walk more often than when it travelled (Table 7). Indeed, they climbed and walked twice as much feeding as when travelling. If it was necessary to cross a gap during feeding, P. rubicunda did so by dropping down or bi-manually swinging (Davies, 1984). Leaping was used only a quarter as much when feeding as when travelling. Davies suggested that this was because there were fewer strong supports from which to spring.

Semnopithecus obscura.

This species was found most often foraging in the main canopy and emergents where substrates are more continuous (Curtin, 1976). Fleagle (1978) stated that because of its concentration of efforts in the main canopy, S. obscura spent more time in quadrupedal locomotion than any of the other categories (Table 7). During travel which was not associated with feeding, walking and running accounted for 50% of the distance

travelled, leaping and hopping 40% of the distance and climbing approximately 9%. Semnopithecus obscura preferred to travel on larger boughs if possible.

Semnopithecus obscura utilized a significantly different pattern of locomotion when feeding than it did when travelling. Quadrupedal walking and running accounted for practically 70% of all observations while the remainder were equally divided between leaping and climbing. Not unexpectedly, when feeding S. obscura utilized branches of small diameter which lead to a greater use of climbing and a decrease in leaping.

Cercopithecus aethiops.

Rose (1979) reported on the amount of time spent moving by a population of vervets in Kenya. Locomotion, regardless of the social or maintenance activities with which it is associated, accounted for only 4.5% of the vervets' time. Rose (1979) commented that this may be a low value compared to other populations of vervets, but not far off from the typical time budget of the species. Of the time engaged in locomotor behaviors, 20% of it was spent on the ground. No matter what the substrate, more than 50% of the vervets time was spent walking, close to 30% climbing, and 10% leaping. When feeding, vervets spent more of their arboreal time on smaller, deformable branches than on medium-sized ones.

Macaca fascicularis.

Cant (1988) reported that most (70%) locomotion in M. fascicularis was along continuous substrates. While travelling the majority of

locomotion was by quadrupedal walking and running (65%) with leaping (11%) and climbing (5%) less important. Leaping occurred at a higher frequency in M. fascicularis when it travelled than during feeding or foraging bouts. Though they more often (58%) chose paths that allowed walking across gaps, M. fascicularis leapt to cross gaps between trees. In these latter cases, lianas proved to be very important. Ripley (1967) reported that macaques always walked more cautiously in all parts of the tree than did langurs. The macaques did not bound or lope like langurs did, in part because they required a new handhold or foothold before they would release their last one (Ripley, 1967). Furthermore, young macaques did not seem able to manage the gaps in the canopies and at these crossings the adults had to bridge the gap with their own bodies. Consequently, macaques would go out of their way to avoid gaps in the canopy that required leaping, especially if the leaping had to be between flexible supports. Cant (1988) recorded little difference in the size of the substrates used for take-off and landing during leaping. On the whole, the majority of leaps (80%) were between relatively small branches and the leaps were relatively short, averaging 2.2 m in length. Practically one-quarter of locomotion was between branches or across substrates. Across-substrate locomotion, defined as clambering by Cant, generally occurred on smaller branches.

The frequency of along-substrate locomotion (quadrupedal walking, running and climbing) increased during feeding in M. fascicularis and leaping decreased substantially (Table 7). Cant (1988) reported that M. fascicularis used larger substrates when feeding than when foraging or

travelling, in contrast to the pattern seen in colobines.

Papio anubis.

Because baboons do not have as discrete activity periods as do arboreal animals, no distinction is made here between locomotion associated with feeding and with travel. Walking was the most common means of progression in P. anubis, accounting for 19% of all activity (Rose, 1977). Running was fairly infrequent, making up only 2% of all activity while climbing occurred less than 1% of the time. Leaping was extremely rare and was mostly associated with ascending or descending trees or fence posts.

Several major features emerge from these studies. The first is that colobines engage in leaping much more frequently than do cercopithecines. Second, the frequencies for leaping (and climbing) behavior are strongly correlated with activity (Table 7). In colobines, leaping occurs twice as often while travelling than when feeding. When feeding, colobines climb twice as often than when travelling. This is not unexpected given that most feeding takes place in the small branch setting of the canopy. Third, a small branch setting requires more climbing or clambering than does a large branch setting. These few distinctions may be used in predicting the sort of positional behavior one expects to see in animals which frequent different parts of the forest.

Habitat Utilization by Cercopithecids

Recent studies (Curtin, 1979; Dunbar and Dunbar, 1974; Gautier and Gautier-Hion, 1969; Moreno-Black and Maples, 1977; Rodman, 1973, 1979; Struhsaker and Oates, 1975) have demonstrated how sympatric forest primates avoid competing directly with each other, by either utilizing different strata in the forest, or if occupying the same stratum, by feeding on different food sources. Furthermore, when cercopithecids coexist in the same stratum they are not usually as closely related to each other as they are to a species allopatric to them. Charles-Dominique (1974) argued that relative height in the forest is not so important to the segregation of species as is the diameter and orientation of supports, which are characteristics that cross the boundaries between strata (Gautier-Hion et al, 1981). While this may be true for lorises (cf. Charles-Dominique, 1974; Crompton, 1984) it is not necessarily the case for cercopithecids (Fleagle, 1978; Waser, 1982b, 1984a). Furthermore, for most primates these types of data are simply not available, whereas there is some documentation of the type of forest in which they are found and the stratum they most frequently occupy. While this information is far from ideal for correlating skeletal differences with behavior (Ripley, 1967) it does provide a crude basis for their interpretation.

Gross estimates of overall positional behavior for species in which it is not known, can be generated by considering the specific positional behaviors documented above. These observations confirmed that there is some correlation between substrate type and positional behavior. Furthermore, as will be presented in the next chapter, there are a number

of studies on closely related species which correlate skeletal differences with documented differences in positional behavior (Fleagle, 1977a,b; Hurov, 1987; Jolly, 1965; Rodman, 1979). Together, these observations should allow some prediction of the biomechanical requirements imposed by the habitat on a particular cercopithecoid species. As such, they will not only allow sorting convergent features from homologous ones, but should assist in interpreting the functional implications of features which characterize related species.

The following pages provide a brief summary of the major morphological features of primate habitats. This is followed by a summary of the literature on the habitat utilization of most cercopithecoid species, concentrating on those studied in this work.

Habitats Available to Cercopithecoids

Cercopithecoids are the most widespread of non-human primate families, extending from well north of the Tropic of Cancer to south of the Tropic of Capricorn. Within this vast latitudinal range a variety of biomes are available to and exploited by cercopithecoids. Jolly (1965) suggested that the major limiting factor to their spread beyond the currently inhabited latitudes is the number of daylight hours available in which to search for food. Otherwise, few habitats provide significant barriers to cercopithecoids' occupation.

The major tropical biomes exploited by cercopithecoids are evergreen and seasonal forests, woodland, thornwood, shrubland, savannas and semi-desert scrub (Richard, 1985). The main distinctions between evergreen

and seasonal forests are whether leaves are shed or not, the timing of their reproductive cycles, and the extent of stratification in their canopy.

In evergreen forests, there is little synchrony among trees in shedding leaves and in reproduction. In mature evergreen forests the canopy is stratified and four layers can be identified: lower, middle, upper and emergent. Because the dense canopy of mature evergreen forests prevents much light from reaching the lower levels, there is little undergrowth on the forest floor. As a consequence, the lower and middle layers are usually less continuous than the upper layer. However, where there are gaps in the forests, such as along rivers or at a tree fall, the greater exposure to light produces an abundance of undergrowth on the forest floor. As a result, such forest edge sites require animals to manipulate small, obliquely oriented branches if they occupy the lower layers. The upper layer of the canopy presents greater continuity and fewer gaps between the crowns of trees, which means that animals need not leap as often as they would lower in the canopy. Emergents generally rise above the continuous upper layer of the canopy and can be vertically separated from the upper layer by quite a gap.

In seasonal or deciduous forests there is synchrony in shedding leaves and in reproduction. If the deciduous forest is mature the canopy is consolidated and continuous. However, stratification within deciduous forest is not so well developed as in evergreen forest.

Savannas, woodlands and shrublands are all defined as regions with little tree cover. Obviously, these habitats require that cercopithecids

occupying them spend considerable amounts of time on the ground in locomotion.

In the following section the utilization of habitats by cercopithecoid species is reviewed. The order of presentation is taxonomic. Thus, cercopithecine, papionin, and then colobine species are presented.

Habitat Utilization by Individual Cercopithecoid Species

Erythrocebus has a continuous distribution throughout the savanna and semi-desert scrub country of Africa, north of the Equator and south of the Sahara Desert (Hall et al., 1965). Its southern range in the west is limited by the rain forest, but in the east there is no obvious ecological barrier to its expansion. Therefore, its current restricted distribution, as compared for example to C. aethiops, is not readily explicable (Struhsaker, 1969). Within this vast territory it avoids the riverine forests frequented by other savanna forms such as baboons and vervets (Hall, 1965b). It seems, therefore, to be more independent of trees than its relative C. aethiops, although it may enter trees occasionally to feed, rest, shelter from predators, and survey its environs (Struhsaker, 1969). It is noteworthy as the primate most cursorially adapted to terrestrial life, running with exceptional speed if disturbed (Tappen, 1960).

Haplorhina inhabits the edges of primary and regenerating evergreen forests, swamp forests and estuarine mangrove swamps (Emmons et al., 1983; Gautier-Hion, 1966, 1972, 1973, 1978). Its typical habitat is primary evergreen forest which is inundated periodically, but it is

also found in secondary forests near human settlements and in the low brush of abandoned farms (Malbrant and MacLatchy, 1949; Sabater Pi and Jones, 1968). At the edges of the primary evergreen forests, Miopithecus prefers dense vegetation cover, where its light weight allows it to use thin supports (Gautier-Hion, 1978). While Miopithecus frequents all levels of the forest, it is usually observed at heights between 2 and 10 m and rarely descends to the ground (Gautier-Hion, 1978). However, it is known to steal soaking manioc and therefore must occasionally descend to the river-beds (Gautier-Hion, 1966), which poses little threat since it is an avid swimmer. Rollinson and Martin (1981) suggested that Miopithecus may be a recent immigrant to the forest canopy because of similarities in its gait to those seen in terrestrial cercopithecids.

The members of the C. cephus species group (cephus, ascanius, petaurista) are small-bodied (3-4 kg), highly arboreal, forest-edge monkeys which are reported to prefer the dense vegetation characterizing the secondary growth at lower levels of the forest, approximately 5-20 m from the ground (Gautier-Hion et al., 1981, 1983; Sabater Pi and Jones, 1968; Struhsaker, 1969). In this milieu, the dominant supports are narrow liana tangles (Oates, 1985). Gautier-Hion et al. (1981) found that C. cephus enters higher levels of the canopy for fruit eating and sleeping but spends the majority of its day time hours in the dense undergrowth resting. Cercopithecus cephus tends to avoid higher levels of the forest and instead searches out the densest understory. However, when C. cephus is in polyspecific associations with C. pogonias and C. nictitans it can be displaced from this stratum into the higher levels,

while the latter species search in the understory for insects (Gautier-Hion, 1988). While C. cephus is found at lower levels in the forest it does not voluntarily descend to the ground (Tappen, 1960).

Cercopithecus petaurista, like C. cephus, flourishes in forest edge and riverine forest habitats (Oates, 1988). It, too, is relatively rare in mature high forest although it can be found where fallen trees leave gaps in the canopy, conditions favorable to dense secondary growth (Booth, 1956). However, unlike C. cephus, it is also reported in the middle and lower layers of the forest (Tappen, 1960).

In the Congo forest block, C. ascanius is reportedly found in every type of lowland rain forest where, like the other members of its species-group, it is often associated with the forest fringes, within which it stays in the lower and middle layers (Clutton-Brock, 1973; Haddow, 1952; Struhsaker, 1978). Unlike C. cephus, C. ascanius is not reluctant to descend to the ground to raid farmers' gardens. Tappen (1960) reported that along the NW shore of Lake Victoria C. ascanius is found at all levels of the canopy in the center of primary forest rather than along the edge. Tappen (1960) suggested that the explanation for this is that in the Congo forest there is more competition for the primary forest zone.

The species of the C. mitis group (C. mitis, C. albogularis, C. nictitans) are medium-sized monkeys (4-9 kg) which show some lability in the habitats they exploit. C. nictitans is perhaps the most restricted in this regard, since it is generally found along the fringes of lowland primary evergreen forest and the secondary growth of the forest-edge

(Lumsden, 1951; Sabater Pi and Jones, 1968). Because C. nictitans includes a substantial amount of foliage in its diet, which is unusual for a cercopithecine, it can probably tolerate relatively dry forests and gallery forests in the savanna zone (Oates, 1988). C. nictitans reportedly exploits the upper part of the forest canopy (Gautier-Hion, 1980; Oates, 1988) and zones of open foliage although it is also reported in lower layers of brush in secondary forest (Malbrant and Maclatchy, 1949). However, C. nictitans does not frequent the densest type of undergrowth as does C. cephus (Gautier-Hion et al, 1981). Although C. nictitans has been seen occasionally on the ground where it may raid cultivation (Lumsden, 1951), It is thought to rarely come to the ground, even to traverse gaps in the forest (Tappen, 1960),

Cercopithecus mitis is restricted to Central and East Africa. Within this range it is versatile in the habitats that it frequents. Cercopithecus mitis is considered to be typical of highland forest, where it is reported from altitudes of 2870 m, but it is also found in lowland forest (Aveling, 1984; Lumsden, 1951). Within this altitudinal range it frequents bamboo forests, primary forest, gallery forest and even ventures into savanna woodland (Booth, 1962; Rahm, 1970; Tappen, 1960). It is said to prefer feeding in the lower to middle storey of the canopy (Clutton-Brock, 1973; Struhsaker, 1978).

Although C. albogularis is known from coastal scrub and relatively dry woodland (e.g., Brachystegia woodland), it is usually found in thick primary evergreen forest (Brain, 1965; Cords, 1987; Moreno-Black and Maples, 1977). Indeed, because C. mitis and C. albogularis are found in

such habitats Brain (1965) noted their similarity to C. aethiops in showing some tendency towards a shift from forest to woodland to savanna. However, usually C. albogularis and C. mitis extend from the lush forest to the forest edge while C. aethiops extends from the scrub vegetation towards the forest edge (Booth, 1962). Furthermore, both C. albogularis and C. mitis are reported to differ from C. aethiops in showing little tendency to terrestrial behavior (Oates, 1988). According to Haddow (1956) they usually do not venture to the ground to raid gardens. But this is very likely dependent upon their habitat, since in a Kenyan coastal forest they were observed on the ground quite often (Moreno-Black and Maples, 1977) and Booth (1962) reported that they are known to raid crops. Moreno-Black and Maples (1977) reported them feeding both on the ground and in trees and noted that when in flight from observers they generally travelled along the large branches of the lower canopy.

The C. mona group species (mona, campbelli, pogonias) are among the smallest in the genus (2.5-5 kg) and are found in a variety of forest habitats such as primary and secondary forest. Cercopithecus mona is reportedly most abundant in secondary rain forest/savanna mosaic zones, such as forest outliers, as well as in mangrove swamps where it has been seen swimming (Lumsden, 1951; Oates, 1988; Sabater Pi and Jones, 1968; Struhsaker, 1969). Booth (1956) stated that C. mona and C. campbelli occupy the lower and middle layers of the trees, rarely ascending to the highest levels in the canopy. Struhsaker (1969), however, reported that it is seen at all heights in the forest but prefers the lower levels.

Cords (1987) reported that it is often found at ground level. Although there is some stratification by sex and body size with females at lower heights (15-20 m) than males (20-25 m), C. pogonias is successful in more mature forest and is usually found in the upper levels (Gautier-Hion, 1980; Gautier-Hion et al., 1981; Lumsden, 1951; Struhsaker, 1969).

As is well known C. aethiops is a savanna and arid-country species, occurring in nearly all such country south of the Sahara Desert. Within this zone it is found in a variety of habitats from semi-arid savanna to rain-forest edge but it is most typical in riverine forests (Hall, 1963, 1965a; Hall and Gartlan, 1965; Moreno-Black and Maples, 1977; Struhsaker, 1969). Throughout this range C. aethiops appeared to be limited only by its need for sleeping trees and water (Fedigan and Fedigan, 1988). Compared to all other Cercopithecus species C. aethiops is noteworthy for its ability to live in marginal habitats and it is reported to move into disturbed areas of secondary growth as well as such habitats as mangrove swamps (Galat and Galat-Luong, 1976; Gartlan and Brain, 1968; Struhsaker, 1967). This ability to tolerate such a variety of habitats is undoubtedly related to C. aethiops' propensity to include a large proportion of leaves in its diet, as does C. ascanius (Hall and Gartlan, 1965). Another important influence is C. aethiops' willingness to cross large expanses of open country to reach other woodlands (Tappen, 1960). As a consequence, this species is second only to E. patas among the cercopithecins in its degree of terrestriality. Whether C. aethiops is prevented from colonizing the lush forests by other species of monkeys which inhabit them as Booth (1962) suggested or

whether C. aethiops is exploiting a niche unavailable to its congeners, is a question to be settled. This description of C. aethiops applies equally well to C. pyrrhythrus.

Napier (1981) discussed how macaques are renowned for their ability to occupy any ecological zone. Because of this, most species are found over broad altitudinal or latitudinal ranges and it can be difficult to specify significant differences among species in their habitat preferences. Nevertheless, some distinctions have been made and are summarized below.

Macaca sylvanus, along with the Japanese macaque (M. fuscata), is one of the most northerly distributed extant species in the family (Deag, 1977). Macaca sylvanus is found in boreal mixed cedar and oak forests at altitudes of up to 2000 m, where it is thought to be more at home in trees than on level ground (Deag, 1977; Sanderson, 1957; Tappen, 1960). Macaca sylvanus also inhabits rocky regions in mountains and in these localities is forced to spend all of its time on the ground passing the nights on cliffs or in caves (Alvarez and Hiraldo, 1975). Taub's (1977) extensive survey of the distribution of M. sylvanus revealed that while many populations are widely disjunct in marginal habitats their greatest density is in cedar forests.

In contrast to M. sylvanus, M. nemestrina, the pig-tailed macaque, keeps largely to the center of dense evergreen forests at low altitudes throughout its range. Within this altitudinal band, however, it does range from forests at the base of hills (up to 900 m) to coastal swamps (McCann, 1933). In the evergreen forests of W. Thailand it is recorded

in medium-sized and low trees about 15-45 m off the ground (LeKagul and McNeely, 1977). There is some difference among the mainland subspecies in their use of the forest floor. Fooden (1975) considered the subspecies M. n. leonina, in the northwestern part of the species range (India, Burma), exclusively arboreal, but Tilson (1982) reported observing individuals foraging and travelling on the forest floor. Tilson did note, however, that the troops kept mainly to the lower canopy (5-10 m from the ground). The southeastern (Malaya, Sumatra, Borneo) subspecies, M. n. nemestrina, is found as often on the ground as in the trees (Fooden, 1975; Medway, 1969; Rodman, 1979). This has been suggested to be due to the low density of their preferred fruit trees in the deep forests which requires considerable movement between feeding trees (Rodman, 1979). Medway (1969) also reported that in Malaya and western Indonesia M. nemestrina spent considerable time on the forest floor foraging. But it is most typical for M. n. nemestrina, when feeding, to do so in the middle canopy (Rodman, 1979). The distinction between the subspecies is also noticeable in response to human disturbance: M. n. leonina flees from danger through the canopy while M. n. nemestrina descends to the forest floor where it disappears into the undergrowth (Bernstein, 1967; Fooden, 1975; Rodman, 1979).

There are few reports on the natural history of M. nigra, the Celebes black ape. It apparently has a predilection for the upper canopy of primary forests at moderate altitudes (c. 2000 m) (Groves, 1980; Hill, 1974) and is thus most likely highly arboreal. But it has also been sighted raiding crops and crabbing along the coast (Hill, 1974) and

therefore, like its congeners, is probably not strictly tied to any one milieu.

Fooden (1982) reported that M. assamensis is restricted to a narrow altitudinal zone between 150 and 1900 m above sea level. But they have been collected at altitudes of 2750 m as well as in tidal mangrove swamp. Within this mid-elevation altitudinal distribution they are usually found in the denser parts of subtropical broadleaf evergreen rain forest (Fooden, 1982). Some troops, however, have been recorded in deciduous forests, bamboo forests, and raiding cultivated fields. Fooden (1982) suggested that all these sightings were near primary evergreen forests and interpreted their presence in these other localities as representing temporary forays. Within the evergreen forests they prefer to be high in the canopy, much like M. nemestrina and M. nigra. Eudey (1980) reported that they will flee from danger either through the tree tops or by descending to the ground. Their movements are reported to be much slower and more deliberate than those of M. mulatta (Fooden, 1982).

Macaca thibetana is a poorly known species generally found in subtropical broadleaf evergreen forest. The temperatures can be quite cool in these forests, remaining above 10° C for only three-quarters of the year (Fooden, 1983). Macaca thibetana is thought to be generally restricted to these forests within its range but it has been sighted on rocky cliffs, indicating some ability to maneuver on the ground (Fooden, 1983).

The species of the M. fascicularis group are very widespread within the tropical belt of SE Asia and tolerant of a variety of habitats.

Indeed, the most ecologically widespread macaque is M. fascicularis. The classic habitat of fascicularis is usually given as coastal mangrove swamp but they are also found in primary and secondary forest as high as 2000 m. Macaca fascicularis has also been sighted in agricultural areas where it raids crops and in isolated patches of woodland (LeKagul and McNeely, 1977). Given this distribution M. fascicularis appears to be well adapted to edge habitats in contrast to the sympatric M. nemestrina which occupies the deeper forest (Fooden, 1982).

Macaca fascicularis is reportedly very agile in the trees where it often stands bipedally to feed. It also walks bipedally during foraging bouts while holding on to branches above its head (Kurland, 1973; Poirier and Smith, 1974). Macaca fascicularis is also reported to be a spectacular leaper, often covering 5 m or more while crossing breaks in the canopy (Kurland, 1973). Cant (1988) suggested that these spectacular leaps were likely due to their desperation during flight from humans. The leaps he observed in a more habituated group were considerably shorter (2.2 m) and more inept. This contrast may be due to differences in the troop's learned behavior (Ripley, 1967). The route M. fascicularis prefers in the canopy is along older, more solid, branches (Kurland, 1973; Poirier and Smith, 1974). Whereas Kurland (1973) rarely saw any terrestrial behavior Poirier and Smith documented it quite often as did Kawabe and Mano (1972). Rodman (1979) reported it only when M. fascicularis left and approached its sleeping trees near the river. Otherwise, Rodman found them strictly arboreal. As might be expected for most macaques, terrestriality is probably a situation-dependent behav-

ior.

Macaca mulatta has been classified an upland species by Fooden (1971) and a lowland form by LeKagul and McNeely (1977) which, in part, reflects its adaptability. Within the subtropics it lives in a wide variety of habitats including cities, primary and secondary non-broadleaf lowland forests, some mountain forests and semidesert environments (Fooden, 1982; Tilson, 1982). Macaca mulatta's altitudinal range is from 500 m to 1500 m. It is less arboreal than many of its congeners, as at home on the ground as in the trees. Because of this M. mulatta is successful as a commensal with humans.

Macaca fuscata is similar to other members of its species-groups in ranging from coastal mixed temporal forests to mountain forests. Macaca fuscata is reported to avoid clearings, but is apparently equally adept on the ground as in the trees (Sugiyama, 1976).

Macaca arctoides is both a tropical and subtropical animal, found in the same kind of habitat as M. thibetana and M. nemestrina, i.e., broadleaf evergreen forest (Fooden, 1982). M. arctoides is considered the most terrestrial of all the macaques and its gait is described as much slower and less agile than that of arboreal macaques (McCann, 1933). When crossing gaps in the canopy it does leap. But its leaps cover only a few meters compared to the more spectacular leaps of M. fascicularis (McCann, 1933). When climbing trees M. arctoides is reported to shinny up the tree using bear-climbing postures (McCann, 1933).

Turning to Africa, there is a fundamental ecological distinction

between the torquatus group of mangabeys and the albigena group in their habitat preference and their vertical range within the canopy. Cercocebus torquatus and C. galeritus are typically found in swamp forests or other seasonally inundated lowland forests (Gautier-Hion, 1978; Groves, 1978; Jones and Sabater-Pi, 1968; Waser, 1982, 1984). During the dry season the C. torquatus-group species are reported to spend as much time on the ground as in the trees. On the forest floor these species walk slowly, foraging in the leaf litter (Groves, 1978; Groves et al., 1974; Waser, 1984). The C. torquatus group species are also known to raid farmers crops (Malbrant and Maclatchy, 1949). Oates (pers. comm.) suggested that mangabeys are being outcompeted by P. (Mandrillus) leucophaeus in the drier rainforests of Cameroon and for this reason these mangabeys are found more often in swampy forests.

Cercocebus albigena is typically found in primary and secondary moist evergreen forest although it has also been sighted in swamp forests (Lumsden, 1951; Sabater Pi and Jones, 1968; Waser, 1976, 1984b). Although it has been reported to come to the ground when frightened and to feed on low vegetation (Lumsden, 1951), C. albigena is, for all practical purposes, entirely arboreal, rarely descending to the ground (Groves, 1978; Haddow, 1952). The typical feeding level for C. albigena is the middle storey of the canopy (Clutton-Brock, 1973; Struhsaker, 1978).

Papio (Mandrillus) sphinx preferentially inhabits the lower levels of the lowland primary and secondary forests in west central Africa (Emmons et al., 1983; Harrison, 1988; Sabater Pi and Jones, 1968; Stam-

mbach, 1987). While P. (Mandrillus) sphinx is most commonly found at ground level or in the lower-level vegetation it has been seen feeding at the highest level in the canopy (Harrison, 1988). Lahm (1986) found that they spent the majority of their time in forests free of dense undergrowth and close to streams. P. (Mandrillus) sphinx appears to avoid forests with dense undergrowth from ground level to 3 m. However, supplementary foods are gathered in secondary, inundated and riparian forests and they are known to raid manioc gardens. There is some segregation of the habitat by larger and smaller members of the species: males remain largely on the ground while females and young are semiarboreal, inhabiting the undergrowth and middle layers of the forest canopy (Jouventin, 1975). The preferred trees are of moderate height and are used for feeding and resting purposes (Tappen, 1960).

Papio (Mandrillus) leucophaeus is also a lowland rain forest form (Struhsaker, 1969). This animal apparently forages on the forest floor for roots, nuts and other plant foods (Tappen, 1960). However, it does sleep in trees (Malbrant and MacLatchy, 1949).

The species of P. (Papio) are all essentially ground-dwelling animals, but do spend considerable amounts of time feeding and sleeping in trees. They are encountered in a wide range of climates and altitudes, since they range over most of sub-Saharan Africa, except for the interior of the Congo block. When P. (Papio) has been sighted in the Congo forest it was always on the ground (Tappen, 1960). Papio ursinus was typically found frequenting the coastal cliffs and treeless kopjes in the rocky country of S. Africa (Hall, 1962, 1963; Tappen, 1960).

Papio hamadryas appeared to avoid woodland in Ethiopia, preferring rocky gorges (Dunbar, 1977) whereas P. cynocephalus is reported to avoid open country, preferring to be near trees (Moreno-Black and Maples, 1977; Tappen, 1960). However, P. cynocephalus certainly ventured into the savanna to feed (Hall, 1965a). Rowell (1966) reported that in Uganda P. anubis spends more than 60% of its time in the forest even though open grassland is available to it. While this information is limited, it appears that there is a cline in the commitment of baboon species to terrestriality, with P. hamadryas and P. ursinus the most terrestrial, P. anubis intermediate and P. cynocephalus the least terrestrial (Kalter, 1977).

The currently monotypic Theropithecus occupies rocky ravines and open spaces in the restricted highlands of Ethiopia. It is found at elevations above 2000 m where maximum temperatures range from 7-15 °C and below zero temperatures at dawn are not uncommon throughout their range (Iwamoto and Dunbar, 1983). Theropithecus is one of the few primates which do not enter trees at night for sleep, but instead choose the steep faces of ravines for protection (Dunbar, 1977). Therefore, like E. patas, they are highly committed to terrestriality (Jolly, 1965).

The African colobine (sub)genera are clearly vertically segregated in the rain forests of W. Africa (Booth, 1954, 1957) although when not sympatric this stratification may be less clear. For instance, when the subgenera are sympatric P. (Piliocolobus) is found at the highest levels of the canopy, Colobus at the middle levels and P. (Procolobus) at the

lowest levels (Booth, 1954; Clutton-Brock, 1973, 1974; Groves, 1973; Struhsaker, 1975, 1978; Struhsaker and Oates, 1975). If P. (Piliocolobus) is absent from a forest Colobus will move into a higher stratum of the forest as well as into the lower (Booth, 1954; Moreno-Black and Maples, 1977). P. (Procolobus), however, always stays within the lowest levels of the forest (Struhsaker and Oates, 1975).

Among Colobus species C. polykomos tolerates a wide variety of habitats. Earlier reports suggested that it was primarily a lowland rain forest form (Lumsden, 1951; Malbrant and Maclatchy, 1949) but it appears to thrive in dry forests as well as in riverine forests (Oates, 1977). Colobus satana is the most restricted in distribution of all the black-and-white forms and is found in coastal evergreen forests (McKey, 1978; Oates, 1977; Sabater-Pi, 1973; Sabater Pi and Jones, 1968). Colobus angolensis is found in both lowland and montane rain forests (Nishida et al., 1981; Oates, 1977; Tappen, 1960). Colobus guereza is probably the most widespread because it is more successful in secondary, relict and gallery forests than it is in mature rain-forest (Struhsaker and Oates, 1975). It is also found in a broad range of altitudes from sea level to 3300 m (Oates, 1977). Some Colobus species are reported to raid crops and have been often observed on rocky outcrops travelling between patches of gallery forest or on the ground ingesting dirt (Buxton, 1951; Lumsden, 1951; Oates, 1977; Sabater-Pi, 1973). Colobus satana (Sabater-Pi, 1973) and C. angolensis (Moreno-Black and Maples, 1977) are reported to flee danger through the highest strata of the forest.

Procolobus (Piliocolobus) is primarily a rain-forest animal al-

though some forms live in more secondary habitats (Booth, 1954; Clutton-Brock, 1973, 1974; Struhsaker and Oates, 1975). As mentioned above, P. (Piliocolobus) occupied the highest level of the canopy where it was reported to be a more accomplished leaper than C. angolensis or C. guereza (Booth, 1956; Clutton-Brock, 1973; Groves and Dandelot, ms.). Procolobus (Piliocolobus) generally feeds in the periphery of tree crowns, often in the middle canopy, but rests near the center of the trees where branch diameters are large. P. (Piliocolobus) also spends many hours sunning itself high in the crown (Groves et al., 1974). Clutton-Brock (1973) reported that P. (Piliocolobus) badius rarely comes to the ground, but does do so when in a patch of forest in which the distance between trees precluded leaping, or when feeding on soil.

Procolobus verus is a rain forest form which is successful in edge habitats, tending to be concentrated around swamps and river banks (Booth, 1954, 1957). As mentioned above, it is found in the thick lower layers of the forest (Booth, 1954, 1957). Unlike the other African colobines, P. verus always stays in the lowest levels of the forest, never venturing into higher and presumably richer parts of the canopy, even if no other colobines are present.

Given the greater number of Asian colobine species than African, relatively less is known about them since only six species have been studied to any extent (S. cristata, S. obscura, S. entellus, P. melalophos, P. rubicunda, N. larvatus). Because of the greater similarity among species of each genus than between genera (Washburn, 1942, 1944) it is probable that the ecology and behaviors reported below

for the Presbytis species (melalophos, rubicunda) are characteristic of the group.

Sennopithecus (Trachypithecus) cristata is found at elevations from sea-level up to 1700 m in evergreen forests, at the junction of mangrove and terrestrial coastal forests and in mangrove swamps (Medway, 1969, 1970). In Thailand most groups are found higher in the trees (40-50 m), but in Malaya some populations spend much of their time on the ground (LeKagul and McNeely, 1977).

Sennopithecus (Trachypithecus) obscura is found in a wide range of habitats, from coastal to montane forests. Like S. (Trachypithecus) cristata, it seems to prefer tall trees, especially emergents, but it is known to raid rubber gardens and therefore descends to the ground (Curtin, 1976; LeKagul and McNeely, 1977). Curtin (1976) reported that this species prefers broad firm substrates in the main canopy level.

The range of S. entellus is rather broad, extending from low altitude plains to heights of 4267 m in the Himalayas (Roonwal and Mohnot, 1977). Within this altitudinal band S. entellus is found in relatively dry tropical forests, wet deciduous forests, scrub jungles, arid rock areas with xerophytic vegetation and cold evergreen forests (Oppenheimer, 1977; Roonwal and Mohnot, 1977; Sugiyama, 1976). In India, S. entellus is said to differ from other langurs in that it is largely restricted to deciduous forest, avoiding dense evergreen forests. In Sri Lanka, S. entellus is reported in lowland mixed deciduous and evergreen forests (Ripley, 1970) and in the Himalayas it is found in evergreen forests (Sugiyama, 1976). Within these forests S. entellus is found

anywhere from ground level to heights greater than 15 m. On average, S. entellus spends half of its time on the ground and the other half in the trees (Ripley, 1967; Sugiyama, 1976).

Presbytis melalophos is found in both inland and coastal forest and in coastal swamps (Curtin, 1976). LeKagul and McNeely (1977) reported that where P. melalophos is sympatric with S. (Trachypithecus) obscura there is some altitudinal stratification with S. (Trachypithecus) obscura more abundant above 600 m and P. melalophos below. Where P. melalophos is alone, however, its range can extend to as high as 2200 m. Presbytis melalophos, therefore, appears to have a broader altitudinal range than does S. (Trachypithecus) obscura (Curtin, 1976). Curtin (1976) stated that its vertical range in the forest is also broad. Presbytis melalophos preferred the middle story but entered the emergents as well as the understory. Presbytis melalophos also occasionally forages on the ground and is known to raid rice fields (Curtin, 1976; Wilson and Wilson, 1973). In contrast to S. (Trachypithecus) obscura, when P. melalophos is in the canopy it utilizes slender flexible supports (Curtin, 1976).

Nasalis larvatus is widely distributed throughout a variety of habitats from mangrove swamps, riparian forests to rain forest (Bennett and Sebastian, 1988; Kawabe and Mano, 1972; Salter et al., 1985). Salter et al. (1985) report that N. larvatus prefers primary forest over more disturbed forests which are in fact avoided by this species. Moreover, given the opportunity, N. larvatus prefers more inland mature forest than coastal or riverine forest (Salter et al., 1985). However, most N.

larvatus are found along the river (Bennett and Sebastian, 1988; Kern, 1964). Nasalis larvatus is mostly arboreal but does swim to escape observation (Bennett and Sebastian, 1988; Kawabe and Mano, 1972; Kern, 1964). Although N. larvatus was occasionally seen on muddy flats at low tide, it is reported that terrestrial locomotion is relatively rare in the mangrove swamps (ibid.) However, terrestrial locomotion was much more common on the floor of the riparian forests, where N. larvatus apparently foraged for food (Kawabe and Mano, 1972).

The habits and habitat of the golden monkey Pygathrix (Rhinopithecus) roxellanae are poorly known. It appears to be restricted to high altitude (3350-4000 m) dense conifer forests in the mountains of Thibet and the Yunnan Province, China (Li et al., 1982). The structure of these forests are reportedly simple with the top of the canopy between 40-75 m high, dense stands of bamboo undergrowth and a carpet of moss on the forest floor. Apparently P. roxellanae spends most of its time in the canopy where it is very nimble. It feeds on conifer needles and hanging moss for most of the year, but also eats the shoots of the underlying bamboo when they are available (Li et al., 1982).

Pygathrix (Pygathrix) nemaeus is equally poorly known. Gochfeld (1974) reported on some animals which he observed at an altitude of 696 m in South Viet Nam. He watched two groups feeding in the canopies of trees, which he said they inhabited, and noted that they rarely came to the ground. Lippold (1977) reported their presence in heavily forested areas of primary and secondary growth. P. nemaeus was occasionally seen on the ground raiding crops. The douc langur appears, however, to be

primarily arboreal.

Summary

Table 8 summarizes the distribution of cercopithecoid species in their respective habitats as well as their likely emphasized locomotor behaviors. Four conclusions can be drawn from the material presented above and summarized in Table 8. First, species which dwell exclusively in the lower canopy and undergrowth (P. verus, M. talapoin, C. cephus) rarely or never descend to the ground. This initially may seem a paradox, since these are the species which are closest to the ground. However, at least in the cases of P. verus and C. cephus, these animals are extremely reclusive and the density of the undergrowth provides them with the optimal conditions for avoiding disturbance. Given the nature of their habitat (small branch setting, tangled vines) it is likely that their locomotor modes emphasize stealthy and cautious quadrupedalism as well as climbing, activities which require a secure grasp as well as strength.

Second, with the exception of C. albigena, most species that inhabit the lower to middle layers of the forest show little reluctance to descend to the ground. These lower to middle layers of the forest canopy contain numerous gaps that require either agility in order to cross them by leaping, or necessitate descent to the ground to reach another tree. The same agility which facilitates leaping across gaps must translate into an ability to move across open stretches of the ground, at speeds which are possibly unfamiliar to the more stealthy species restricted to

the undergrowth. In the case of colobines, their propensity to leaping in an arboreal milieu apparently predisposes them to bounding and hopping when on the ground. It seems likely that the species which preferentially occupy the middle layers of the forest canopy would show the greatest diversity in locomotor behaviors, as well as the greatest ability to leap across gaps.

Third, the species which occupy the upper layer of the canopy, where supports are continuous, have less need to cross gaps by leaping. Presumably, they also have less need to descend to the ground because of the continuity of pathways. As a consequence, arboreal quadrupedalism and some climbing would most likely be the primary locomotor behaviors. While this may seem odd for P. badius, who has been reported to make spectacular leaps, it appears reasonable in light of Struhsaker's (1975) observation that it is also one of the clumsiest leapers he had witnessed.

Fourth, the baboons, T. gelada and E. patas, which spend the majority of their time on the ground, would be expected to show adaptations for cursoriality, as would S. entellus.

Table 7. Frequencies of locomotor modes during travel and feeding.
Sources in text. quad w/r, quadrupedal walking and running; leap,
leaping; hop, hopping; climb, climbing; armswing, armswinging.

Species	quad w/r	leap	hop	climb	armswing
<u>C. quereza</u>					
travel	42.1%	34.5%	4.5%	17.6%	1.3%
feeding	48.4%	15.4%	-	36.2%	<0.1%
<u>P. melalophos</u>					
travel	20.7%	42.5%	25.0%	8.4%	3.4%
feeding	35.5%	10.6%	20.9%	30.1%	.9%
<u>P. rubicunda</u>					
travel	32.0%	45.0%	2.5%	10.0%	2.0%
feeding	51.0%	12.0%	2.0%	22.0%	5.0%
<u>S. obscura</u>					
travel	50.6%	40.2%	-	9.2%	-
feeding	68.6%	15.0%	-	16.4%	-
<u>H. fascicularis</u>					
travel	65.2%	10.8%	-	5.4%	-
feeding	74.0%	3.6%	-	8.8%	-
<u>C. aethiops</u>					
locomotion	53.9%	9.6%	-	29.5%	-

Table 8. Species classification according to habitat use and predicted emphasized locomotor behavior.

Species	Habitat Preference	Emphasized Behaviors
<i>S. entellus</i>	Ground to middle canopy; spends 50% time on ground.	Terrestrial and arboreal quadrupedalism, bounding
<i>P. frontata</i>		
<i>P. hosei</i>		
<i>P. melalophos</i>	Primarily middle canopy	Leaping, hopping, climbing,
<i>P. rubicunda</i>	dwellers; will descend to	terrestrial and arboreal
<i>P. aygula</i>	ground to raid crops, feed	quadrupedalism, bounding
<i>C. polykomos</i>	on earth or move between	
<i>C. angolensis</i>	patches of trees	
<i>C. guereza</i>		
<i>C. satana</i>		
<i>C. vellerosus</i>		
<i>H. larvatus</i>		
<i>S. cristata</i>		
<i>S. obscura</i>	Upper canopy; generally do	Arboreal quadrupedalism
<i>P. badius</i>	not descend to ground, but	and leaping on large branches
<i>P. nanaeus</i>	depends upon situation.	
<i>P. roxellanae</i>		
<i>P. verus</i>	Lower canopy; never descends to ground.	Climbing and arboreal quadrupedalism on small branches

Table 8. (cont.)

Species	Habitat Preference	Emphasized Behaviors
<i>E. patas</i>	savanna	Terrestrial quadrupedalism
<i>C. pygerythrus</i>	savanna and forest edge	Semi-terrestrial quadrupedalism, leaping, climbing
<i>C. ascanius</i>	dense vegetation of secondary	Arboreal quadrupedalism and climbing
<i>C. nona</i>	forest or various forest types;	
<i>C. mitis</i>	lower to middle strata;	
<i>C. albogularis</i>	where known will descend to	
<i>C. petaurista</i>	ground	
<i>C. campbelli</i>		
<i>C. nictitans</i>	open vegetation of mature forest;	Arboreal quadrupedalism and leaping
<i>C. pogonias</i>	middle to upper strata; where known rarely descends to ground	
<i>H. talapoin</i>	dense vegetation of forest edge;	Stealthy quadrupedalism and climbing
<i>C. cephus</i>	lower stratum; rarely descends to ground	

Table 8. (cont.)

Species	Habitat Preference	Emphasized Behaviors
<i>P. gelada</i>		
<i>P. hanadryas</i>	Primarily terrestrial	Terrestrial quadrupedalism
<i>P. ursinus</i>		
<i>P. anubis</i>		
<i>P. cynocephalus</i>	Primarily terrestrial but	
<i>P. sphinx</i>	do use trees for feeding	Terrestrial quadrupedalism
<i>P. leucophaeus</i>	and sleeping	and some climbing
<i>C. galeritus</i>		
<i>C. torquatus</i>		
<i>H. sylvanus</i>	Canopy level uncertain but	Terrestrial quadrupedalism
<i>H. thibetana?</i>	spend much time on ground	and more climbing
<i>H. arctoides</i>		
<i>H. nenestrina</i>		
<i>H. fascicularis</i>	Canopy level variable;	
<i>H. mulatta</i>	primarily arboreal but will	Arboreal quadrupedalism
<i>H. fuscata</i>	descend to ground	and more climbing
<i>H. nigra</i>		
<i>H. assanensis</i>		
<i>H. tonkeana</i>		
<i>C. albigena</i>	Mature forest; middle stratum;	Arboreal quadrupedalism
	rarely descends to ground	and much climbing

Chapter 4. BIOMECHANICS AND GAIT ANALYSIS

Introduction

It follows from the last chapter that the cercopithecoid positional repertoire includes standing, sitting, quadrupedal arboreal and terrestrial walking, trotting, galloping and bounding, climbing as well as bipedal hopping and leaping. Generalized biomechanical descriptions are presented below for the actions of the hindlimb and its segments during standing and sitting and three of these locomotor modes, quadrupedalism, leaping and climbing. The description for the relative positions of the hindlimb and its segments for standing are taken from Jolly (1965) and for sitting from Rose (1974). The positions of the hindlimb, its segments, and the actions of muscles in quadrupedalism is based on a variety of sources, including Muybridge (1899), Manter (1938), Jolly (1965), Grand (1968), Stern (1971), Fleagle (1977a,b), Kimura et al. (1979), Jungers et al. (1983) and Dykyj (1988). The biomechanical description for leaping is based on Wells et al.'s (1977) description of a vertical leap in C. sabaeus with some modifications taken from the publications of Fleagle (1977a,b) on the leaps of P. melalophos. The very brief description of climbing is taken from Sarmiento (1985, pers. comm.). These biomechanical descriptions are followed by some predictions of which morphological features should be altered to optimize cursoriality and leaping. The chapter is concluded with a summary of previous work correlating specific morphological features with arboreal quadrupedalism, terrestrial cursoriality, leaping and climbing in

several cercopithecoid species.

Posture

Standing.

In arboreal quadrupedal standing the long axis of the body is parallel to the substrate and the body weight is borne partially by the forelimbs and partially by the hindlimbs. Because the center of gravity is typically caudally positioned (Kimura et al., 1979; Rollinson and Martin, 1981) up to 60% of the body's weight is taken by the hindlimbs. Jolly (1965) described the limbs during standing as nearly fully extended and oriented at 90° to the body. The forearms are held in a neutral position with the volar surface of the hands facing medially and grasping the branch. The foot is slightly inverted and engaged in a hallux grip so that the lateral digits are appressed to the outside of the branch, the web between the hallux and lateral digits is on top of the branch, and the hallux is appressed to the inner side of the branch. Because the limbs are strongly extended, with no passive "locking" mechanism to hold them in this position, they can be easily upset or knocked out of equilibrium. Grasping is likely to be important in this position. In addition, one or another limb will periodically act as a lever to maintain balance via the forces exerted by the extrinsic musculature around it. This is especially critical in branch-standing since the transverse base of support can be very narrow. As a consequence, the weight-line of the body can be easily displaced out of the base of support. Forces not only act on the limb as a whole but also upon the

major segments of the limbs. In the hindlimb, these tend to flex the knee and ankle and must be resisted by the action of intrinsic muscles.

Terrestrial quadrupedal standing is not so precarious as branch-standing because a wider base of support is possible. If instability should occur, one or another limb can be shifted appropriately so that a new quadrilateral base of support is defined which encloses the center of gravity. Additionally, the foot is not inverted in terrestrial standing, but is flat on the ground and the hallux performs no special function against the other digits.

Tripedal standing, which is generally part of feeding behavior, involves supporting the body's weight within a triangle defined by the hindfeet and one of the forefeet. Tripedal standing is practically as stable a posture as quadrupedal standing and again involves the limbs acting as struts. The major difference is that each limb bears more of the body's weight than in quadrupedal standing and may be more extended.

Bipedal standing is the most precarious standing posture for monkeys since their center of gravity must stay along a narrow line of support and is very easily shifted off of the line. The hindlimbs must bear a greater porportion of the body's weight than in quadrupedal standing. This posture is most easily maintained when some assistance in balancing is possible by grasping nearby branches or bushes.

Sitting.

Rose (1974) described the variations in sitting postures in Old World monkeys and the following is taken from his work. Essentially all

cercopithecids sit in a fairly characteristic manner, especially in the small-branch setting. Animals can sit either along or across a branch. In the former position they generally try to form a stable triangular support base using the ischial callosities and the two hindfeet. The trunk is always flexed and inclined forward to bring the center of gravity well within the support base. The hindlimbs are generally abducted at the hip. On especially large branches colobines typically extend their legs forward or let them hang on either side of the branch whereas cercopithecines usually flex their hindlimbs. The feet are either applied in a plantigrade manner to the branch or they engage in a hallux-grip to assist in maintaining stability.

If the branches are too small for an animal to maintain contact with its ischial callosities an across-branch posture is assumed. In this posture, cercopithecids grip the branches with the lateral digits atop and the hallux below. The trunk is strongly flexed so that the animal leans over the branches and the rump is generally held level with the branch or below it. In this posture, the foot is subjected to more compressive forces than is typical in sitting. However, if an animal has its foot propped up while sitting along a branch then the foot will also be subjected to some tensile forces.

Quadrupedal Gait Cycle

The use of the limbs during a cycle of quadrupedal walking is subdivided into two phases: the stance phase and swing phase (Fig. 1). The stance phase is that portion of the gait cycle when contact is made

with the substrate and weight is supported by the foot. The swing phase is that portion of the cycle when the foot is off the substrate and being repositioned for the next stance phase. As a heuristic device, and by analogy to the human gait cycle (Dykyj, 1988), the stance phase in quadrupedal walking is here further subdivided into three periods during which the foot is initially loaded (contact), supporting the weight of the animal (midstance) or pushing off (propulsive). A complete cycle consists of both limbs of a pair engaging in stance and swing phases. Figure 2 illustrates the probable relative positions of the hindlimb segments during a stride. Part A of Figure 2 was taken from Fleagle (1977a) and was the basis of the schematic diagram of the hindlimb segments in Part B. The relative positions of the segments were estimated by measuring the angles between the major segments in Part A, relative to a reference vertical line dropped from the likely position of the hip joint to the ground.

Stance Phase.

The contact period of stance phase in the hindlimb is initiated by heel strike when the dorsiflexed foot is lowered to the ground (Fig. 1). It is apparent in Figure 1 that at heel strike the foot is positioned anterior to the estimated center of gravity of the body. The center of gravity is passing from a position posterior to the foot to one directly over the foot. When the center of gravity is in line with the foot the midstance period begins. Midstance is initiated when the heel is lifted from the ground and the alternate foot begins its swing phase. As the

center of gravity continues to move anteriorly, the support of body weight is shifted distally in the foot and the complete sole lifts from the ground. Total lifting of the sole marks the beginning of the propulsive period. It should be noted that the terms "heel lift" and "forefoot loaded" are taken from the literature on the human gait cycle (Dykyj, 1988). In humans, the forefoot is loaded at the beginning of midstance and heel-lift marks the beginning of the propulsive phase. These terms have been reversed here since it is a more accurate description of the the postures of the foot during a cercopithecoid quadrupedal stride, given the illustrations by Muybridge (1899) and Fleagle (1977a). Additional evidence for heel-lift marking the beginning of midstance in cercopithecoids is provided by electrical activity in m. gastrocnemius early in the stance phase (Kimura et al., 1979), the carrying angle of the distal calcaneus (Gebo, 1989) and experimental analyses of elastic strain energy storage in the plantar ligaments of cercopithecoid feet, which showed a "reversed arch" during walking (Bennett et al., 1989). Thus, in cercopithecoids, midstance apparently begins with the calcaneus being lifted and the propulsive period begins when the foot is lifted onto the metatarsophalangeal joints. During the propulsive period, support of body weight is shifted completely to over the toes and this period ends when the toes are lifted from the substrate. Simultaneously, the alternate swing phase limb has made contact with the substrate to begin its stance phase.

At the end of swing phase the hip is strongly flexed, the knee is somewhat less strongly flexed, the ankle is dorsiflexed and the hindlimb

is anterior to the center of gravity (Figs. 1 and 2). During much of stance phase the weight-supporting hindlimb acts as a strut between the body as it moves forward over the foot and the substrate. In the stance phase hindlimb, motion occurs at the hip joint, knee joint, upper ankle joint and intrinsic joints of the foot (Fig. 2). At the hip joint the major movement is thigh extension. At the knee joint the major motions are first flexion and then extension of the leg. At the upper ankle joint the major motions are dorsiflexion followed by plantarflexion of the foot. Complex movements also occur within the foot, as discussed below.

During the contact period of stance phase the body moves over the hindlimb primarily as a function of its kinetic energy. Thus, most muscular activity in the hindlimb during contact is involved with stabilization of the joints. The hamstring and gluteal muscles are in an anatomical position to decelerate flexion of the hip joint and provide stabilization until partial support of body weight by the hindlimb is achieved at midstance (Fig. 2). The dorsiflexors of the upper ankle joint, *mm. tibialis anterior* and *extensor digitorum longus*, are also positioned to decelerate the foot while it is being lowered to the ground (Fig. 2). The plantarflexors of the upper ankle joint are activated at the end of the contact period to resist the passive dorsiflexion that occurs when the momentum of the body carries the leg over the lowered and fixed foot. Within the foot, there is progressive loading of the foot distally, from heel strike to full foot support. This loading, plus the muscular activity around the upper ankle joint, causes

pronation of the forefoot. The pronated position of the foot is a flexible, rather than stable, position. Flexibility allows the foot to adapt to the substrate's surface, to function in shock absorption, and to store elastic strain energy.

By analogy to the human gait, it is likely that at midstance, because the opposite limb is in swing phase, the adductors of the stance phase hip internally rotate the swing phase pelvis to stabilize it, using the stance phase hip as the pivot (fig. 4.1). As a reaction to the hip being used as a pivot, the hindlimb externally rotates in all of its segments to the ankle. The movement of the body forward over the fixed foot causes the ankle to passively dorsiflex. These movements are resisted by the triceps surae and hamstring muscles. Additionally, once the leg passes beneath the acetabulum, the hamstrings are activated to help extend the thigh and flex the knee (Fig. 2). During the contact period the plantarflexors had acted as antagonistic muscles in decelerating pronation of the foot. In midstance these muscles become prime movers and supinate the foot into the close-packed position of the tarsus. The action of the plantarflexors during supination also contributes to external rotation of the leg and thigh. As the midstance period progresses the foot is prepared to load more distally. This involves stabilizing the distal tarsals by the synergistic action of m. tibialis posterior (the strongest invertor of the foot) and the peronei (evertors of the foot). The plantarflexing and everting potential of m. peroneus longus is resisted by the action of the posterior crural compartment muscles which maintain pressure on the lateral border of the

foot. As a consequence, the cuboid is held in a fixed position to act as a pulley for the tendon of m. peroneus longus. M. peroneus longus produces a force which presses the distal tarsals against each other, as well as, in arboreal forms, pressing the head of the first metatarsal against the substrate.

The propulsive period begins when most of the body's mass is over the metatarsophalangeal joints. Extension of the hip is likely effected by the hamstrings while extension of the knee is likely effected by m. quadriceps femoris. Plantarflexion of the ankle is a result of complex interactions between body momentum and resistance by the plantarflexors to dorsiflexion at the upper ankle joint. During the propulsive period the foot continues to be plantarflexed and body weight is shifted totally anteriorly onto the metatarsal heads. The metatarsal heads form the fulcrum for the foot which is acting as a second-order lever. The extensor digitorum longus and hallucal extensor tendons terminate in extensor tendons which stretch around the metatarsophalangeal joints and insert on the medial and distal phalanges. The long extensor and flexor muscles of the toes are likely to synergistically act to brace the toes against the substrate, thus stabilizing the fulcrum. However, the metatarsals and phalanges do not form the most stable arrangement for weight bearing. This is not a significant problem because by the end of the propulsive period, much of the body weight is shared by the opposite foot which has begun its own stance phase (Fig. 1). The stance phase terminates when the toes are lifted from the ground.

Swing Phase.

At the end of stance phase the hip is extended, the knee is partially extended, and the hindlimb is completely posterior to the acetabulum. During swing phase the limb must be repositioned anteriorly to complete the gait cycle. To effect this repositioning, motion occurs around the hip joint, knee joint and upper ankle joint. At the hip joint the thigh is simply flexed. At the knee joint, however, movement is somewhat more complex. The knee must first flex to clear the foot from the substrate (Fig. 2). Secondly, the knee must extend to position the foot anterior to the center of gravity for contact with the substrate. Third, the hip must extend again to decelerate its flexion and to bring the heel into contact with the substrate. During swing phase the upper ankle joint is dorsiflexed and the foot is carried forward by the leg.

The primary accelerator of thigh flexion at the beginning of swing phase is probably mm. iliopsoas and quadriceps femoris. During the majority of swing phase the momentum of the limb carries it forward so that muscular activity is unnecessary. Because the swing phase limb, by definition, loses contact with the substrate, it can no longer support body weight. As a consequence, body weight must be shifted to the stance phase limb. Furthermore, the swing phase hip itself is unsupported and will tend to tilt downward relative to a transverse axis. Because there is no external support for the swing phase limb, support has to be provided by muscular activity. This is probably provided by the m. erector spinae of the swing side and is assisted by the mm. gluteus medius and minimus of the stance side in lifting and leveling the swing

side hip. While the swing side hip is being stabilized about the transverse axis, it is also being rotated anteromedially about the sagittal axis. This is accomplished by the adductor muscles on the stance side pulling the pelvis medially, with rotation of the pelvis taking place around the stance side hip joint. Some assistance is probably provided by mm. gluteus medius and minimus and tensor fasciae latae on the swing side. This rotation should help to advance the swinging limb and to increase stride length.

During swing phase the leg is flexed around the knee joint, thus lifting the foot for clearance of the substrate. The movement of the leg forward is largely a function of the momentum produced by the thigh. Once the leg and foot clear the ground directly below the center of gravity, extension of the leg around the knee joint occurs (Fig. 2). Knee extension is achieved by the contraction of the quadriceps femoris group. M. quadriceps femoris is a group made up of four muscles. Three of these, the vasti, are one-joint muscles, while m. rectus femoris crosses two joints. As a consequence, m. quadriceps femoris acts in both hip flexion and knee extension. Towards the end of the swing phase, extension of the knee is decelerated by the hamstring muscles. The three hamstring muscles (mm. semimembranosus, semitendinosus and biceps femoris) are all two-joint muscles, taking origin from the ischial tuberosity and inserting on either side of the leg. They therefore function in both extending the thigh at the hip and flexing the leg at the knee. These actions combine to pull the leg back so that the foot can come down into contact with the substrate at heel strike, thus

terminating the swing phase. Because the hamstrings insert on either side of the leg they also function in stabilizing rotation at the knee joint.

During swing phase, the anterior compartment muscles of the leg function to clear the foot from the substrate by producing dorsiflexion at the upper ankle joint. The positions of the tendons of the anterior compartment muscles and their insertions, relative to the functional axes of the tarsus, affect the intrinsic postures of the foot. Thus, the dorsiflexors of the upper ankle joint secondarily produce the actions of inversion and eversion at the lower ankle joint and supination and pronation at the transverse tarsal joint. Swing phase reaches its conclusion when the foot is being positioned for heel strike. In humans, *m. tibialis anterior* is reportedly producing the strongest action at this time and therefore the foot is slightly supinated at contact. If this were also the case in arboreal monkeys, it would be advantageous for positioning the foot to grasp a branch.

At heel strike, the hip and knee joints tend to be flexed by the reaction force from the substrate. Resistance to this reaction is provided at the hip by the hamstrings and *m. gluteus maximus* and at the knee by the antagonistic muscular couple of *m. quadriceps femoris* and the hamstrings. Thus, at heel strike, the hip and knee are well stabilized for their subsequent role in weight bearing.

Arboreal versus terrestrial quadrupedalism.

The description presented above was for a quadrupedal stride on the

ground. Branch-walking differs from terrestrial walking in two regards. First, the base of support is narrower along a branch than on the ground. As a consequence, the center of gravity could more easily move outside of the base of support provided by a branch and lead to an animal falling. Cercopithecids reportedly deal with this by flexing their limbs to lower the center of gravity (Jolly, 1965; Rose, 1973). As a result, the knee joint is likely to be more flexed during the stance phase of a stride, as reported by Fleagle (1977a) for S. obscura (Fig. 2A), than is the case for the terrestrial baboons photographically documented by Muybridge (1899) (Fig. 1). Second, Jolly (1965) states that in branch-walking, during the propulsive period of the stance phase, the fulcrum of the foot is at the web between the hallux and lateral digits. He contrasts this with the position of the fulcrum at the lateral metatarsophalangeal joints in terrestrial cercopithecids. An important consequence of the position of the fulcrum is in the use of the hallux. In terrestrial walking the hallux is abducted in cercopithecids and does not contribute a propulsive boost during the final period of the stance phase, whereas in arboreal walking the hallux plays an important role in grasping the branch and securing the web of the fulcrum (Jolly, 1965).

Leaping

Rose (1973) defines leaping as differing from jumping or dropping in terms of the strength of the hindlimb thrust given at take-off while Horbeck (1976) describes leaping as similar to bounding in that the

hindlimbs work synchronously. Rose (1973) divides the leap into five stages: preparatory, take-off, flight, landing, and recovery. The following description of the relative positions of the segments of the body during the preparatory and take-off stages is taken from Wells et al. (1977). Wells and colleagues define a "take-off stage" that is equivalent to Rose's preparatory stage. These authors describe only the take-off stage of the vertical leap in C. sabaeus. All of Wells et al.'s (1977) observations were of vertical leaps that occurred at the termination of a run, from the ground to a tree.

Wells et al. (1977) divided the take-off stage of a leap into three different phases: lifting, transition and preparatory (Fig. 3). The lifting phase comprises approximately one-half the time of the take-off stage. At the initiation of lifting the direction of body momentum is horizontal. This direction must be changed to a more vertical one if the animal is to avoid running into the tree. Change in the direction of momentum is initiated in the lifting phase by extension of the trunk around the hip which produces a large decelerating force. During the transition phase, which comprises one-quarter the time of the take-off phase, the thigh takes on the more active role in translating the momentum from a horizontal direction to a vertical one. During the final preparatory phase, which again is one-quarter the time of the take-off phase, most of the body mass is in motion and the foot contributes a final impulse by plantarflexion.

While the trajectory of a leap is basically determined at the take-off, the movements of the body during the flight stage can affect the

trajectory of the leap (contra Wells et al., 1977). Because the limbs must be placed in positions for landing their movement, plus that of the tail, could effect the trajectory of the flight. Thus, the posture of an animal in flight (tucked versus splayed-out) will determine the relative effect of air drag, and consequently the speed of the flight, as well as the distance covered in flight. There has been no formal study of the cercopithecoid body during flight comparable to that of Wells et al. (1977) for take-off. However, some observations and illustrations are available in the literature from which to extract information as is also the case for landing and recovery.

It was reported in the last chapter that when cercopithecoids leap in the trees it is often from a fairly firm substrate, such as a medium-sized or large branch. Additionally, in colobines (and probably cercopithecines), the leaps are often part of a galloping or bounding sequence. Therefore, the leaps analysed by Wells et al. (1977) are probably reasonable representatives of those that would occur in the trees. Nevertheless, several differences might be expected between animals which habitually take-off from the ground and those that take-off from a branch. First, arboreal leapers may have to maintain contact with the substrate by actively grasping it. As a consequence, the phalanges will not be as hyperextended as those of a terrestrial animal at take-off. Secondly, Fleagle (1977a) illustrated the angular changes between segments in the hindlimb of Presbytis melalophos during the take-off stage of a leap (Fig. 4.4A). The sequence which Fleagle illustrated differs from that of Wells et al. (1977) in that (1) the knee

joint is not flexed as strongly during the transition phase in P. melalophos as in C. sabaeus, and (2) the knee joint is extended more strongly in P. melalophos during the preparatory phase than in C. sabaeus.

Figure 4 illustrates the relative positions of the hindlimb segments and some lumbar vertebrae during the take-off stage of a leap. Like Figure 2, the schematic diagram in Figure 4B was based on Figure 4A from Fleagle (1977a).

Lifting Phase.

In C. sabaeus the movement of the trunk about the hip joints during the lifting phase is very rapid. Wells et al. (1977) reported that it is the rapid movement of the trunk about the hip, followed by deceleration, which allows the translation of the body's momentum from horizontal to vertical during the subsequent transition phase. It is also likely that a part of the translation of the body's momentum is due to extension of the vertebral column itself, as suggested by the reports of Morbeck (1976) on the movement of the trunk in C. guereza and the documentation of vertical leaping in Galago senegalensis (Hall-Craggs, 1965). Furthermore, in the sequence illustrated in Figure 4B, trunk extension at the hip is not as rapid as reported by Wells et al. (1977). Nevertheless, in C. sabaeus, the main action at the hip is powerful extension of the trunk, until the termination of the lifting phase when the action becomes flexion. Two single joint muscles, mm. gluteus medius and minimus, are anatomically positioned to initiate powerful extension

of the trunk (Fig. 4B). Extensor action is then taken over by the two-joint hamstring muscles. In order for these muscles to extend the trunk, the knee must be fixed upon the thigh. Wells et al. (1977) stated that this fixation is effected by the architecture of the knee as well as the activation of the extensors of the knee. The knee extensors function as synergists (with the hamstrings) in retarding knee flexion and thus fix the knee, providing the thigh with a stable base.

Along with the leg, the foot is also providing a stable base of support against which rapid extension of the hip and trunk can occur. Wells et al. (1977) reported that for the majority of the lifting phase the displacement of the foot on the ground was minor. The major motion at the upper ankle joint is dorsiflexion, due to total body momentum carrying the animal over the fixed foot and to contraction of the extrinsic extensors of the foot (Wells et al., 1977). Wells et al. (1977) stated that, at this time, body weight was transferred directly to the ground through the astragalus and calcaneus.

Transition Phase.

The termination of the lifting phase, and the initiation of the transition phase, is marked by rapid deceleration of the extending trunk and lifting of the heel. The motion of the pelvic section, and the remaining upper body (all segments which are even more distal to the fixed point of the foot) is critical in translating the body's momentum from horizontal to vertical and forward. The pelvis continues to extend throughout the transition phase but its rate is slow due to the

decelerating action of the hip flexors. The more distal segments, such as the abdomen, are slower in responding to deceleration of the pelvis because of inertia, the high concentration of mass in the trunk and the flexible lumbar region of the vertebral column. Once the translation of motion from horizontal to vertical and forward has been achieved by the trunk, the hindlimb can engage in powerful extension for lift-off; powerful deceleration of the trunk leads to a sequence of segment extensions along the entire hindlimb. The muscles responsible for deceleration of the trunk include the single-joint muscle *m. iliopsoas* and the two-joint muscle *m. rectus femoris* (Fig. 4B). Because of its action on the knee as well as the hip, *m. rectus femoris* is especially important for coordinating the actions of the trunk and hindlimb.

Under the influence of *m. rectus femoris* and the remaining quadriceps group muscles (*mm. vasti*) the knee is powerfully extended (Fig. 4B). Powerful knee extension contributes to propelling the body, which is already in motion, along its new trajectory. Strong dorsiflexion of the ankle retards extension of the leg on the thigh. As a consequence the two-joint *m. rectus femoris* powerfully extends the thigh on the pelvis by acting against the stable base of support provided by the knee.

Dorsiflexion of the foot is powered in part by the momentum of the body but also, as mentioned above, by contraction of *mm. tibialis anterior* and *extensor digitorum longus*. Since *m. tibialis anterior* also functions as an invertor of the foot and *m. extensor digitorum longus* as an everter, these two muscles synergistically stabilize the tarsus. This

is especially important because as dorsiflexion occurs the lower ankle joint becomes everted, which is an unstable position for the tarsus. Wells et al. (1977) suggested that because of the inherent instability of eversion, inappropriate movements of the tarsus are probably guarded against by the simultaneous operation of many muscles in the foot.

Contraction of m. extensor digitorum longus not only dorsiflexes the ankle but also extends the lateral phalanges at the metatarsophalangeal joints. Thus, at the same time that distal transference of weight to over the metatarsophalangeal joint is occurring, the fulcrum is being braced by extension of the phalanges. By the end of the transition phase the upper ankle joint is close to a neutral position as plantarflexion of the upper ankle joint becomes more powerful and plantarflexion of the toes against the ground is effected. This plantarflexion increases the stability of the lateral metatarsophalangeal joints by additionally bracing the toes.

Preparatory Phase.

During the final, preparatory phase of take-off, the role of the ankle changes from one of stable support to one of actively contributing thrust to the body. By this stage of take-off, however, little of the body's weight is supported by the feet so that the contribution of ankle plantarflexion to the total body's momentum is minor. Indeed, the initial orientation of the body for the leap and the majority of the take-off force have already been accomplished.

For the first half of the preparatory phase the trunk continues to

decelerate on the pelvis. Prior to take-off this deceleration is reversed as extensors of the pelvis are activated. The extensors responsible for this motion are likely the two-joint hamstring muscles which are also acting to stabilize the knee through flexion and mm. gluteus medius and minimus. If the hamstrings were not acting on the knee joint while the ankle was undergoing powerful plantarflexion much of the thrust generated by the ankle would be dissipated as the thigh reacted by moving backwards and extending at the knee joint. Indeed, the knee joint is extending during the preparatory phase but is limited by the antagonistic action of the hamstrings. Furthermore, fixation of the knee permits the pulling momentum of the moving upper body to lift the lower limbs from their base of support.

Rapid plantarflexion of the ankle is effected primarily by mm. gastrocnemius, soleus, and plantaris. These muscles are likely the most important of any of the plantarflexors of the ankle because they have the most powerful lever arms. However, mm. flexor hallucis longus and flexor digitorum longus could also aid in plantarflexion due to their action in plantarflexing the extended phalanges.

Flight, Landing and Recovery.

The motions of the body that take place during the flight stage concern repositioning the limbs, so that the cheridia meet the substrate first, (Fig. 5) and controlling air drag. In small animals, where the ratio of surface area to body mass is great and the terminal velocity is low, deceleration due to air resistance occurs relatively quickly, so

that ample time is available to prepare for landing. In larger animals, the ratio between surface area and body mass is low and the terminal velocity is higher, so that positioning the limbs and tail to maximize air resistance may be important to increase the available time for preparing to land.

Mittermeier and Fleagle (1976) reported that C. quereza usually lands hindlimbs first, but also frequently lands on all four limbs simultaneously. The movements of the limb segments during flight illustrated by Mittermeier and Fleagle (1976; Fig. 5) are similar to those involved during the swing phase of a quadrupedal gait. In the hindlimb this involves flexing the hip and extending the knee and upper ankle joints to position the foot for grasping. Because C. quereza's landing sites are usually flexible (Mittermeier and Fleagle, 1976; Morbeck, 1976) the branches can absorb and dissipate much of the impact of landing. The recovery stage would likely be very variable, depending upon subsequent aspects of locomotion as well as the details of the landing site.

Climbing and Shinnying

Cartmill (1974), Bock and Winkler (1978) and Sarmiento (1985, 1989) have provided excellent discussions of the forces and movements of the limbs involved in vertical climbing in primates. The only detailed description of a cercopithecoid climbing is by Jolly (1965). Jolly describes the relative positions of the limb segments during ascent of a vertical support, as illustrated by Huxley (1899) for P. anubis. The

relative segment positions and the inferred muscular actions are similar to those described above for quadrupedal diagonal sequence, diagonal couplet symmetrical walking.

During shinnying (=bear climbing), as described by Sarmiento (1985; pers. comm.) there is contact between the substrate and most of the major segments of the body: the palmar surface of the hand and plantar surfaces of the foot are always in use and, occasionally, the ventral surfaces of the trunk, chin, arm, forearm, thigh and leg are employed. In shinnying, both lateral and dorsoventral spinal flexion and extension, as well as shoulder depression and elevation, are the major sources of motion and, therefore, propulsion (Sarmiento, pers. comm.). Lateral flexion of the spine pivots the shoulder and hip girdles toward each other and, depending upon the security of the hand- and foot-holds, a grasp by a contralateral member is released and regained further above. However, the extension of the extremities is limited, since this throws the animal off balance.

Factors which enhance speed during cursorial locomotion

A significant factor in increasing speed in locomotion is to change the gait used by an animal (Alexander and Maloiy, 1984; Vilensky, 1980). In cercopithecids this usually means a transition from walking to trotting, galloping and bounding (Rollinson and Martin, 1981; Alexander and Maloiy, 1984; Grand, 1976). Therefore, the foot falls are more asymmetrical at higher speeds in cercopithecids, which is essential for at least one of the adaptations for increasing speed described below

(spinal flexion/extension). Speed is the product of the length of the stride and the rate of the stride (Hildebrand, 1988) and therefore can be increased by altering either component. Indeed, increasing speed usually requires that both components are magnified. However, there is evidence that primates use lower stride frequencies at high speed than do non-primates (Alexander and Maloiy, 1984). The following discussion on factors which enhance speed during cursorial locomotion and on factors which enhance leaping is taken from Hildebrand (1988).

Stride length can be increased in four ways. The first way is to effectively elongate the limbs. Effective elongation can be achieved by: (a) increasing the length of the limbs relative to body size; (b) altering the posture of the foot from a plantigrade posture to a digitigrade or unguligrade one; or (c) reorienting the scapula on the thorax so that the pivot of forelimb lies further up the scapula from the shoulder joint.

The assumption of a digitigrade or unguligrade posture has repercussions for the weight-bearing role of the phalanges (Fig. 6; pers. comm. Sarmiento). In a plantigrade foot, body weight passes primarily from the leg through the upper (=talocrural) and lower (=subtalar) ankle joints to the ground, and the major function of the tension produced in the long flexor tendons is to maintain the integrity of the interphalangeal and metatarsophalangeal joints. Because the reaction force which must be resisted by the phalanges in this position is minimal, they can afford to have a relatively long lever arm. In a digitigrade or unguligrade foot, as illustrated in Fig. 6B,C, weight is no longer

transferred to the ground through the more robust proximal tarsal bones, but, instead, is passed to the ground through the metatarsus and phalanges. As a consequence, the reaction force which must be resisted by the phalanges has increased. Because the amount of tensile force in the long flexor tendons is limited, either the lever arm of the tendon around the metatarsophalangeal joint must increase, or the lever arm (phalangeal length) of the reaction force must decrease. This latter lever arm can be decreased by posture (Fig. 6B) and by shortening the toes (Fig. 6C).

The second way to increase stride length is to dorsoventrally flex and extend the vertebral column during the stride. Flexion and extension are synchronized with limb movement so that flexion occurs when the forelimbs are in contact with the ground and extension occurs when the hindlimbs contact the ground. During spinal flexion, the forelimbs prevent the rostral half of the body from moving backwards or decelerating so that the length the body shortens is added to stride length. Spinal extension occurs when the hindlimbs are in contact with the substrate. Hindlimb contact prevents the caudal half of the body decelerating so that the increase in length of the body due to spinal extension is added to stride length.

The third way to increase stride length is to include unsupported or suspended intervals in the stride. This is identical to changing the gait since galloping and bounding include periods of suspension. The fourth and final way to increase stride length is to alter the muscle mechanics by moving muscle insertions closer to the joints (Smith and

Savage, 1956). As a consequence, for a given contraction of a limb flexor, for instance, the distal end of the limb will move through a greater arc.

There are three likely ways to increase the rate of the stride in cercopithecids. The first is to move muscle insertions closer to joints. This altering of the muscle mechanics also affects the length of the stride, as indicated above. Shortening the in-lever arm of a muscle transforms a joint from a "low gear ratio" to a "high gear ratio" by altering the in-lever:out-lever ratio and thereby increasing the velocity of the bone or segment. Not only does a high gear ratio move a limb, for example, through the same distance as a low gear ratio but in less time, but "the muscle gains an important physiological advantage by doing the job without shortening as much" (Hildebrand, 1988:484). On the other hand, the transformation of lever arms into a high gear ratio means that force, or torque, is sacrificed.

The second way to increase the rate of the stride is to synchronize the movement of as many joints as possible in the limb in the same direction so as to sum the individual velocities they produce. Thus, the synchronization of spinal flexion and extension, along with the addition of an extra joint through digitigrady, lead to increasing velocity of the body. The velocity of a swing-phase limb is also increased by shortening the axis of the limb and thus reducing the period of its rotation around its proximal attachment.

The third way to increase the rate of the stride is to reduce the time spent by a limb in stance phase while maintaining a constant time

for the swing phase limb (Prost, 1965).

Theoretically, non-explosive cursors not only need to optimize speed but also their endurance. This is especially important for larger animals because the energetic cost of locomotion increases with speed and with mass. Endurance can be increased in three ways. The first is to reduce or eliminate as many oscillating motions as possible, since these require energy to control. Thus, the feet may not be lifted very high during the swing phase of a stride, the amount of dorsoventral flexion of the back is reduced so that the center of gravity undergoes less vertical displacement, and unsupported intervals of the stride are reduced, since these must follow vertical acceleration.

The second way to enhance endurance is to reduce the force that must be developed to reverse the direction of an oscillating limb. The force that must be developed is in proportion to the square of the angular velocity of the limb (kinetic energy of rotating limb equals $\frac{1}{2}I\omega^2$, where I is the moment of inertia of the limb, which increases with the length and distal mass of the limb, and where ω is the angular velocity). Therefore, the force needed to reverse the direction of a limb can be reduced by reducing the angular velocity of the limb. If the major muscle mass of a limb is close to the body it does not have to move so far. Therefore, the angular velocity of the proximal limb can be reduced.

The third way to enhance endurance, and thus reduce the cost of running, is by storing and releasing elastic strain energy. Elastic potential, or strain, energy equals $\frac{1}{2}kx^2$, where k is the restoring force

per unit displacement of the elastic material which is stretched and s is the amount of displacement. Because ligaments are elastic, the energy they acquire while they are deformed can be recovered when they are unloaded. Ker et al. (1987) have demonstrated that energy-saving springs exist in the tendons of mm. gastrocnemius, soleus and plantaris as well as in the ligaments of the longitudinal arch in humans. They calculated that 17% of the mechanical energy needed by a running human could be provided by the elastic energy stored in the ligaments of the longitudinal arch, while an impressive 35% could be provided by the energy stored in the tendons of the triceps surae muscles.

Factors which enhance Leaping

There are two parameters of a leap that can be optimized: the vertical height of the leap and the horizontal range of the leap. The height (h) to which any animal can jump depends upon the upward velocity at take-off ($h=v^2/2g$) and is a function of the acceleration (a) required to achieve this velocity ($v^2=a2d$). Since velocity depends the distance (d) through which the applied force acts, increasing d increases the height of the leap or jump. In a leaping animal, d is the vertical distance that the center of gravity is displaced in the time that the hindlimb, from its initial flexed position at the beginning of the leap, reaches its final extended position at the end of the leap (Figs. 3-4). Therefore, elongating the hindlimb increases d . The horizontal range of a leap depends, in part, upon the take-off velocity and the angle of take-off. Theoretically, the maximum range is achieved when the angle of

take-off is 45°.

Demes and Günther (1989) have recently developed a model which predicts the effect of size on the performance and proportions of leapers. Their model is useful in that it explicitly and formally presents the reasoning that lay behind much of the work done on leaping by previous authors (e.g., Hall-Craggs, 1965; Jouffroy and Gasc, 1974; Jouffroy and Lessertisseur, 1978; Schultz, 1963b). Demes and Günther (1989) demonstrated that in small animals, the time available for acceleration and the distance through which the body can be accelerated during take-off are short. As a consequence, small-bodied leapers must optimize the time available for acceleration as well as the distance through which the body can be accelerated. Demes and Günther (1989) suggested that small-bodied prosimians accomplish this in four ways: (1) increasing the angular excursions of the hindlimb joints; (2) altering the proportions of the skeletal lever arms for propulsive muscles, so that the power arms are short and the load arms are long; (3) elongating the hindlimbs, especially the distal segments; and, (4) adding an extra joint to the tarsus.

Demes and Günther (1989) also demonstrated that with increasing body size, the time available over which to accelerate the body is no longer a problem. Instead, because large animals have proportionately weaker muscles than small animals, they must optimize the use of their available muscle force. Demes and Günther (1989) suggested that large-bodied prosimians accomplish this in five ways: (1) acceleration in energetically profitable joint positions; (2) avoidance of acute joint

angles, especially at the distal joints where muscles work against the highest percentage of body mass; (3) moderate elongation of the hindlimbs with short distal segments; (4) long lever arms of the muscles that extend the hindlimb joints; and, (5) utilizing non-hindlimb muscles for acceleration, by swinging the arms (and extending the back).

If Demes and Günther's (1989) model is to have any generality, then their predictions should not be specific to prosimians but apply to other leaping forms as well. It is worth pointing out here, that while time for acceleration is indeed a limiting factor for small-bodied animals, small-bodied forms are relatively stronger than larger-bodied forms and therefore can achieve a higher velocity through a shorter distance than can large-bodied forms.

Morphological Correlates of Locomotion in Primates

Several studies have documented skeletal and muscular differences in closely related cercopithecoid species that are a function of differences in locomotor behavior. In particular, the studies of Jolly (1965), Fleagle (1977a,b), Rodman (1979) and Hurov (1987) stand out and were summarized below. Only those results which described specializations of the hindlimb were presented under the relevant locomotor mode.

Arboreal quadrupedalism.

Semnopithecus obscura was described in the last chapter as an arboreal quadruped which prefers walking along the large boughs in the continuous main canopy and emergent stratum. Fleagle (1977a,b) found a

number of morphological features in S. obscura that appear to enhance quadrupedal behaviors and which distinguish it from its close relative, the leaping P. melalophos.

In the hindlimb skeleton, S. obscura has relatively asymmetrical femoral condyles and an asymmetrical astragalar trochlea. The asymmetry of the femoral condyles suggests that the femur is habitually abducted and that excursion of the femur over the tibial platform involves some rotation of the femur about its long axis. Fleagle (1977b) argued that an abducted femur is expected in an arboreal quadruped since it contributes to a lowered center of gravity. He also suggested that abducted hindlimbs contribute to an inverted set of the foot, which was indicated by the trochlear asymmetry.

The muscular anatomy of the hindlimb in S. (Trachypithecus) obscura also showed some specializations for arboreal quadrupedalism. The m. biceps femoris had an extensive crural insertion, which would enhance its moment arm about the knee for flexion (Fleagle, 1977a). An extensive crural insertion may also indicate an advantageous lever arm for m. biceps femoris throughout a wide range of motion. The remaining, two-joint, hamstring muscles (mm. semitendinosus and semimembranosus) were well developed and also had distal insertions on the leg. The large size of these hamstrings suggested their importance in extending the thigh during the stance phase while their distally placed insertions on the leg increased their moment arms around the knee (Fleagle, 1977a). These large lever arms indicated the importance of knee flexion during the initial period of stance phase (Fleagle, 1977a). As mentioned above,

this would be expected in an arboreal, but not necessarily a terrestrial, quadruped. The m. quadratus femoris in S. (Trachypithecus) obscura has an extensive femoral insertion. This muscle was described by Fleagle (1977a) as being in an anatomical position to act as an extensor of the hip during the stance phase and as a decelerator of the thigh at the end of the swing phase. The large femoral insertion of m. quadratus femoris in S. (Trachypithecus) obscura should enhance the power of this muscle around the hip during its activity as an extensor. M. tensor fascia latae was well developed in S. (Trachypithecus) obscura and anatomically positioned to flex the thigh during the swing phase of a stride. The two-joint m. sartorius was also well developed in S. (Trachypithecus) obscura with an extensive crural insertion. It was in an anatomical position to flex and laterally rotate the thigh while also flexing and medially rotating the knee. Fleagle (1977a) suggested that this muscle might be important at the end of the stance phase and at the initiation of the swing phase.

Jolly (1965) documented two features in cercopithecines which are associated with arboreal quadrupedalism. The first was that in arboreal quadrupeds the limbs are short relative to body size. Jolly (1965) suggested that this would be advantageous to an arboreal animal since it lowers the center of gravity. He further argued that for arboreal cercopithecids, which walk above branches, lowering the center of gravity is the major option available to maintain stability because they cannot broaden their support base to minimize displacement of the body's weight line. Arboreal cercopithecines also had a narrower pelvis than did

terrestrial or semiterrestrial forms. Jolly (1965) also interpreted this as an adaptation for minimizing displacement of the body's mass out of the narrow support base.

Terrestrial Quadrupedalism.

Rodman (1979) postulated that Macaca nemestrina, as a terrestrial quadruped, should be adapted to a more efficient mode of locomotion than the more arboreal M. fascicularis. As described in the last chapter, M. nemestrina is larger than M. fascicularis and travels further between food sources. Given the reasoning developed above about the cost of large body size in locomotion, one would predict that efficiency should be maximized. Cursorial adaptations which increase stride length would produce more efficient locomotion. This is because each stride is associated with vertical and transverse movements, and by increasing the distance travelled per stride the number of oscillations of the body, per distance travelled, is decreased. Rodman (1979) documented that M. nemestrina indeed had such cursorial adaptations relative to M. fascicularis. The limbs are expected to be relatively longer in a cursorially adapted animal and, indeed, M. nemestrina had a higher brachial index than M. fascicularis. A higher brachial index not only means that the stride is lengthened but that the speed of the limb in swing phase is also increased. However, this distinction was not apparent for the crural index because the tibia was also increasing in length in M. fascicularis as an adaptation to leaping (see below).

Cursors are also expected to have relatively short in-lever rela-

tive to out-lever arms around joints which show a lot of excursion (e.g., elbow, shoulder, hip). This increases the speed of movement of the out-lever for a given muscle contraction. Rodman's (1979) predictions were borne out in the comparison of M. nemestrina and M. fascicularis. Macaca nemestrina had a relatively shorter trochanteric in-lever arm around the hip joint as well as a shorter ilium and ischium relative to femoral length. The mechanical effect of these are discussed below in the section on climbing adaptations.

Jolly (1965) also found longer limbs and a higher brachial index in terrestrial cercopithecines than in arboreal ones. Furthermore, he confirmed Pocock's (1925b) observation that terrestrial cercopithecines have shorter phalanges and a more reduced hallux than do arboreal cercopithecines. If terrestrial cercopithecids assumed a digitigrade posture of the foot, then for the reasons given above, it is reasonable to expect reduction in the length of the phalanges. Additionally, short phalanges are not as susceptible to bending stresses when they are extended, and weight-bearing, as would be the case for long phalanges. Furthermore, one might expect the paraxial phalanges to be reduced in a cursor, since this lightens the distal load of the limb (Hildebrand, 1988). Huybridge's (1877) photos illustrated, and Jolly (1965) observed, that the hallux was not used during the propulsive period of the stance phase in baboons. Therefore, it appears that there is a tendency in terrestrial cercopithecines to reduce the distal load of the limb by reducing the size of the hallux.

Bennett et al. (1989) have recently documented the role of the long

plantar and plantar calcaneocuboid ligaments as energy-saving springs in the feet of cercopithecoid monkeys. These authors calculated that, in trotting monkeys, 12.5% of the energy cost of half a stride is provided by the strained plantar ligaments and an additional 5% by the tendons of the triceps surae. This is most likely a significant savings in the energy cost of locomotion for monkeys.

Hurov (1987) compared the high-speed locomotor behavior and back anatomy of C. aethiops and E. patas. He documented that as galloping speed increased five-fold in C. aethiops, the range of sagittal back motion also increased. Increasing the amplitude of back motion directly translates into a longer stride length. In E. patas, which is practically twice the size of C. aethiops, there was no significant increase in the amplitude of sagittal back motion as galloping speed increased five to six-fold. This observation is in keeping with those made above about the effect of large body size in cursors. Large cursors are expected to reduce the amount of back movement in order to sustain their economy of motion or endurance.

Hurov (1987) also found significant differences in the anatomy of the axial skeleton between these two species. Cercopithecus aethiops has thicker intervertebral discs, relative to the vertebral bone, and a dorsoventrally smaller diameter of the thorax than does E. patas. The increase in pliant material within the vertebral column facilitated an increase in the range of back motion, while the dorsoventrally shallower thorax also enhanced back mobility. These anatomical specializations enabled C. aethiops to utilize high speeds when on the ground. Hurov

(1987) found that E. patas increased its stride length by virtue of longer forearms and legs (high brachial and crural indices) as well as by their long fore and hindlimbs relative to skeletal trunk length (Biegert and Maurer, 1972). Hurov noted that Wood (1973) found that the propulsive musculature of the hindlimb in E. patas was organized around the proximal limb joints to ensure the generation of large ground reaction forces, as well as to minimize rotary inertia during limb recovery. Additionally, Wood (1973) found that the pattern of hindlimb joint mobility was regulated within parasagittal planes, thereby reducing the deviations of limb segments from rectilinear motion.

Leaping.

Presbytis melalophos was described above as travelling more in the discontinuous understory and consequently engaging in more leaping than does the sympatric S. (Trachypithecus) obscura. Similar observations were made for P. rubicunda (Davies, 1984). Washburn (1942) described a number of differences in the proportions of the hindlimb which distinguished P. rubicunda from S. (Trachypithecus) cristata while Fleagle (1977a,b) described a number of features in the hindlimb which distinguished P. melalophos from S. (Trachypithecus) obscura. For the sake of convenience, and where relevant, the two Presbytis species and two S. (Trachypithecus) species will be discussed together.

In terms of skeletal anatomy, Presbytis had a lower intermembral index than did S. (Trachypithecus), indicating longer hindlimbs (Washburn, 1942; Fleagle, 1977b). Presbytis also had relatively longer feet,

due to elongated metatarsals (Washburn, 1942; Fleagle, 1977b). Longer hindlimbs enhance leaping by increasing the distance over which the animal's applied force acts, and thus increases the animal's velocity at take-off.

Fleagle (1977b) suggested that the hindlimb in P. melalophos was likely to be more adducted than in S. (Trachypithecus) obscura because the femoral head articular surface was extended onto the neck, the femoral condyles were symmetrical with a well developed lateral margin to the patellar groove, and the astragalar trochlea was symmetrical. The ischium was also relatively longer in P. rubicunda than S. (Trachypithecus) cristata (Washburn, 1942). As a result, the moment arm of the hamstrings around the hip joint, when the thigh is flexed, is longer. A longer moment arm in this position would provide powerful extension of the hip during leaping. Finally, Fleagle (1977a) reported that in P. melalophos the femoral neck is buttressed superiorly, and that the neck is set perpendicular to the femoral shaft. Fleagle (1977a) suggested that these differences assisted the femoral neck in withstanding the large bending forces generated in leaping.

The muscular anatomy also showed some specializations in P. melalophos compared to S. (Trachypithecus) obscura (Fleagle, 1977a). The femoral insertion of m. biceps femoris was relatively larger in P. melalophos, while the crural insertion was close to the knee joint (Fleagle, 1977a). Because the femoral portion of m. biceps femoris is the only hamstring muscle to insert on the femur, proximal to the center of rotation of the knee, it would be expected to be enlarged in a leap-

ing animal (Fleagle, 1977a). The remaining hamstrings, like the crural portion of *m. biceps femoris*, also flex the knee while extending the hip during leaping. In order to reduce the effect of these muscles on the knee during hip extension, the insertions of these muscles, in particular *m. semitendinosus* and *m. biceps femoris*, are close to the knee joint. Similarly, in *P. melalophos* the insertion of *mm. gracilis*, another two-joint muscle, was close to the knee (Fleagle, 1977a). The *mm. vasti*, which are major extensors of the knee, were very well developed in *P. melalophos* (Fleagle, 1977a). These muscles are not only important in extending the knee during a leap, but also must resist the action of the hamstrings which concomitantly flex the knee while extending the hip (Fleagle, 1977a). This latter function is probably less important than knee extension, if the hamstrings insert close to the knee joint.

Rodman (1979) also found some indication of leaping adaptations in *M. fascicularis*, which he described as engaging in more leaping than the sympatric *M. nemestrina*. Specifically, *M. fascicularis* had a lower intermembral index and a higher crural index, both features associated with increasing the length of the hindlimb, as described above.

Climbing.

Macaca fascicularis was described above as being one of the most arboreal macaques, and Rodman (1979) described it as engaging in much more climbing than *M. nemestrina*. Rodman (1979) identified a number of skeletal features which he interpreted as associated with climbing

behavior. Rodman's major prediction about the expected differences between a climber and nonclimber was that the former should have structural adaptations for power. In particular, the in-lever arms for propulsive muscles used in climbing should be large relative to their out-lever arms.

As described above, extension of the hip joint is, in part, effected by mm. gluteus minimus and medius, which arise from the surface of the ilium and pass backwards to insert on the major trochanter. The in-lever arm for these muscles can be increased by elongating the greater trochanter so that it projects above the femoral head or by reducing the length of the femur. Rodman (1979) found that the greater trochanter projected above the femoral head to a greater extent in M. fascicularis than it did in M. nemestrina. Similarly, the lesser trochanter, which provides attachment to the flexors of the hip (mm. iliacus, psoas major) was found to lie farther distal to the femoral head in M. fascicularis than in M. nemestrina. Macaca fascicularis was also found to have a relatively longer ilium. This increases the power of the two-joint muscles, mm. sartorius and tensor fascia latae, which flex the thigh and knee (Rodman, 1979). A long ilium also increases the power of the one-joint muscle, m. iliacus, a flexor of the thigh. Additionally, a long ilium stabilizes the back in climbing, by decreasing the the magnitude of the rotational forces around the lumbar joints that have to be counteracted by muscular forces (Sarmiento, 1985). Finally, Rodman found that H. fascicularis, like P. melalophos, had a long ischium relative to femoral length. This ratio increases the power of the

hamstrings to extend the hip.

Summary.

It has been amply demonstrated that cercopithecoid species which emphasize particular locomotor modes, such as terrestrial cursorial quadrupedalism or leaping, have altered the relations of relevant muscles and their lever arms to enhance these behaviors. It was also shown, in the preceding chapter, that large groups of cercopithecoid species, varying in body size, probably have similar locomotor profiles. It remains to be seen what effect body size has on the proportions of the musculoskeletal system in animals which apparently engage in similar behaviors. This topic is dealt with in the next chapter.

Figure 1. The main subdivisions of the gait cycle in Papio. H.S., heel strike; H.L., heel lift; F.F.L., forefoot loaded; T.O., toe off. (After Dykyj, 1988 and Jolly, 1965).

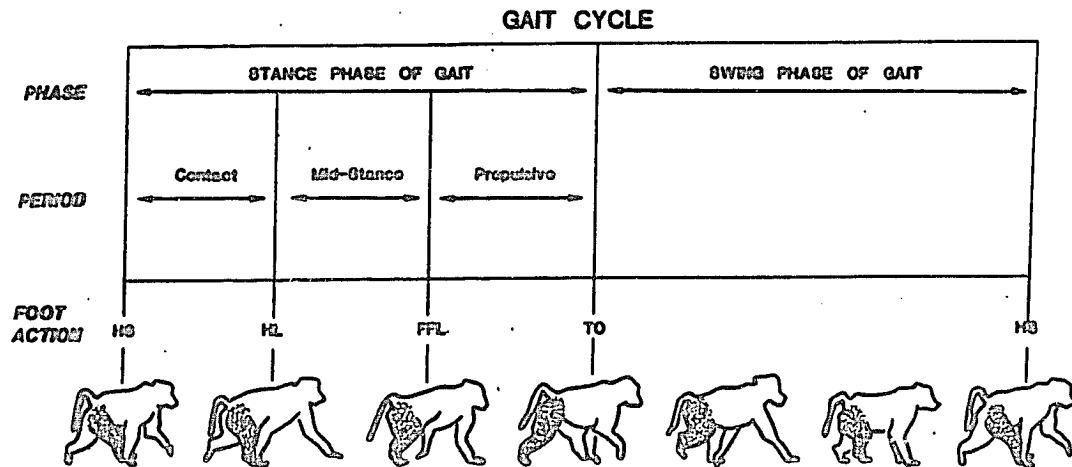


Figure 2. A. Angular changes in the main segments of the hindlimb during an arboreal diagonal sequence walk in *Trachypithecus obscura*. (Taken with permission from Fleagle, 1977a). B. Schematic diagram of angular changes in main segments of hindlimb, during a terrestrial diagonal sequence walk, based, in part, on A. g, mm. gluteus medius and minimus; h, hamstrings; e, long extensors of toes; t, triceps surae; q, m. quadriceps femoris.

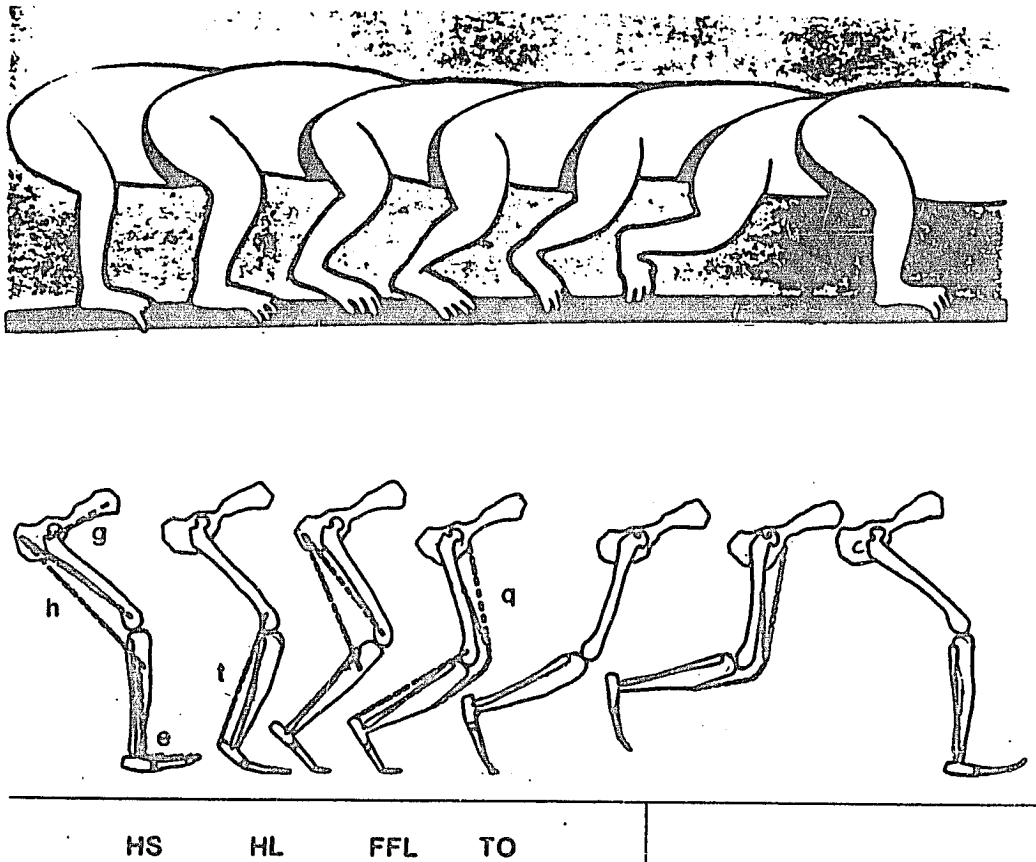


Figure 3. Angular changes in the main segments of the body during the take-off stage of a leap in *Cercopithecus sabaeus*. 1, forearm; 2, arm; 3, thorax; 4, abdomen; 5, pelvis; 6, thigh; 7, leg; 8, foot. (After Figure 2 in Wells et al., 1977).

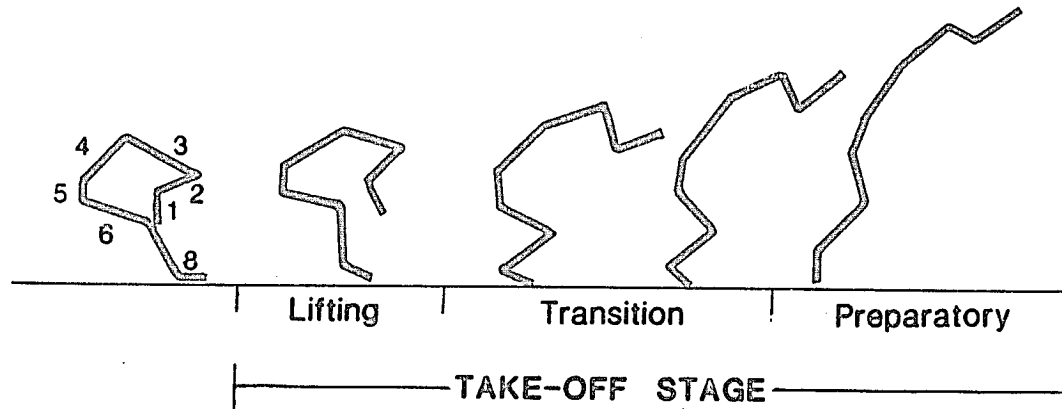


Figure 4. A. Angular changes in the main segments of the hindlimb during the take-off stage of a leap in Presbytis melalophos. (Modified, with permission, from Fleagle, 1977a). B. Schematic diagram of angular changes in main segments of hindlimb, based, in part, on A. g, mm. gluteus medius and minimus; h, hamstrings; s, short head biceps femoris; e, long extensors of toes; t, triceps surae; r, m. rectus femoris;

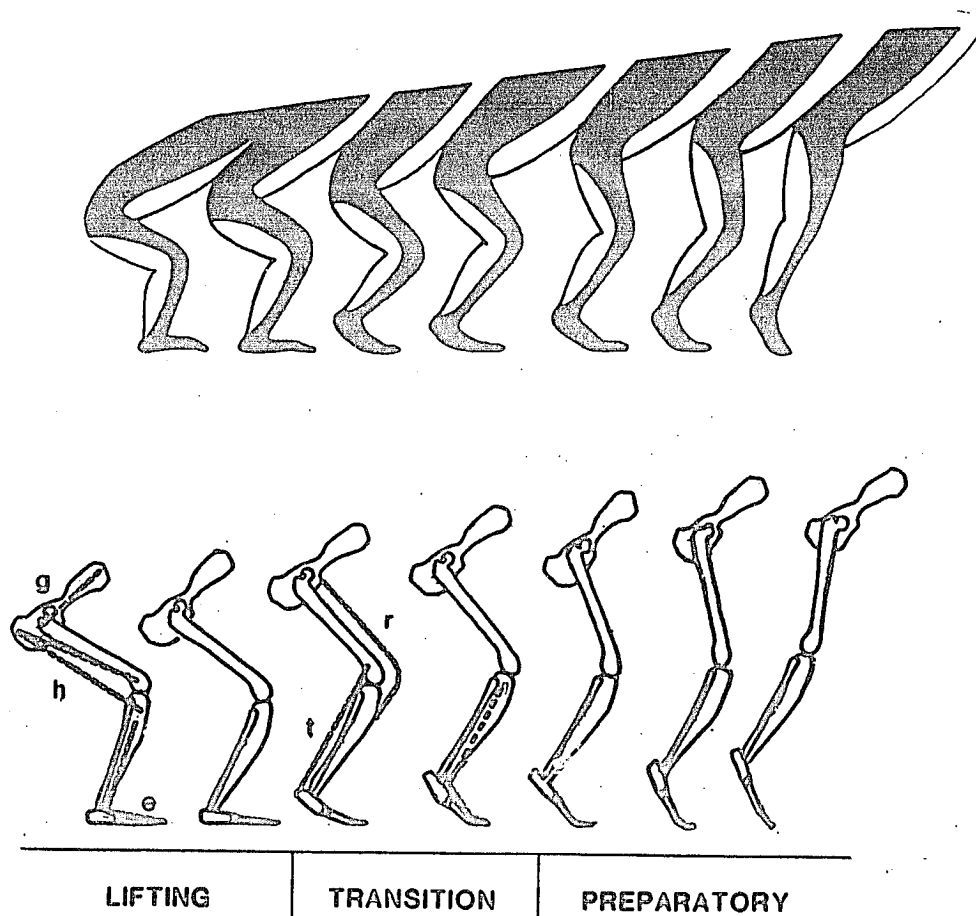


Figure 5. A typical leap sequence in Colobus guereza. (Taken, with permission, from Hittermeier and Fleagle, 1976).

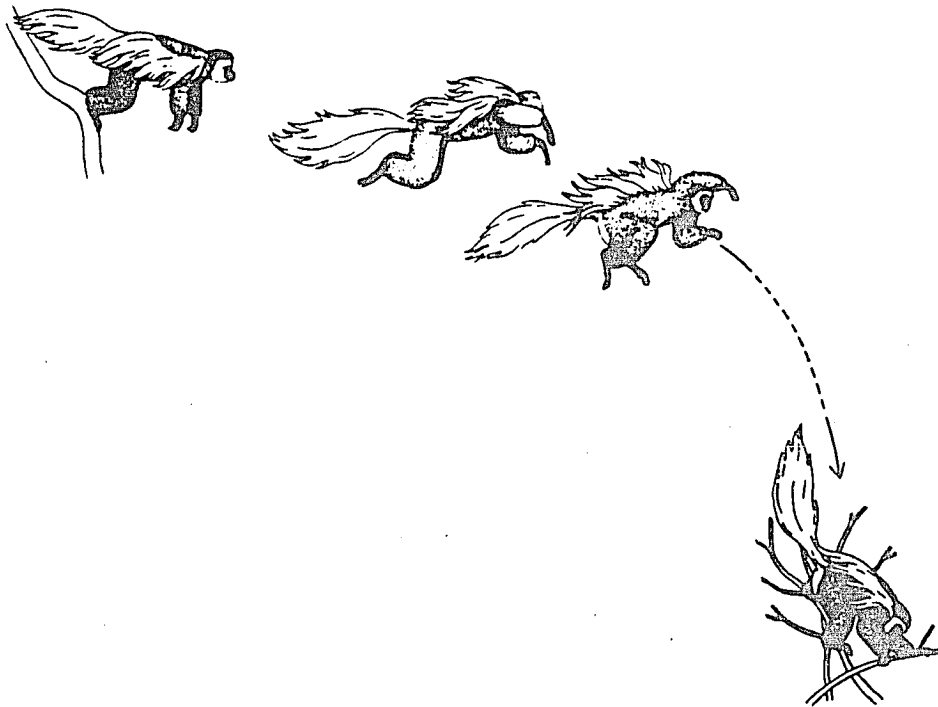
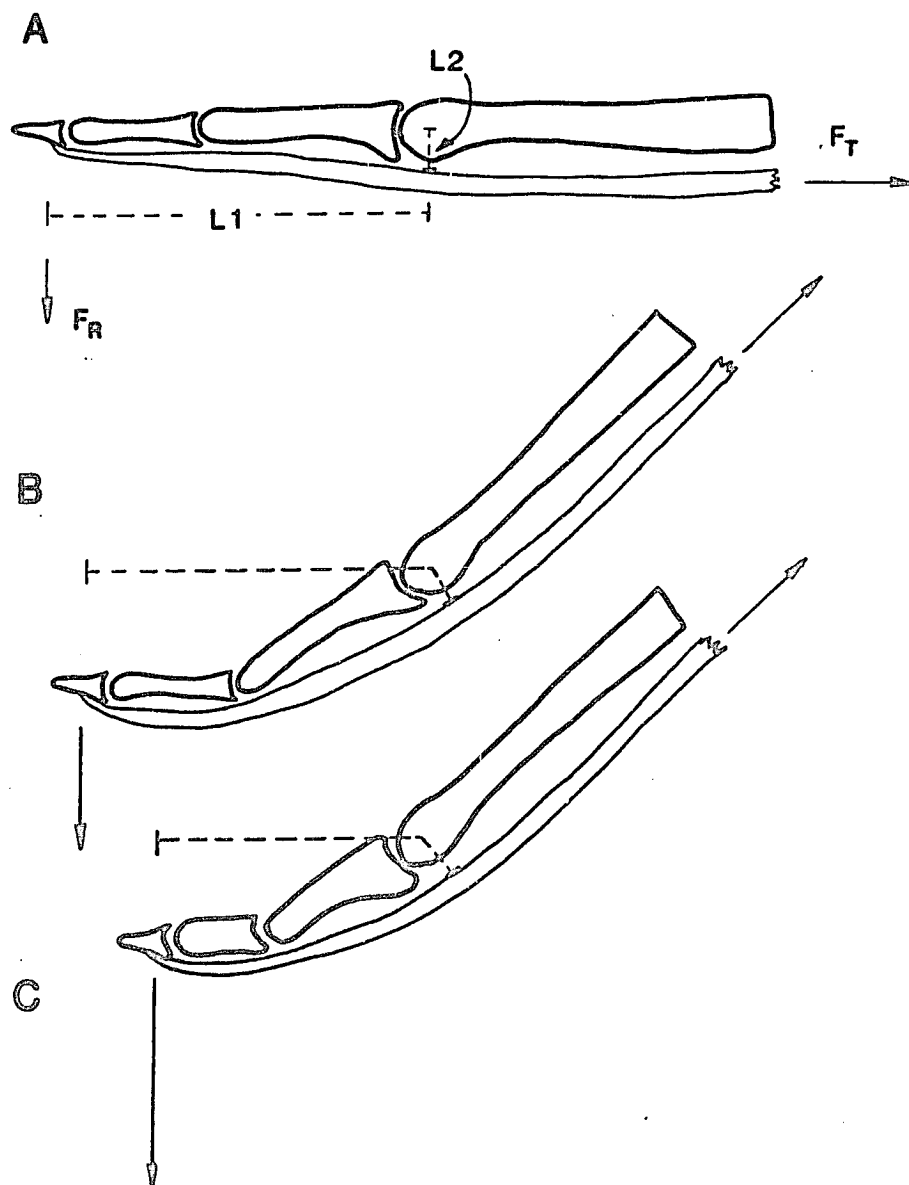


Figure 6. Schematic diagram of some forces operating around the metatarsophalangeal joint. A. Reaction force minimal at digital pads. B. Reaction force increase at digital pads when posture changes to dorsiflexion at proximal interphalangeal joint. C. Reaction force greater because of posture and short digits. F_T , tensile force of long flexor tendon; F_R , reaction force at digital pads; L1, lever arm for F_R ; L2, lever arm for F_T . Note that $F_R(L1) = F_T(L2)$.



Chapter 5. ALLOMETRIC CONSIDERATIONS

Introduction

The topic of this dissertation concerns the interpretation of cercopithecoid hindlimb and pedal indices, as well as the relative robusticity of the pedal rays. As discussed in Chapter 2, it is difficult to interpret many of the indices describing the shape of pedal segments in cercopithecoids. This is because many indices do not conform to functional segments of the foot, because it is impossible to tell from the value of the index which dimension is changing, and because many values appear to change with body mass. The most efficient way to interpret the value of indices is to examine the scaling of their constituent dimensions against body mass.

Recent years have witnessed an overwhelming demonstration of the pervasive effect of mass on the structural design of skeletal elements (see Gould, 1966 and Schmidt-Nielsen, 1984 for excellent reviews). Indeed, the impact of mass on the functional integrity of an organism is so profound that Gould (1966) and Schmidt-Nielsen (1984) argue the necessity of studying the effects of scaling for understanding the physiological and mechanical parameters of systems in a wide variety of organisms. To understand the effect of mass on the primate postcranium, it is imperative to have some biomechanical model of locomotion which provides the basis for predicting the effect of mass on the scaling of the dimensions. Otherwise, it is difficult to interpret the scaling exponents. Indeed, this is why the "engineering approach" has been

strongly advocated (Fleagle, 1985). Such an engineering approach has been successfully used in examining the proportions of a number of primate groups (Aiello, 1981; Burr et al., 1989; Dykyj, 1982; Jungers, 1978, 1979, 1985, 1988; Rodman, 1979; Ruff, 1988; Schaffler et al., 1985; Steudel, 1982a,b, 1984). A summary of some studies which examined the effect of scaling on the value of indices in the cercopithecoid postcranium is presented below, but it is worthwhile first briefly considering two models which are commonly used as null hypotheses for evaluating the effect of mass on dimensions.

Allometric Models

Geometric Similarity.

A series of different sized organisms are geometrically similar, or in isometry, if they are identical in shape. If a series of organisms are isometric, then the ratio of different dimensions, such as length or area to volume, will not be the same in smaller and larger organisms: the larger the organism, the smaller the ratio of its dimensions. It is well known that many physiological and mechanical functions are dependent upon length:area or area:volume relationships. As a consequence, those functions which are dependent upon a constant relationship between two dimensions cannot be equivalent in isometric organisms of different size. If an organism is to maintain the same function when it is built to a different size, its relevant dimensions must change non-geometrically (allometrically) so as to compensate for the overall size difference (Gould, 1966). The model of geometric similarity has tradi-

tionally been used as the null-hypothesis in biomechanical studies to evaluate the proportionate dimensions of the musculoskeletal system in a size-graded series of organisms. The geometric similarity model predicts that bone lengths and diameters should scale as mass to the one-third power and that cross-sectional areas of bones and muscles should scale as mass to the two-thirds power (Table 5.1).

The tensile strength of a muscle is a function of its cross-sectional area (Schmidt-Nielsen, 1984). The torque that a muscle can produce around a joint is a function of its size and lever arms around a joint. In an isometric series of related organisms, the length of the lever-arms scale to a lower exponent than do the cross-sectional areas of the muscles or body mass. As a consequence, the mechanical advantage of the lever arms of larger animals in an isometric series will be less than those of smaller animals, and therefore the larger animal will be relatively weaker. If a larger animal is to maintain the same mechanical advantage for its muscles as a smaller animal, either the ratio of its lever arms around joints must change or the size of its muscles must change. If the size of a muscle does not change, then one or both lever arms must scale allometrically with body mass in order to compensate for the changing ratio of muscle cross-sectional area and mass.

The ability of a bone to resist static, axially directed compressive stress (which is a function of body mass) is a function of its cross-sectional area. Therefore, in a geometrically similar series, larger animals will have bones with relatively smaller cross-sectional areas, which could fail due to compression. In order for bones to sup-

port larger body size their cross-sectional areas must increase in a positive allometric manner to compensate for the larger body mass. In fact, cross-sectional areas are expected to scale as body mass, yet this is not the case in animals (Gould, 1966; Schmidt-Nielsen, 1984). As a consequence, while larger animals do have more robust skeletons than smaller ones, their bones are not so robust as expected if they were scaled to resist static compressive stresses (McMahon, 1973; Schmidt-Nielsen, 1984). This failure of bones to have the proportions expected given a compressive stress model is due to the fact that this model is too simplistic (Scott, 1985). No long bones are loaded only centrically along their major axis. Aside from compressive loads, long bones are also subjected to bending moments that arise from eccentric loading. The consideration of bending moments has lead to the construction of an alternative similarity model, which considers the effects of forces other than static compression on the proportions of limbs.

Elastic Similarity.

The elastic similarity model was first proposed by McMahon (1973) to account for the effect of bending and buckling forces on the proportions of columnar structures such as tree trunks, branches and limb bones. The term "elastic" refers to the ability of materials to change their dimensions when under stress, but to regain their original shape when the stress is removed. When the elastic limit is reached, due to bending or lateral deflections, permanent deformation occurs, and when the elastic limit is exceeded, the structure breaks. Given this

relationship McMahon (1973, 1975a,b, 1984) has proposed that the major determinant of bone shape is its ability to withstand bending or buckling forces, which is a function of the elastic properties of its materials, as well as of its length and diameter. Furthermore, he suggested that as related animals increase in size, the dimensions of their bones will change so as to maintain the same elastic resistance to bending, buckling or torsional stresses. Specifically, given the modulus of elasticity for bone, McMahon (1973) suggested that bone lengths should scale as mass to the one-quarter power, diameters should scale as mass to the three-eighth power and cross-sectional areas should scale as mass to the three-quarter power (Table 5.1).

McMahon's model has stimulated a great deal of research on the scaling of limbs and locomotion in a variety of mammalian groups, because of the specificity of the predicted relationships. It is beyond the scope of this work to expand on the details of the biomechanical basis of the model, but the reader is referred to excellent discussions in McMahon (1973, 1975), Wainright et al. (1976), Currey (1984), Prange (1977) and Schmidt-Nielsen (1984). Some examples of its application to groups other than primates can be found in Alexander and colleagues (1977, 1979), Scott (1985) and Bou et al. (1987).

In summary, these two models, which predict the effect of size on bone proportions, differ in one significant way. The classic model of geometric similarity predicts exponents for the scaling of various dimensions with body size which are not expected to be seen for proportions which are the basis for a mechanical function. Therefore, these

exponents serve as a "criterion for subtraction" to determine the extent of change for maintaining mechanical similarity. In contrast, the model of elastic similarity predicts exponents which are expected in the scaling of bone dimensions with body size in order for mechanical similarity to be maintained.

Examples of the Effect of Size on the Proportions of Bones

Three indices of the limbs have traditionally been used to describe either taxonomic or locomotor assemblages of primates: the intermembral, brachial and crural indices. Biegert and Maurer's (1972) seminal paper, which included among other things, the correlation between body size and the value of the intermembral index, has stimulated a number of researchers to examine this relationship in greater detail. The success of researchers in interpreting the scaling exponents was directly linked to the structure of their analysis; i.e., predictions were based on biomechanical models (e.g., Jungers, 1985).

Intermembral Indices.

Until recently, most studies on the value of the intermembral index in primates used trunk length as the estimator of body size (e.g., Biegert and Maurer, 1972; Lumer and Schultz, 1941; Schultz, 1953). This is undoubtedly a valid measure of size for studies of closely related species, such as that conducted by Lumer and Schultz (1941) on M. mulatta and M. fascicularis or Jungers' (1979) work on lemurs and lorises. However, it is questionable when applied to a broad cross-

section of primates in which there is scaling of trunk length itself with body mass (e.g., Biegert and Maurer, 1972). Jolly (1965) was aware of this problem in his re-analysis of the limb proportions calculated by Mollison (1910), in which the denominator was trunk length. He circumvented it, to a certain extent, by restricting his analysis to species within Cercopithecini and Papionini (his Cercocellini). While his concern was not directly with allometry, his arrangement of species along an arboreal-terrestrial cline coincided with an increase in body mass. Because Jolly's results and conclusions were identical to those of Jungers (1985) (see below), who did perform a direct allometric analysis of limb proportions with body size, they were not separately reported here.

Because Biegert and Maurer (1972) used skeletal trunk length as the independent variable in their examination of relative limb proportions in catarrhines, there has been some question as to whether their results, which indicated that the intermembral index increased with body mass, were valid. Aiello (1981), Steudel (1982a,b) and Jungers (1985) have pursued this question in great detail by examining a large variety of primates.

Aiello (1981) reported that the positive allometry of the forelimb described by Biegert and Maurer (1972) was an artefact of the samples which they used in their analysis, as well as of their choice of skeletal trunk length as the independent variable. In her analysis of more homogeneous assemblages of primates, such as colobines and branch-walking cercopithecines or terrestrial cercopithecines, she found no

evidence for an increase in intermembral index with increasing body size. Instead, Aiello (1981) reported that limb lengths scaled isometrically with body mass in all cercopithecids. Aiello (1981) further argued that skeletal trunk length was not a reliable indicator of body size because it scaled isometrically with body mass in branchwalking cercopithecines and colobines and scaled negatively with body mass in terrestrial cercopithecines.

Steudel (1982a,b) also found that the fore- and hindlimbs, as represented by their proximal elements, scaled isometrically with body mass in cercopithecids. However, Steudel (1982a,b) also reported a consistent difference between colobines and cercopithecines in the elevation of their lines for the scaling of femoral and humeral lengths on body size. At comparable body sizes, colobines had higher values for the lengths of limb bones than did cercopithecines. Steudel interpreted the greater length of the femur relative to body size in colobines as an adaptation for increasing speed at the take-off of a leap. Steudel (1982a,b) interpreted the greater length of the femur as complementary to her earlier reported results (1981) of a significantly shorter ischium in colobines, compared to cercopithecines at comparable body sizes, which she interpreted as an adaptation to enhance acceleration at the beginning of a leap. However, Demes and Günther's (1989) model for leaping predicted that large leapers, such as colobines, need to enhance the power arms of muscles generating the force for a leap. The distance from the ischium to the acetabulum describes the power arm for the hamstrings around the hip. A shorter ischium would not enhance the power

arm of the hamstrings. Indeed, Washburn (1942) and Fleagle (1977b) both found that the ischium in the more frequently leaping Presbytis species was longer than the ischium in the less frequently leaping S.

(Trachypithecus) species. Steudel (1981) was aware of the contradictory nature of her data to what was predicted by theory, and suggested that the contradiction might be explained by the fact that colobines are often reported to run towards their take-off and do not leap vertically as do prosimian leapers.

Jungers (1985) came to a quite different conclusion from Aiello (1981) and Steudel (1982a,b). Jungers (1985) confirmed Biegert and Maurer's (1972) observation that the cercopithecoid intermembral index increased with increasing body size and reported that this was especially the case for colobines. Jungers (1985) found that, in cercopithecids, an increase in intermembral index with body size was the result of strong positive allometry of the forelimb coupled with strong negative allometry of the hindlimb. The strong positive allometry of the forelimb was due to the positive scaling of both humeral and radial elements with body mass. In colobines, the strong negative allometry of the hindlimb was due to both elements scaling negatively with body mass, but in cercopithecines only the tibia scaled negatively with body mass.

Jungers (1985) used two biomechanical models to explain the scaling of limb lengths with body mass in cercopithecids. First, Jungers (1985) argued that an increase in intermembral index with increasing body mass was to be expected, given the biomechanical principles related to climbing in clawless animals (see Cartmill, 1974; Jungers, 1977, 1978; Bock

and Winkler, 1978; and Sarmiento, 1985, 1988 for a fuller discussion of the principles related to climbing). Long forelimbs and short hindlimbs would increase the normal force of the feet against the vertical substrate, thus enhancing friction (Cartmill, 1974; Sarmiento, 1985). Second, Jungers (1985) suggested that in arboreal pronograde quadrupeds, a relatively short hindlimb would contribute to increased stability by lowering the center of gravity, which is posteriorly positioned in primates (Kimura et al., 1979; Rollinson and Martin, 1981).

Presumably part of the explanation for the differences in the results reported by Aiello (1981), Steudel (1982a,b,) and Jungers (1985) has to do with the taxonomic composition of their samples, as well as with the methods which they used to estimate the scaling exponent. Steudel (1984) discussed the fact that Aiello's (1981) results may have been biased because she combined Cercopithecus and Cercocebus with colobines as an "arboreal group" to contrast with terrestrial cercopithecines. As Steudel (1982a,b) demonstrated, there was a large difference between colobines and cercopithecines in the elevation of their lines, which suggested that samples which were not taxonomically homogeneous would be biased.

There are two likely reasons for the difference between Steudel's (1982a,b) results and those of Jungers' (1985). The first, again, has to do with the composition of the sample. Secondly, Steudel examined only the proximal elements whereas Jungers considered both proximal and distal elements. Because the distal elements in both limbs scaled very strongly with body size, they were undoubtedly important in determining

the values of the exponents which Jungers (1985) reported.

Crural Index.

The data presented by Aiello (1981) indicated that the value of the crural index decreased with an increase in body mass. Jungers (1985) also found that the crural index decreased in value with increasing body mass. In colobines both the femur and tibia scaled negatively with body mass, but the tibia scaled more negatively than did the femur. In cercopithecines, the femur scaled isometrically with body mass while the tibia scaled negatively. Rodman (1979) reported similar results to Jungers' in his comparison of the small-bodied M. fascicularis and larger M. nemestrina.

Sarmiento (1985) discussed the biomechanical basis for a low crural index in climbers and its negative scaling with body mass. Essentially, reducing the length of the tibia reduces the out-lever arm of the thigh adductors and increases the resultant force at the foothold. As a consequence, the force which must be exerted by the thigh adductors in climbers can be decreased, leading to energetic efficiency (Sarmiento, 1985).

According to the arboreal pronograde quadrupedalism model (Rollinson and Martin, 1981; Jungers, 1985; Sarmiento, pers. comm.), a decrease in the crural index with increased body size would decrease the amount of power that needs to be generated by two-joint muscles which stabilize the knee and hip.

Brachial Index.

The data presented by Aiello (1981) indicated that the brachial index increased with increasing body mass in most primates. However, her data also suggested that humerus length scaled more rapidly with body mass than did radial length, which is counterintuitive and may be related to the inconsistent taxonomic composition of her samples across comparisons. Jungers (1985) also reported that the brachial index in cercopithecids increased with body mass, because the radius scaled more rapidly with body mass than did the humerus. Jungers (1985) did not present a biomechanical explanation for an increased value of the brachial index with increasing body size, perhaps because it is indeed difficult to conceive of one. Just the opposite trend is expected, as was the case for the crural index.

Robusticity.

There is little question that within a homogeneous assemblage of primates, as body size increases the long bones become more robust (Schultz, 1953). However, as noted above, the biomechanical basis for this robusticity is open to some question. Thus, there have been several studies which have specifically tested in primates McMahon's (1973) predictions on the elastic scaling of long bones (Aiello, 1981; Dykyj, 1982; Jungers, 1984; Steudel, 1984). All agree that his predictions have not been verified.

Aiello (1981) reported that in branchwalking cercopithecines and colobines, the circumferences and midshaft diameters of the humerus and femur, as well as their lengths, all scaled isometrically with body

mass. On the other hand, the exponents she reported, in most cases, lie between those predicted by geometric and elastic similarity, and the confidence interval included both values. Therefore, the data are actually equivocal in this regard.

Steudel (1984), like Aiello, found that cercopithecoid humerus and femur lengths scaled isometrically with body weight. However, the confidence intervals around the exponents for femur diameters on mass did include elastic similarity. Steudel (1982a,b) also found that the colobine lines for diameter and cross-sectional area were transposed above the cercopithecine ones. She interpreted these transpositions as indicating an adaptation for leaping in colobines. She argued (1982b:439-440) that "The accelerations encountered at the end of a leap seem likely to be greater than what would be encountered in normal terrestrial locomotion...The increased bone diameters would reduce the stresses placed on the bones, decreasing the likelihood of breakage".

Schaffler et al. (1985) examined the intraspecific scaling of femoral and humeral mid-diaphyseal cross-sectional moments of inertia (CSMI) and the polar moment of inertia (J), with body mass in *M. nemestrina*, *M. fascicularis* and *S. cristata*. The CSMI directly reflects bending rigidity of bones while J directly reflects the torsional rigidity of bones (Schaffler et al., 1985). These authors found that the CSMI and J scaled positively with body mass in all three species, but that *S. cristata* differed from the macaques in that the exponent was much higher, indicating more rapid scaling. Schaffler et al. interpreted the higher exponents in *S. cristata* as an adaptation to the larger

impulsive loads the femur would be subjected to during leaping, compared to the loads born by femora during pronograde arboreal quadrupedalism.

Summary

It is clear from the above that the study of bone scaling with body mass can clarify the meaning of indices as well as the causes for proportionate differences. With the exception of the brachial index, allometric studies have demonstrated that the proportions of bones deviate from geometric similarity in a direction predicted by biomechanical models. The lengths of the limbs scale with body mass as expected for climbing or pronograde arboreal quadrupedal animals. The lengths of the bones within the hindlimb scale with body mass so as to insure either greater stability at the knee joint with increasing size or to generate adequate adductory forces by the hip musculature for vertical climbing. The cross-sectional dimensions of the long bones scale with body mass to resist bending stresses. No study has addressed the scaling of pedal dimensions with body mass. It is likely that the foot, which is in direct contact with the substrate, would most obviously show not only adaptations to particular locomotor modes (cf. Walker and Pickford, 1983), but would scale with body mass in a manner consistent with those patterns established above.

Table 9. Predicted exponents for the scaling of dimensions.

Dimensions	Geometric Similarity	Elastic Similarity
Length scales as Mass	.33	.25
Diameter scales as Mass	.33	.38
Cross-sectional Area scales as Mass	.67	.75
Length scales as Cross-sectional Area	.50	.33
Length scales as Diameter	1.00	.67

Chapter 6. MATERIALS AND METHODS.

Taxonomic Sample

The materials examined in this study are housed in the collections of twenty museums or institutions in the United States, Europe and Africa (Table 10). In total, 826 anthropoid foot specimens were examined, 585 of which were cercopithecids. These cercopithecoid specimens represent 50 species distributed over 17 genera (Table 11). The 50 species are distributed among the three major taxonomic groups which constitute the family: 18 species represent Colobinae, 12 species Cercopithecini and 20 species Papionini. The initial assignment of specimens to specific taxa was based on the identifications made by collectors and curators. The accuracy of these identifications was checked for critical taxonomic categories using the following criteria.

The first category checked was the specimens' assignment to the appropriate family. The criteria used to distinguish cercopithecoid feet from those of other anthropoid families were morphological, based on my experience in studying the two well-curated collections of the American and National Museums of Natural History. The second category verified was the allocation of specimens to subfamily. Again, the criteria used to allocate specimens to either subfamily were morphological. There are a variety of features in most bones of the foot, from the proximal to distal end, which distinguish the subfamilies (Strasser, 1988). Individual features, in isolation, would not allow complete confidence about taxonomic attribution but, in combination, they form a pattern

which is distinctive. As a consequence, I am confident that the samples attributed to the two extant subfamilies indeed represent those groups. The assignment of specimens to the remaining, lower, taxonomic categories was based on the identifications made by curators of the collections. This was especially the method of choice at institutions where one of three criteria were met: (1) that the collections were recently or well curated; (2) that there were limited numbers of species represented; and (3) that the collections comprised large series of animals taken from few localities in the wild. Whenever there was any reason to doubt taxonomic allocation (e.g., when the specimens were not part of large series) I would check the skins and locality data against a catalogue I had compiled based on Napier (1981, 1985), Fooden (1969, 1975, 1980), Dandelot (1971), LeKagul and Heester (1977), Groves (1970), Kingdon (1971), Malbrant MacLachy (1949), Hedway (1969), Pocock (1907, 1925a,b, 1928, 1936), Rahm (1970), and Schwartz (1928a,b, 1929).

An attempt was made to collect data only from wild-caught specimens for which provenance data were available. The majority of specimens for most of the species in this study are from large series (see Appendix 1). For instance, most of the specimens of C. albigena and all the specimens of C. ascanius were collected at a few localities in Uganda by Dr. N. Tappen. Similarly, the majority of S. (Trachypithecus) cristata and P. rubicunda specimens were collected by Drs. A.H. Schultz and S.L. Washburn in Borneo. P. (Piliocolobus) badius is made up primarily of one series from Cameroon with some smaller series added to it. Indeed, most species are represented by what appear to be bona fide populations.

However, for seven species, specimens for which there were no locality data were included. In the cases of M. talapoin, E. patas and P. (Papio) cynocephalus, the specimens either had field numbers which, given their sequence, suggested that they were from the wild, or they were a part of the KNM osteology collection, and were presumably wild-caught. A specimen of C. vellerosus was from a zoo in Sierra Leone, which suggests that the specimen was of local origin. In the cases of M. sylvanus and M. fuscata, the provenance data were either vague (e.g., Barbary, Japan) or non-existent, but these species would not have been represented in this study if these specimens had not been used. Finally, the complete M. mulatta sample is from the collection of Dr. Schultz. While there was no provenance data associated with the specimens, they formed part of the basis for Dr. Schultz's extensive studies and were therefore used in this one.

Age and Sex of Sample

All individuals analysed in this study were considered adults as judged by the eruption of the third molar and epiphyseal fusion. Individuals were considered young adults (YA) if the third molar had just erupted and showed no wear, adults (A) if there was some wear to the third molar, old adults (OA) if the third molar was very worn and very old adults (VO) if the whole molar series was worn to the cervix. Dental eruption patterns do not correlate strongly with epiphyseal fusion, so that individuals judged to be adult by their dental eruption pattern did not necessarily have fully fused epiphyses of the long bones, calcaneus

or digits. However, in no case was an individual included in this analysis if the epiphyses of the leg and foot bones were not securely, albeit not necessarily completely, fused with the diaphysis. Age categories were identified in order to isolate specimens which might skew analyses and are presented in Appendix 1. However, they were not used as categories for analysis.

The sex of specimens was taken from the collection labels and corroborated by examining the size of the canines. In the case of three specimens, there was no indication of the sex on the labels, the skulls and mandibles were missing, and no skins were available for examination. Because these specimens were wild-caught, it was worthwhile to determine their sex based on the absolute lengths of their calcanei or femora (Table 12). The degree of sexual dimorphism for these bones in the relevant species is significant, as judged using a student's t-test to compare the means of the sexes (Table 12). Each specimen was assigned to a sex by comparing its calcaneal length, or in the case of NMNH 239743, its femoral length, to the estimated population parameters. Approximately equal numbers of individuals from each sex were sampled for cercopithecins and colobines but in the papionin sample there are far more males than females (Table 11).

Body Size.

In order to examine the effect of body size on the shape and proportions of bones, some estimate of it must be presented. The estimator used in this study was body mass. Body mass was a particularly

useful estimator of body size for two reasons: (1) values for this dimension are widely available in the literature, and (2) it is approximately equivalent to volume which is, theoretically, the independent variable in allometric models. Estimates of average body mass were calculated for each sex of each species. Table 13 presents sex-specific body mass estimates for cercopithecids derived from data taken from the literature and specimen labels. The body mass estimates were calculated for each sex by taking a weighted mean of the reported estimates. The criterion used for weighting was the sample size reported for each datum. If no sample size had been reported, then it was treated as if the sample size were one. Thus, the average body mass (in grams) for males of P. rubicunda was calculated as follows: $6190 + 6339 + 6588*(11) + 5707*(7) / 20 = 6247$.

It should be noted that, to my knowledge, there are no well-documented estimates of body mass for P. (Rhinopithecus) roxellanae. Birchette (1982) used an estimate of 35 kg which Ruth Happel reported to him. This value is one-half again as large as that of male Nasalis larvatus and seems very unlikely given the size of P. (Rhinopithecus)'s skeletal elements. Fleagle (1988) reported an estimate of 27 kg, but this also seemed large; in scatter diagrams an estimated mass of 27 kg caused P. (Rhinopithecus) to fall out as an exceptionally extreme outlier. Dr. Karl Koopman (pers. comm.) reported that individuals of P. (Rhinopithecus), which he had seen in a zoo in China, were the same size as Nasalis larvatus. Therefore, the estimate which Fleagle (1988) gave for females of P. (Rhinopithecus) was used, because it was similar to

those of Nasalis. However, a value for males was estimated by doubling the value of females. This seemed appropriate because of the sexual dimorphism reported by Dr. Koopman, as well as that which appears in the skeletal elements.

Measurements

Thirty-one measurements taken on disarticulated specimens were analysed in this study. Their codes and definitions are given in Table 14 and are illustrated in Figure 7. All measurements were taken using an electronic digital caliper (Fowler Max-Cal) attached to a portable computer (Compaq or NEC PC-8201A). Long bone lengths were taken using a stainless-steel 18 inch ruler with a metric scale on one side to which an epoxy stop and slide were added. All caliper measurements were taken to the nearest 0.01 cm while the ruler measurements were taken to the nearest 0.1 cm.

The original measurements were used to construct ten derived measurements (Table 15). Most of these derived measurements were used by Midlo (1934), Washburn (1942), Gabis (1960) and Schultz (1963a,b) to construct indices which quantify the proportions of the foot or hind-limb. Midlo's measurements were taken on cadavers, using landmarks which approximated the joints between skeletal elements beneath them. Washburn's (1942) measurements for the foot were taken on articulated specimens using the techniques described by Schultz (1930, 1937). Gabis' (1960) measurements were based on specimens in which the tarsus was separated from the metatarsus and phalanges. Although Gabis did not

explicitly state it, it is likely that the phalanges were separate from the metatarsals. Schultz's (1963a,b) measurements were taken on articulated specimens and were either direct lengths or projective lengths.

Foot length (Table 15) was arrived at by adding the maximum calcaneal length to the maximum medial cuboid length to the metatarsal three length and proximal phalanx three length. (Only the proximal phalanges were measured because they could be assigned with a strong degree of confidence to specific rays. Isolated middle and distal phalanges are difficult to assign to specific rays.) Washburn's (1942) foot length was a direct measurement taken from the proximal point of the calcaneal tuber to the distal point of the distal phalanx of the third ray. Gabis' (1960) foot length is the sum of tarsal length, taken on an articulated tarsal specimen from the proximal point of the calcaneal tuber to the distal midpoint of the ectocuneiform, and ray 3 length, which includes the metatarsal and all the phalanges. Thus, the foot length used in this study differs from Washburn's and Gabis' in terms of the tarsal elements included and the numbers of phalanges included. Because the difference in distal projection between the ectocuneiform and cuboid in an articulated cercopithecoid specimen is minimal, the difference between Gabis' tarsal length and the one used here is probably unimportant. However, the fact that both Washburn's and Gabis' foot measurement included the length of the intermediate and distal phalanges of the third ray, whereas the foot length of this study does not, undoubtedly caused our results to differ.

Sole length (Table 15) was arrived at by adding the maximum cal-

canal length to the maximum medial cuboid length to the length of the third metatarsal. Midlo's (1934) sole length was a projective measurement from the most proximal point of the heel to the plantaro-digital line distally. The comparable length used by Schultz (1963a,b) was a direct measurement, taken on articulated specimens, from the most proximal point of the calcaneal tuber to the distal end of the third metatarsal. The sole length used in this study differs from Midlo's in that the plantaro-digital line is distal to the third metatarsophalangeal joint, at about the level of the midshaft of the proximal phalanx, and therefore is longer than the length used here. However, it is likely that the sole length used in this study is comparable to Schultz's sole (=lever) length.

Tarsus length (Table 15) was estimated by the sum of the maximum calcaneal length and maximum medial cuboid length. Gabis' (1960) tarsus length was described above and is identical to Schultz's (1963a,b). As also discussed above, the difference in measurement technique and bones used will probably not affect the results, since the distances measured are comparable.

Power arm length (Table 15) was estimated by subtracting one-half the length of the calcaneal proximal astragalar-calcaneal facet from a measurement taken from the proximal point of the calcaneal tuber to the distal point of the calcaneal proximal astragalar-calcaneal facet. Schultz's (1963a,b) power arm length was a projective measurement from the proximal end of the calcaneal tuber to the midpoint of the astragalar trochlea. These two estimates of the foot's power arm are

comparable, since the midpoint of the astragalar trochlea lies above the midpoint of the calcaneal proximal astragalar-calcaneal facet in the neutral position of the foot.

Calcaneal load arm length (Table 15) was arrived at by subtracting one-half the length of the calcaneal proximal astragalar-calcaneal facet from a measurement taken from the distal point of the calcaneus to the proximal point of the calcaneal proximal astragalar-calcaneal facet. This length was estimated in order to calculate the load arm of the foot.

Load arm length (Table 15) was estimated by the sum of the calcaneal load arm length, maximum medial cuboid length and metatarsal three length. Schultz's (1963a,b) load arm length was a projective measurement taken from the midpoint of the astragalar trochlea to the distal point of the third metatarsus. For the reasons cited above, the estimate of load arm length used in this study is comparable to the one used by Schultz.

Ray1-5 lengths (Table 15) were estimated by the sum of metatarsal length and proximal phalangeal lengths. Gabis' (1960) and Schultz's (1963a,b) ray1 and ray3 lengths were also sums of the metatarsals and phalanges. However, both of these authors measured all three phalanges whereas only the proximal phalanx was measured in this study. It is unlikely that the estimates of ray1-5 length used in this study are directly comparable to those of Gabis and Schultz, because Schultz (1963b) reported that the middle phalanx in terrestrial monkeys, as in humans, was the one most reduced by effect of terrestriality.

Metatarsal cross-sectional areas (Table 15) were estimated by the product of the height and breadth of the shaft at its estimated midpoint. These products were used to construct metatarsal robusticity formulas and in bivariate plots of the relationship between metatarsal length and cross-sectional area.

Hind length (Table 15) was estimated by summing the maximum bicondylar femur length, maximum tibial length and the estimated length of the foot. This length was used as the denominator in three indices, which were calculated to provide complete and comparable comparisons to the foot/femtib index described below.

Femtib length (Table 15) was estimated by summing the maximum bicondylar femur length and maximum tibial length. Washburn (1942) used a similar sum as the denominator of an index describing the relative length of the foot.

Data Description

Indices.

Certain of the original measurements and the derived measurements were used to construct twenty-three indices (Table 16). Six indices describe the relative proportions of the segments of the hindlimb. Washburn (1942) used the tibia/femur (=crural) and foot/femtib indices in his study of macaques and langurs. The remaining four hindlimb indices were constructed for this study to provide additional descriptions of the hindlimb segment proportions. The foot/tibia index was constructed to describe the relation of the foot to the hindlimb without

the influence of the femur. Three indices (femur/hind, tibia/hind, foot/hind) were calculated so that each segment of the hindlimb was described with reference to the same denominator.

Ten indices describe the relative proportions of the non-hallucal segments of the foot. The tarsus/foot, mt3/foot and ph3/foot indices were used by Gabis (1960) and Schultz (1963b) to describe the proportions of the non-hallucal segments of the foot using a common denominator. The ph3/sole index was used by Midlo (1934) and Schultz (1963a) to describe the development of the phalanges relative to the rest of the foot. The tarsus/sole and mt3/sole indices were constructed for this study to determine the relative contribution of the tarsus and metatarsus to the sole. These indices are complementary to each other and are related to the mt3/tarsus index. The ph3/tarsus index was studied by Gabis (1960) while the ph3/mt3 index was used by Schultz (1963b). Both indices, again, describe the length of the third digit relative to part of the sole. The power/load ratio was used by Schultz (1963a,b) to describe the relative development of the lever arms of the foot during the push-off stage of the stance phase.

Two sets of bivariate relationships were not summarized as indices, but are most appropriately described here. These involve the relationship between the lengths of the third metatarsal and proximal phalanx relative to their cross-sectional dimensions. While indices could have been constructed from these variables, such indices would not be intuitively and immediately comprehensible. It seemed more reasonable, instead, to summarize these data as bivariate plots. Because these data

were drawn from the axial digit ray, they were presented with the indices from the non-hallucal segments of the foot.

Seven indices describe the relative development of the hallux. The ray1/foot index was used by Schultz (1963b) while the ray1/mt3 index was used by Gabis (1960). The ray1/sole index was constructed here to balance the comparisons which included the phalanges of the third ray (ray1/foot) and that which excluded the tarsus (ray1/mt3). The ray1/ray3, mt1/mt3 and ph1/ph3 indices were all studied by Schultz (1963b) and the first was also analysed by Gabis (1960). These indices attempt to take into account the relative development of the individual elements in the comparisons of the hallux and lateral digits. The ph1/mt1 index was used by Schultz (1963b) to determine which segment of the hallux contributed to the relative difference in its length among primates.

The indices were summarized by presenting the mean and range of values for the sex of each species. The indices were also summarized for the cercopithecine tribes and colobines by presenting the mean of species means, the range of species means and the standard deviation of the overall mean. These data were used to construct box-and-whisker plots, providing a useful visual aid of the discriminating value of the index among cercopithecids. Another means for evaluating the discriminating value of indices is to examine their relative correlation with body mass. If species of similar body size have substantially different values for an index, this suggests that the index is useful as a descriptor of locomotor or taxonomic differences. Therefore, bivariate

plots were constructed of the species-by-sex mean index values against mean body mass.

Linear Regression.

Two regression models exist which are based on significantly different assumptions (Sokal and Rohlf, 1981). Two of these assumptions are particularly relevant to this study. The first assumption involves the logical nature of the relationship between the dependent and independent variables in the regression analysis. The second assumption is statistical and concerns the amount of error associated with measuring the variables. Model I problems are those in which it is assumed that there is a cause-effect relationship between the values of the independent variable and the values of the dependent variable. It is also assumed that the independent variable is fixed and measured without error. Model II problems are those in which there is no cause-effect relationship between variables. Model II variables may covary, but this is because of a third variable which is not considered in the problem. Furthermore, the values of two variables in a Model II problem are both random and measured with error.

The difference between the two models, in terms of their assumptions, is not trivial, and has been the cause of a great deal of controversy in the literature about which model is appropriate to use in allometric studies (Steudel, 1982a,b; Aeillo, 1981; Dykyj, 1982; Jungers, 1985; Rayner, 1985; Harvey and Mace, 1982; Pagel and Harvey, 1988). However, as described in the previous chapters, Newton's second

law provides the justification for treating allometric relationships as Model I regressions, because there is a logical foundation for interpreting the allometric coefficients which describe the relationship between length and/or areal dimensions with mass. Mass is fundamental to any object, and the value of all other dimensions are logically considered to be dependent upon its value. Therefore, the logical assumption of Model I regression is met in allometric studies.

Much of the controversy over which model is appropriate for allometric studies revolve around whether the statistical assumption is violated or met. In engineering or experimental biology, the values of the independent variable are under the control of the investigator and can be manipulated as needed. Therefore, they are truly fixed and measured with a minimum of error. In studies such as this one, of biomechanical relationships, body mass could not be manipulated. However, one can argue that the variety of body masses which is present in life represent the results of a "natural experiment" (Diamond, 1989). On the other hand, the assumption that the independent variable is measured without error is very likely violated. While there were certainly problems associated with the comparability of the mass estimates taken from a variety of sources, they were nevertheless treated as if measured without error in this study.

It was mentioned above that the difference between the two regression models was not trivial. One especially important reason for this is that the choice of a model dictates which method can be used to calculate the linear regression equation. This is important, because the

method used determines whether the regression equation parameters of two or more groups can be tested for the statistical significance of their difference. The Least Squares (LS) method is always used for Model I problems whereas a number of methods are available for Model II problems (e.g., major axis, reduced major axis). One difference between the methods is that the LS method minimizes only the error due to measurement and natural variation in the dependent variable, around the Y axis, whereas Model II methods minimize the error around the X axis as well as around the Y axis. The second difference between the methods is that there are a number of tests widely available for testing the LS regression parameters but none are widely available to test Model II parameters.

Most researchers currently estimate the regression coefficients with both Model I and II methods and test the significance of the former parameters (e.g., Steudel, 1982a,b; Aeillo, 1981; Dykyj, 1982; Jungers, 1985). The regression coefficients were estimated using only the LS method in this study, for two reasons. First, while most researchers reported the Model II coefficient, it was rarely discussed, because it cannot be tested. Secondly, for the linear regressions presented in the next chapter, both the LS coefficient as well as the relevant statistics necessary to calculate a reduced major axis (RMA) coefficient were presented.

For all the LS regression analyses discussed in the next chapter the following data are presented: the size of the sample (n), the LS regression coefficient (slope), the standard error of the slope (SE),

the y-intercept, and the coefficient of determination (r^2). These data are necessary and sufficient for calculating such quantities as the upper and lower confidence limits around the LS slope and the RMA. The upper and lower limits to a 95% confidence belt around each slope were calculated by multiplying the SE of a LS slope by the relevant student's t-value (e.g., from Appendix Table 2 of Simpson, Roe and Lewontin, 1960) at $n-2$ degrees of freedom, and adding or subtracting this product to the value of the slope. A small SE (e.g., 0.01) yields a narrow confidence belt around the slope. A narrow confidence belt indicates that the functional relationships between two variables is strong. An estimate of the RMA slope was calculated by dividing the LS slope by r . The SE and y-intercept of the RMA lines are the same as those for the LS lines. The 95% confidence belt is important for determining whether the observed coefficients differ significantly from the a priori predicted coefficient of geometric similarity. The coefficient of determination (r^2) indicates the degree to which the variation in the dependent variable is explained by the variation in the independent variable in a linear regression of a particular sample. Therefore, in the linear regressions presented in the next chapter, the value of r^2 indicates the strength of the functional relationship between body mass and particular variables. The coefficient of determination is theoretically not the same as the common correlation coefficient (a.k.a. r , Pearson's correlation coefficient, product-moment correlation coefficient), which indicates the strength of an interdependent relationship between two variables, which may be due to yet another, third, variable (Sokal and Rohlf, 1981).

However, many researchers report the correlation coefficient rather than the theoretically different coefficient of determination. This may be because the value of r is always higher than r^2 , because r is the square root of r^2 , and therefore suggests a stronger relationship.

All LS linear regression equations were calculated for the cercopithecin subtribes and for colobines. The regression equations were calculated with variates which were the natural logs of the means of a variable for the sexes of each species. One reason for using mean sex-species values was that the body mass estimates were available only at the level of species and sex. More importantly, however, is that it is inappropriate to use the observations of individuals as the variates for examining patterns at higher taxonomic levels. This is because the variation within a species would be added to that among species. As a consequence, the regression equation would not be an accurate description of the bivariate relationship between variables for the taxonomic categories used here. The reasons for using natural logs are: (1) it makes the data homoscedastic (variance equal across the range of values); (2) it transforms curvilinear data into linear data, allowing widely available linear regression techniques to be used rather than more complex techniques which describe curvilinear relationships, such as those described by the allometric equation, and; (3) natural logs, rather than logs to the base 10, are traditional in allometric studies (Simpson, Roe and Lewontin, 1960; Sokal and Rohlf, 1981). The codes for the logged means of the variables used in the linear regression analyses are given in Table 17.

The residual values for the variates of each subfamily from their respective subfamilial lines were also calculated. The residual values were standardized to a mean of 0 and standard deviation of 1 in order to identify which variates, if any, fell outside of the 95% confidence interval of the subfamilial lines. The outlying variates were indicated on the scattergrams associated with each regression. The standardized residuals were presented for each linear regression analysis. The codes used to identify the residuals of the logged mean values for each variable are also given in Table 17.

Digit Length and Robusticity Formulas.

The digit ray measurements for all the lateral digits were used to calculate relative length and robusticity formulas between adjacent rays. The formulas presented in the next chapter were constructed for the lateral digits only, for two reasons. First, the lateral digits operate in unison during much of the positional repertoire of cercopithecids, while the hallux usually functions in opposition to them. Secondly, the hallux is usually the smallest digit in length and cross-section in cercopithecids, with the exception of the metatarsal breadth formulas in T. gelada (Jolly, 1965).

The relative length formulas were calculated for digit rays (metatarsal plus proximal phalanx), metatarsals and proximal phalanges. Because the measurements of each bone is to the hundredth place (0.01 cm) it is rare that any two measurements were actually equal to each other. Therefore, I arbitrarily decided that bones were equal in length

if the difference between them was 0.1 cm or less. When bones were considered equal in length, one of the pair nevertheless had a larger value. This was indicated in the formulas by the ordering of the bones. Thus, in the formula "4=3=5=2" digit 4 is larger than digit 3 but not by greater than 0.1 cm. The same applies to the remaining digits in the formula. With regard to metatarsal cross-sectional area, a difference of 0.1 cm^2 or less was sufficient to consider metatarsals equal. As for phalangeal mid-shaft breadths, the maximum difference for two phalanges to be considered equal was 0.05 cm. There are from fifteen to thirty-one permutations of formulas for the lengths of the digit rays, metatarsals and proximal phalanges, forty-three permutations for the metatarsal cross-sectional area formulas, and thirty-two permutations of the proximal phalangeal breadth formulas. Since such a large number of formulas is not a heuristic summary of the data, the formulas were collapsed for discussion of taxonomic groups.

In the case of the phalangeal formulas (both length and breadth), and therefore the digit ray formulas, some bias may have affected the results. This is because, on the basis of my experience with the phalanges of articulated specimens, I identified unassociated phalanges using size as the criterion. Therefore, in some cases, the phalangeal formulas are the direct result of my assignment of phalanges to digits. This is probably not too serious a drawback because the pattern seemed so invariant for associated specimens, especially in cercopithecines. That is, typically, the third phalanx is the broadest and longest followed, in descending order, by the fourth, second, and fifth. In colobi-

nes, however, the third and fourth phalanges are very similar with the third usually slightly larger.

The frequency of length and robusticity formulas were summarized for each species, cercopithecine tribe, and for colobines. Because formulas indicate only the relative ordering of digits but otherwise are uninformative about how much larger or smaller adjacent digits are to each other, two complementary approaches to formulas were used for describing the relative development of adjacent digits. The first approach involved calculating the difference in length or cross-section between pairs of digits: the central digits 3 and 4, the flanking digits 2 and 5, the medial digits 2 and 3, and the lateral digits 4 and 5. The difference between two digits was adjusted for absolute differences in body size by dividing the difference by the sum of the two digits (e.g., $3-4/3+4$). The mean values of these data were given for species and the mean of the species mean values for cercopithecine tribes and colobines. The second approach was to describe the relative proportion which each digit contributed to the sum of all lateral digits. These data were summarized by presenting the mean proportion for each digit per species. They provide the basis for a useful visual aid: box-and-whisker plots of the range, mean and one standard deviation of the species means for cercopithecins, papionins and colobines.

Data Analysis

All data analyses were performed using the Statistical Analysis Systems package (SAS) for personal computers. Three methods were used to

analyze the data described above: analysis of variance, analysis of covariance and G-tests.

Analysis of Variance.

The average adjusted differences between digit length or cross-section measurements among groups (cercopithecine tribes and colobines) were evaluated using a single-classification Analysis of Variance (anova). Analysis of Variance differs from student's t-test in that it can evaluate the differences among the means of more than two groups. The anova produces an F-statistic as well as the probability of a greater F value. If the probability value was significant (≤ 0.01) then a difference existed among the groups. However, an anova only indicates whether there is a significant difference among the groups; it does not specify which groups differ significantly from each other. Therefore, it was necessary to perform supplementary tests of significance between all possible pairs of means (i.e., the cercopithecine tribes against each other and each against colobines). Because the supplementary tests were non-orthogonal (all possible pairs) the critical value for the probability of making a type I error (rejecting the null hypothesis when it is true) had to be adjusted for each t-test so that the probability of making a type I error over the entire series of tests did not exceed the critical value. This altered probability is called the "experimentwise error rate". The Tukey-Kramer method for multiple comparisons among pairs of means, based on unequal sample sizes, was used because the sample sizes were sometimes very unequal. The Tukey-Kramer method is

robust to this situation and yields results close to the intended significance level. The critical value for the experimentwise error rate used in this study was 0.01.

The SAS statements used in performing an anova and supplementary t-tests are given in Table 18 as is an example of an anova table and the supplementary t-tests. However, the information given in these tables was not presented each time the results of an anova was performed. Instead, those groups with means differing from the others at an experimentwise error rate of 0.01 were indicated by an asterisk.

Analysis of Covariance.

A two-level nested Analysis of Covariance (ancova) for unequal sample sizes was used to examine the LS regression coefficients and y-intercepts among cercopithecids. A nested ancova produces a comparison of cercopithecine tribes while simultaneously taking into account the variance within the cercopithecoid subfamilies. As a consequence, the effect of both levels of the taxonomic hierarchy were considered.

The main test in an ancova is whether there are statistically significant differences in the y-intercepts among groups. It is appropriate to use ancova only if the slopes of the regressions among groups are the same. If the slopes were heterogeneous (i.e., different) then two variables have a different functional relationship among the groups and the ancova would be unnecessary. The assumption that the slopes are homogeneous must be tested before performing the actual ancova. The assumption of homogeneity of slopes was tested by examining

the probability of a getting a greater value for the F statistic in the comparisons of tribes and subfamilies (Sokal and Rohlf, 1981). These are reported under the heading 'Pr > F slope', below the tables presenting the LS regression results for cercopithecoid taxa (e.g., Table 25). Most regressions presented in the next chapter show no significant difference in the slopes between the tribes or subfamilies at the 0.01 probability level. However, in a large number of the ancovas, the probability levels associated with the cercopithecine tribal regression lines were suspiciously low, which suggested that the tribal lines were different enough to require further investigation. On these occasions, examination of the scatter diagrams provided for each ancova (see below) indicated that some outlying observations were rotating either the cercopithecine or the papionin regression line away from the other. When this was the case, the outlying observations were removed, the slopes re-calculated and the test re-run. In some of these cases, the departures of species from the more typical cercopithecine slope suggested special adaptations for the outliers, as discussed in the last chapter. For four variables (ph1, mt1 ray1, ph3) the slopes of the re-calculated cercopithecine LS lines were quite different from the original lines because of the effect of the large terrestrial species. Because it was of interest to see how much these terrestrial species differed from a cercopithecine line calculated with arboreal and semiterrestrial species only, the residuals for all cercopithecines were estimated by forcing the re-calculated LS line through the data. These residuals were then standardized as given above.

If the assumption of a common slope holds true, each group's mean

for the dependent variable is adjusted to the common slope. The actual ancova examines the differences among these adjusted group means for their statistical significance. Thus, while it is true that an ancova tests for the differences among y-intercepts, it is more appropriate to refer to this test as an analysis of the homogeneity of adjusted group means. The test for significance of differences among adjusted group means relies on the probability of getting a greater value for the F statistic for comparisons of two groups. The results of the actual ancova are given under the heading "Pr > F mean", below the tables presenting the LS regression results (e.g., Table 25).

The exact calculations and SAS statements used in testing the hypothesis that the slopes are homogeneous and for performing an ancova are given in Appendix 2. However, only a few SAS statements are needed to achieve the same results enumerated in Appendix 2 and those for a nested ancova are given in Table 19.

It was found that practically all the differences between the subfamilies in the regressions of dimensions on mass were due not to differences in their slopes but to differences in the adjusted group means. In other words, there was generally a transposition of the lines so that the line of one subfamily lay above and parallel to that of the other. This means that at comparable values of X there is a fundamental difference in the values of Y. Explanations for these differences were given in Chapter 8, using biomechanical models. In addition, for many bones, there was also a difference in shape (i.e., allometry) between smaller and larger species of the same tribe or subfamily. In those

cases where allometry was demonstrated, an explanation for it was also sought in biomechanical models.

G-test.

The frequencies of the various digit formulas among the three groups were evaluated using a G-test (a.k.a. Least Likelihood Squares Test). G-tests have several advantages over the traditional Chi-Square test (Sokal and Rohlf, 1981). The most significant of these advantages is that the G values are additive. As a consequence, it is possible to compare the G values obtained at one level of analysis to those obtained at another level. A G value is obtained for all cercopithecids (colobines, cercopithecines and papionins) considered together, for a comparison of the subfamilies and for a comparison of the two cercopithecine tribes. Because the G values are additive, those for the comparisons of subfamilies and tribes sum together to yield the G value for the whole family. In general, as will be seen in the next chapter, the G value is much larger for the comparison of subfamilies than for the comparison of the cercopithecine tribes. As a consequence, one can infer that the differences between the subfamilies are more profound than those between the tribes. G values were considered significant if the probability level was 0.01 or less. An example of the SAS statements used in performing a G-test, as well as the output, are given in Table 20.

Reliability of Literature-Derived Body Mass Estimates

Seventeen percent (n=98) of the 585 specimens had body mass estimates associated with them. Therefore, it was possible to examine if there were differences in the LS regression estimates and statistics based on the sample of specimens with associated estimated masses (Narrow sample) versus those derived for a comparable sample of species in which the body mass estimates were taken from the literature (Broad sample). Table 21 presents the sample size, mean and standard deviations for the variates which make up the narrow and broad samples. The sample statistics were reported for body mass as well as for three variables (about which I have a high degree of confidence in the accuracy of their measurement): femur, tibia and calcaneus length. The narrow and broad samples not only differ in the origin of their body mass estimates, but also in the number of observations from which the sample statistics for the bones were derived. The statistics for most variables in the broad sample were based on more observations than the comparable statistics for the narrow sample. As a consequence, the broad sample means for bone lengths should be better estimates of the parametric means than those of the narrow sample.

The results of ancovas on the data presented in Table 21 are given in Table 22. There are five points worth discussing about the data in Table 22. First, the values of the estimated LS slopes differ very little between the narrow and broad samples. For cercopithecines, the values of the broad sample LS slopes were consistently larger by 1 unit compared to the narrow sample. For colobines, the broad sample values of

the LS slopes were either the same (femur length) or smaller (tibia and calcaneus length) than those of the narrow sample. The most marked difference between the broad and narrow samples is in the values of the LS slope for the regression of calcaneus length on mass in colobines. The higher value of the LS slope in the narrow sample is likely due to the combined effect of the small sample sizes, and the large mean body mass estimates, for C. polykomos and N. larvatus (see Table 21). The combined effect of these factors resulted in a colobine narrow sample LS line which was elevated and rotated in a counter-clockwise direction relative to the colobine broad sample LS line.

Second, the broad sample values of the standard errors (SE) of the estimated LS slopes either decrease or stay the same, but do not increase relative to those in the narrow sample. This means that the 95% confidence intervals around the slopes were the same or narrower compared to those of the narrow sample. It is encouraging that the value of the SE is generally lower in the broad sample, since an expanded version of the broad sample provided the basis for all the regressions reported in the next chapter.

Third, in every regression, the coefficient of determination (CD) had a larger value in the broad sample compared to those of the narrow sample. In cercopithecines, the increase in broad sample CD values ranged from 1-3%, whereas in colobines it ranged from 4-14%. These large improvements in the colobine CDs, and the general improvement in all the CD values, imply that the estimated LS slopes in the broad samples are better estimates of a deterministic relationship between body mass and

bone dimensions than are those of the narrow sample.

Fourth, the probability values for the tests of the homogeneity of the slopes ($Pr > F$ slope) between subfamilies and tribes vary little between the narrow and broad samples. The only difference is that the values are larger in the broad sample. While this increase in value strengthens the conclusions that can be drawn from these tests (i.e., no difference in slopes), it is more important that there is no change in the direction of statistical significance.

Fifth, the probability values for the tests of the homogeneity of adjusted group means ($Pr > F$ means) are stronger in the broad sample (with one exception) compared to those of the narrow sample. Three tests show a decrease in value of the probability of a greater F statistic from the narrow to the broad samples. Two of these smaller values (subfamilial contrasts for femur and tibia lengths on mass) yield a greater likelihood that the differences in adjusted group means is significant. The lower value of the broad sample tribal contrast for tibia length does not change the interpretation derived from the narrow sample: the difference in adjusted group means is not statistically significant at the 0.01 level. The three probability values in the broad sample which increased in value from the contrasts made with the narrow sample (tribal contrasts for femur and calcaneus lengths, subfamily contrast for calcaneus length) also strengthened the interpretation, based on the narrow sample, that there were no significant differences in the adjusted group means.

This comparison of regression estimates, statistics and of ancova

tests suggested that the results of regressions for other variables, based on large sample sizes and literature derived body mass estimates, would not be significantly different from those based on small samples with associated body mass estimates. Therefore, it is likely that the regression estimates and statistics presented in the next chapter are reasonable estimates of the population parameters. Similarly, it is likely that the results of the ancovas on these estimates are an indication of the true similarities and differences that exist among cercopithecid groups.

The Scattergrams

Because 95 sex-by-species variates typically constitute the samples used in the linear regressions, and because the majority of regressions had high values for the CDs, most scattergrams of the variates feature dense clouds of overlapping points. This density of points precluded calling out or identifying the species name of the variates in each scattergram. Furthermore, it is unnecessary to identify variates which make up a dense cloud because the regression equation essentially describes their relative position on the scattergram. The absolute location of a variate can be determined by examining the residual values. However, points representing variates which lie at the edges of, or outside of, the 95% confidence belt around each subfamilial slope, were identified on the scattergrams.

Most scattergrams feature the values of body mass as the variable on the X-axis. Because the range of values for body mass does not change

within the series of scattergrams, it is possible to make some general remarks about the relative positions of cercopithecoid species within the scattergrams. To this end, two identical scattergrams were generated for each subfamily (Figure 8), on each of which the points representing one sex were identified to species. Additionally, I arbitrarily identified clusters of similar-sized species for each sex of each subfamily.

Among colobine females (Fig. 8A), P. (Procolobus) verus (at $\ln$ body mass 8.2) is separated from all the other colobine females, which make up a cluster, with a range in body mass values of $\ln$ body mass 8.6-9.2.. While there is no clear gap among these latter females, to separate smaller from larger variates, it is obvious that the Presbytis and S. (Trachypithecus) species are at the lower end of the range and Colobus, Nasalis and S. (Semnopithecus) are at the upper end of the range. Among colobine males (Fig. 8B), there are three distinct clusters of species as well as P. (Procolobus) verus, at approximately $\ln$ body mass 8.3 body mass. The first cluster (range: $\ln$ body mass 8.6-9.0) comprises the Presbytis and S. (Trachypithecus) species. The second cluster (range: $\ln$ body mass 9.0-9.4) contains the remaining African colobines plus P. (Pygathrix). The third cluster comprises the large bodied (range: $\ln$ body mass 9.4-10.0) Asian colobines, S. (Semnopithecus), P. (Rhinopithecus) and Nasalis.

Within cercopithecine females (Fig. 8C), two groups of species were recognized on the basis of body size and H. talapoin, with a body mass of $\ln$ body mass 7.0 separated from the rest. The first intermediate-sized group of species (range: $\ln$ body mass 7.6-8.2) is made up of the

females in the C. mona, C. cephus and C. pygerythrus groups as well as M. fascicularis. The second, and larger, group is made up of species of relatively larger body mass (range: ln 8.2-9.6). All the papionins, plus the C. mitis groups species, make up this second group. Within the cercopithecine males (Fig. 8D), three groups of species were recognized as well as the tiny M. talapoin, the latter at an average body mass of ln 7.2. The first group, of small-to-intermediate sized species, has the same taxonomic composition as in the females: the C. cephus, C. mona and C. pygerythrus group species plus M. fascicularis. The second group, of intermediate-to-larger species (range: ln body mass 8.5-9.7) contains the C. mitis group species, Erythrocebus and all the Cercocebus and Macaca species. (At first glance it appeared that there were two groups in what I recognized as the third group. However, it will be demonstrated in the next chapter that a gap appears at the position of Erythrocebus because this species is elevated in its observed value for calcaneus length far above its predicted value given body mass.) The third group, comprised of the largest-bodied species (range: ln body mass 9.7-10.3), contains Papio plus Theropithecus.

Five observations emerge from examination of the subfamily by sex scattergrams. First, the range of values for body mass is greater in cercopithecines (ln body mass 7.0-10.5) than in colobines (ln body mass 8.2-9.8). Second, in both subfamilies, it is the great sexual dimorphism at large body mass values that accounts for the distribution of points to the upper right of the scattergram. Third, both subfamilies have one species with a value for body mass which is far lower than that of the

next-smallest species (P. verus, M. talapoin), thus extending the range of values to the lower left of the scattergram. Fourth, within cercopithecines there is strong sexual dimorphism in body mass over all sizes, so that alternating clusters of males and females cause an even distribution of variates across the scattergram. Fifth, within colobines, sexual dimorphism in body mass is great only at the two extremes of the range. For many species in colobines there is little sexual dimorphism. As a result, the density of variates in the middle of the colobine range is not great.

Table 10. Acronyms for museums and collections visited in course of study.

Acronym	Institution
AMNH	American Museum of Natural History, New York, NY, USA
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
BM	British Museum (Natural History), London, England
TER	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
GOT	Zentrum Anatomie der Georg-August-Universität, Göttingen, Germany
PCM	Powell-Cotton Museum, Birchington, Kent, England
STA	Stark Collection, Zentrum der Morphologie der Klinikum der Johann Wolfgang Goethe-Universität, Frankfurt, W. Germany
KNM	National Museums of Kenya, Nairobi, Kenya
RNMH	Rijksmuseum van Natuurlijke Historie, Leyden, Netherlands
MNHM	Muséum National d'Histoire Naturelle, Paris, France
JFO	Personal collection, John F. Oates
ZMUC	Zoologisk Museum, University of Copenhagen, Copenhagen, Denmark
NHMB	Naturhistorisches Museum Basel, Basel, Switzerland
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA
UWHT	Personal Collection, Neil Tappen, The University of Wisconsin-Milwaukee, USA
NMS	Natur-Museum Senckenberg, Frankfurt, W. Germany
PAL	Physical Anthropology Laboratory Collection at Zürich, Switzerland
AS	Adolph Schultz Collection, Zürich, Switzerland
AIUZ	Anthropologisches Institut und Museum der Universität Zürich-Irchel, Zürich, Switzerland

Table 11. Skeletal sample. H male, F female, T total.

Species	H	F	T	Species	H	F	T
<i>Erythrocebus patas</i>	4	2	6	<i>Nasalis larvatus</i>	8	5	13
<i>Cercopithecus albogularis</i>	9	11	20	<i>Pygathrix roxellanae</i>	1	6	7
<i>Cercopithecus mitis</i>	8	12	20	<i>Pygathrix nanae</i>	5	3	8
<i>Cercopithecus nictitans</i>	14	5	19	<i>Sennopithecus entellus</i>	3	6	9
<i>Cercopithecus pygerythrus</i>	16	11	27	<i>Sennopithecus obscura</i>	8	7	15
<i>Cercopithecus petaurista</i>	1	4	5	<i>Sennopithecus cristata</i>	12	13	25
<i>Cercopithecus cephus</i>	17	4	21	<i>Presbytis frontata</i>	2	2	4
<i>Cercopithecus ascanius</i>	10	10	20	<i>Presbytis nelalophos</i>	4	4	8
<i>Cercopithecus campbelli</i>	2	2	4	<i>Presbytis aygula</i>	3	3	6
<i>Cercopithecus nona</i>	11	2	13	<i>Presbytis rubicunda</i>	11	11	22
<i>Cercopithecus pogonias</i>	13	5	18	<i>Presbytis hosei</i>	2	2	4
<i>Hiopithecus talapoin</i>	7	4	11	<i>Colobus quereza</i>	16	14	30
<i>Macaca arctoides</i>	2	0	2	<i>Colobus angolensis</i>	2	4	6
<i>Macaca thibetana</i>	4	0	4	<i>Colobus polykomos</i>	2	2	4
<i>Macaca assanensis</i>	1	0	1	<i>Colobus vellerosus</i>	2	0	2
<i>Macaca sylvanus</i>	4	1	5	<i>Colobus satanas</i>	2	1	3
<i>Macaca nenestrina</i>	5	7	12	<i>Procolobus badius</i>	14	13	27
<i>Macaca nigra</i>	3	1	4	<i>Procolobus verus</i>	6	3	9
<i>Macaca tonkeana</i>	2	1	3				
<i>Macaca fuscata</i>	3	0	3				
<i>Macaca mulatta</i>	10	10	20				
<i>Macaca fascicularis</i>	10	10	20				
<i>Cercocebus torquatus</i>	11	7	18				
<i>Cercocebus galeritus</i>	8	4	12				
<i>Cercocebus albigena</i>	14	10	24				
<i>Papio sphinx</i>	3	5	8				
<i>Papio leucophaeus</i>	2	2	4				
<i>Papio ursinus</i>	4	4	8				
<i>Papio anubis</i>	15	5	20				
<i>Papio cynocephalus</i>	11	8	19				
<i>Papio hanadryas</i>	5	2	7				
<i>Theropithecus gelada</i>	4	1	5				

Table 12. Results of student's t-test for sexual dimorphism in the maximum length of the calcaneus and/or femur.

C. albogularis: calcaneus length

Sex	N	Mean	SD	Min - Max
Female	10	27.53	1.44	25.69-29.96
Male	8	33.04	1.52	31.48-35.84

Pr > t 0.0000, given equal variances [Pr > F', 0.8589]

	calcaneus length	estimated sex
HHHH 18928	35.12	Male
HHHH 35129	22.44	Female

P. anubis: calcaneus length

Sex	N	Mean	SD	Min - Max
Female	5	42.91	1.99	40.46-45.55
Male	14	50.08	3.01	45.94-56.38

Pr > t 0.0001, given equal variances [Pr > F', 0.4373]

	calcaneus length	estimated sex
HHHH 239743	45.72	?

P. anubis: femur length

Sex	N	Mean	SD	Min - Max
Female	5	226.80	10.41	210.00-238.00
Male	12	257.63	10.28	238.50-272.00

Pr > t 0.0000, given equal variances [Pr > F', 0.8732]

	femur length	estimated sex
HHHH 239743	253.0	Male

Table 13. Body mass estimates, in grams. The key to the sources for body mass estimates are: (a) Napier, 1981, 1985; (b) Jungers, 1985; (c) Fleagle, 1988; (d) Clutton-Brock & Harvey, 1977; (e) Rowell, 1985; (f) specimen labels; (g) Smithsonian Institution Catalogue; (h) Fooden, 1988; (i) Fooden, 1971; (j) Booth, 1957; (k) Haldenorth and Diller, 1985; (l) Harvey et al, 1987; (m) Hill, 1974; (n) Sauts, 1985; (o) Fleagle, 1977a; (p) Oates and Trocco, 1983; (q) Hill, 1970; (r) Eurov, 1987; [] Reported sample sizes. * median value. Mean, mean body mass weighted by reported sample sizes.

Taxon	Source	Males	Mean	Females	Mean
<i>Erythrocebus patas</i>	(a)	7000 [1]	8528		5150
	(b)	11100		5900	
	(r)	8180 [3]		4400 [1]	
<i>Cercopithecus albogularis</i>	(g)	8865 [8]	8795	4446 [10]	4878
	(f)	8655 [4]		9194 [1]	
<i>Cercopithecus mitis</i>	(a)	7350 [12]	7607	4231 [14]	4254
	(g)	8634 [3]		4317 [5]	
<i>Cercopithecus nictitans</i>	(b)	6500	5765	4000	4000
	(g)	5150 [4]			
	(f)	7491 [1]			
<i>Cercopithecus pygerythrus</i>	(a)	4582 [17]	4661	3257 [15]	3257
	(r)	5330 [2]			
<i>Cercopithecus petaurista</i>	(a)	3820 [5]	3820	3020 [5]	3059
	(f)			3158 [2]	
<i>Cercopithecus cephus</i>	(b)		4000	2880	2880
	(c)	4000			
<i>Cercopithecus ascanius</i>	(a)	4212 [6]	4212	3300 [2]	3300
<i>Cercopithecus campbelli</i>	(a)	4300 [5]	4300	2200 [2]	2200
<i>Cercopithecus nona</i>	(a)	2733 [3]	3575		2900
	(q)			2500 [1]	
	(k)	*6100		3300	
<i>Cercopithecus pogonias</i>	(c)	4500	4550	3000	3000
	(g)	4600 [1]		3000 [1]	
<i>Hiopithecus talapoin</i>	(b)	1380 [7]	1380	1120 [9]	1120

Table 13. (cont.)

Taxon	Source	Males	Mean	Females	Mean
<i>Macaca arctoides</i>	(f)	10200 [1]	10200		
<i>Macaca thibetana</i>	(h)	15000 [6]	15000		
<i>Macaca assanensis</i>	(h)	11300 [16]	11147		
	(f)	8700 [1]			
<i>Macaca sylvanus</i>	(g)	9300 [2]	9933	9333 [3]	9500
	(l)	11200		10000	
<i>Macaca nemestrina</i>	(a)	9753 [2]	9974	4649 [1]	6155
	(d)			7000	
	(l)	10400		7800	
	(f)	9988 [1]		5826 [3]	
<i>Macaca nigra</i>	(a)	5954 [1]	8065		5168
	(l)	10400		6600	
	(n)	7990 [3]		4690 [3]	
<i>Macaca tonkeana</i>	(n)		6000	9450 [2]	7833
	(g)	6000 [1]		4600 [1]	
<i>Macaca fuscata</i>	(i)	15400 [3]	14475		
	(l)	11700			
<i>Macaca mulatta</i>	(a)	7712 [8]	7502	5367 [9]	5367
	(f)	7221 [6]			
<i>Macaca fascicularis</i>	(a)	6199 [3]	5055	4536 [3]	3430
	(b)	4930 [6]		3130 [6]	
	(f)	4162 [3]		3178 [6]	

Table 13. (cont.)

Taxon	Source	Males	Mean	Females	Mean
<i>Cercocebus torquatus</i>	(a)	10750 [1]	12351		6333
	(g)	11413 [4]		6333 [3]	
	(f)	17706 [1]			
<i>Cercocebus galeritus</i>	(d)	10200	10200	5500	5500
<i>Cercocebus albigena</i>	(a)	7311 [4]	6829	5671 [3]	5369
	(g)	6346 [4]		4915 [2]	
<i>Papio sphinx</i>	(a)	17827 [1]	21153		11500
	(b)	26900			
	(q)	20750 [6]		11500 [2]	
<i>Papio leucophaeus</i>	(c)	20000	18500		10000
	(l)	17000		10000	
<i>Papio ursinus</i>	(a)	31752 [2]	29173		14525
	(f)	28602 [1]		14755 [1]	
	(g)	26880 [2]		14410 [2]	
<i>Papio anubis</i>	(a)	28414 [4]	26435	14744 [2]	13451
	(g)	27700 [4]		17900 [1]	
	(f)	27612 [8]		17619 [3]	
	(n)	24400 [11]		12800 [30]	
<i>Papio cynocephalus</i>	(a)	22979 [4]	22950	11680 [2]	12006
	(g)	22926 [5]		12114 [6]	
<i>Papio hanadryas</i>	(g)	19509 [5]	19585	10225 [2]	9980
	(f)	19660 [5]		9817 [3]	
<i>Theropithecus gelada</i>	(c)	19000	18833	11700	13167
	(e)	21000		14000	
	(f)	16500 [1]		13800 [1]	

Table 11. (cont.)

Taxon	Source	Males	Mean	Females	Mean
<i>Hasalis larvatus</i>	(b)	20370	18649	9820	8727
	(g)	21392 [4]		8363 [3]	
	(f)	15475 [4]			
<i>Pygathrix roxellanae</i>	(c)	*27000	16500	8250	8250
<i>Pygathrix nemaeus</i>	(c)	10900	10839	8200	8132
	(g)	10752 [2]		8064 [1]	
	(f)	10896 [2]			
<i>Sennopithecus entellus</i>	(a)	12748 [19]	12748	9421 [20]	9421
<i>Sennopithecus obscura</i>	(a)	7319 [12]	7487	6602 [22]	6731
	(f)	7945 [4]		7353 [5]	
	(o)	7578 [2]		6595 [2]	
<i>Sennopithecus cristata</i>	(b)	6930 [6]	6656	5950 [6]	5772
	(f)	6421 [7]		5505 [4]	
<i>Presbytis frontata</i>	(c)	5570	5529		5600
	(g)	5488 [1]		5600 [8]	
<i>Presbytis nelalophos</i>	(g)	6478 [25]	6493	6318 [27]	6374
	(o)	6685 [2]		6877 [3]	
<i>Presbytis agnala</i>	(b)	6680	6682	6671	6665
	(g)	6683 [3]		6664 [4]	
<i>Presbytis rubicunda</i>	(b)	6190	6247	5680	6326
	(c)	6339		6056	
	(g)	6588 [11]		6683 [9]	
	(f)	5707 [7]		5999 [7]	
<i>Presbytis hosei</i>	(c)	6200	6200	5570	5566
	(f)			5562 [1]	
<i>Colobus guereza</i>	(a)	9327 [8]	10158	7826 [12]	7826
	(f)	9750 [1]			
	(p)	10800 [11]			
<i>Colobus angolensis</i>	(a)	9679 [2]	9740	7403 [5]	7403
	(p)	9800 [2]			
<i>Colobus polykomos</i>	(a)	8420 [5]	8970	7133 [6]	7500
	(f)	8000 [1]		9700 [1]	
	(p)	9900 [4]			
<i>Colobus vellerosus</i>	(p)	8500 [3]	8500		
<i>Colobus satana</i>	(d)	10000	10250	9000	9000
	(p)	10500 [1]			
<i>Proxolous badius</i>	(a)	9348 [7]	9348	6770 [7]	6770
<i>Procolobus verus</i>	(f)	4280 [4]	4131	4200 [1]	3717
	(g)	4476 [5]		3742 [4]	
	(j)	3800 [7]		3600 [5]	

Table 14. Definition of Measurements. See Figure 7.

Femur

F1. Femur length. Maximum bicondylar length.

Tibia

T1. Tibia length. Distance between medial tibial plateau and distal end of malleolus.

Calcaneus

- C1. Maximum length calcaneus. The maximum distance between the dorsal side of the distal edge of calcaneus and the tuber.
- C2. Calcaneal lever arm. The distance between the proximal surface of the bone and the distal edge of the proximal calcaneal-astragalar facet.
- C3. Calcaneal load arm. The distance between the distal surface of the calcaneus and the proximal edge of the proximal calcaneal-astragalar facet.
- C4. Length proximal calcaneal-astragalar facet. The chord between the proximal and distal edges of the facet, parallel to the long axis of the calcaneus.

Cuboid

Cu1. Medial length cuboid. The distance between the proximal and distal edges of the cuboid on the medial side.

Metatarsals

- Mt1-5. Maximum lengths metatarsals. Distance between the approximate midpoints of the proximal articular surface and distal head.
- BrMt1-5. Mediolateral breadth of shafts. Distance between medial and lateral edges taken at approximate midpoint of length.
- HtMt1-5. Dorsoplantar height of shafts. Distance perpendicular to BrMt1-5.

Proximal Phalanges

- Ph1-5. Maximum lengths phalanges. Distance between midpoints of proximal articular surface and distal trochlea.
- BrPh1-5. Mediolateral breadth phalanges. Distance between medial and lateral edges of shafts at approximate midpoint.

Table 15. Measurements derived from original measurements in Table 14.

Foot	$C1 + Cu1 + Ht3 + Ph3$
Sole	$C1 + Cu1 + Ht3$
Tarsus	$C1 + Cu1$
Power Arm	$C2 - (.5 * C4)$
Calcaneal Load Arm	$C1 - (.5 * C4)$
Load Arm	$(C1 - (.5 * C4)) + Ht3 + Ph3$
Ray1-5	$Ht1-5 + Ph1-5$
Cross-sectional Area Ht2-5	$BrHt2-5 * HtHt2-5$
Hind	$Pl + Tl + Foot$
Pentib	$Pl + Tl$

Table 16. Indices derived from measurements in Tables 14-15.

Hindlimb Segments	Non-hallucal Foot Segments	Hallucal Foot Segments
Tibia/Femur	Tarsus/Foot	Ray1/Foot
Foot/Femur	Ht3/Foot	Ray1/Sole
Foot/Tibia	Ph3/Foot	Ray1/Ht3
Femur/Hind	Ph3/Sole	Ray1/Ray3
Tibia/Hind	Tarsus/Sole	Ht1/Ht3
Foot/Hind	Ht3/Sole	Ph1/Ph3
	Ht3/Tarsus	Ph1/Ht1
	Ph3/Tarsus	
	Ph3/Ht3	
	Power/Load	

Table 17. Codes for logged means of variables used in linear regressions and for residuals of each variate from subfamilial lines.

Variable	Regression Code	Residual Code
body mass	lznass	
hind length	lxhind	Hind
femur length	lxfeantib	Femur
femur length	lxfeantib	Femur
tibia length	lxtiblen	Tibia
foot length	lxfootlen	Foot
sole length	lxsole	Sole
tarsus length	lxtarsus	Tarsus
calcaneus length	lxlnal	Calc
calcaneal load arm length	lxldcal	LdCal
cuboid length	lxlnal	Cuboid
metatarsal 3 length	lxnt3	Ht3
ray 3 length	lxray3	Ray3
phalanx 3 length	lxph3len	Ph3
power arm length	lxpower	Power
load arm length	lxload	Load
ray 1 length	lxray1	Ray1
metatarsal 1 length	lxlennt1	Ht1
phalanx 1 length	lxlenph1	Ph1
cross-sectional area metatarsal 3	lxareant3	Ant3
breadth phalanx 3	lxbrph3	Bph3

Table 18. An example of the SAS statements used in performing an Analysis of Variance and the modified results of this procedure.

SAS Statements:

```
data tmp; set c.ray2_5;
diff34=ray3-ray4; run;
proc means data=work.tmp; by sflabel trilabel;
var diff34; output out=mn34 mean=xdiff34; run;
Proc anova data=work.mn34; class trilabel;
model xdiff34=trilabel; means trilabel / tukey alpha=.01;
run;
```

Output:

Values for difference in length between digit rays 3 and 4.

	N	Minimum	Maximum	Mean	Std Dev
Cercopithecins	10	0.1200000	1.1700000	0.6269222	0.3198406
Papionins	19	-0.5100000	2.0600000	0.8658912	0.8176339
Colobines	16	-3.0800000	-1.0493750	-1.8515412	0.6002324

Analysis of Variance Procedure
Class Level Information

Class	Levels	Values
TRILABEL	3	C O P

Number of observations in data set = 45

Anova Table. Dependent Variable: XDIFP34

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	2	71.96809681	35.98404841	82.32	0.0001
Error	42	18.35832023	0.43710286		
Corrected Total	44	90.32641704			

Table 18. (cont.)

Tukey's Studentized Range (HSD) Test for variable: XDIFP34

Alpha= 0.01 Confidence= 0.99 df= 42 MSE= 0.437103
Critical Value of Studentized Range= 4.355

Comparisons significant at the 0.01 level are indicated by '***'.

TRILABEL Comparison	Simultaneous		Difference Between Means	Simultaneous	
	Lower Confidence Limit	Upper Confidence Limit		Lower Confidence Limit	Upper Confidence Limit
P - C	-0.556	1.034	0.239	-0.556	1.034
P - O	2.027	3.408	2.717	2.027	3.408 ***
C - P	-1.034	0.556	-0.239	-1.034	0.556
C - O	1.658	3.299	2.478	1.658	3.299 ***
O - P	-3.408	-2.027	-2.717	-3.408	-2.027 ***
O - C	-3.299	-1.658	-2.478	-3.299	-1.658 ***

Table 19. Illustration of SAS statements and output for a nested Analysis of Covariance.

Step 1. TEST FOR HETEROGENEITY OF SLOPES (between cercopithecine tribes and between colobines and cercopithecines).

SAS Statements:

```
proc glm data=c.mnlm1; class trilabel sflabel;
model lx2=wght sflabel trilabel(sflabel) wght*sflabel
wght*trilabel(sflabel);
run;
```

Output:

Table A. Test for heterogeneity of slopes. Dependent Variable: LX2 (log of species*sex mean length of metatarsal 2. WGHT, log of species*sex mean body mass.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
WGHT*SFLABEL	1	0.00558088	0.00558088	1.26	0.2643
WGHT*TRILABEL(SFLABEL)	1	0.02250850	0.02250850	5.09	0.0265

Step 2. TEST FOR DIFFERENCES IN ADJUSTED GROUP MEANS (between cercopithecine tribes and between colobines and cercopithecines).

SAS Statements:

```
proc glm data=c.mnlm1; class trilabel sflabel;
model lx2=wght sflabel trilabel(sflabel) ;
run;
```

Table B. Test for homogeneity of adjusted group means.

Source	DF	Type III SS	Mean Square	F Value	Pr > F
SFLABEL	1	0.14610890	0.14610890	31.56	0.0001
TRILABEL(SFLABEL)	1	0.01626125	0.01626125	3.51	0.0641

	Original Mean	Adjusted Mean
Cercopithecines	3.6794856	3.85086721
Papionins	3.8980166	3.80733951
Colobines	3.9223408	3.90327138

Step 3. CALCULATE REGRESSION COEFFICIENTS FOR SUBFAMILIES; CALCULATE RESIDUAL VALUES FOR SPECIES FROM RESPECTIVE SUBFAMILIAL LINES.

SAS Statements:

```
proc glm data=c.mnlmnt; by sflabel;
model lx2=vght;
output out=resid r=r2;
run;
```

Output:

Table C. Coefficients for regression of metatarsal 2 length on body mass. N, sample size; LS slope, least squares slope; y-intercept; SE, standard error of slope; r^2 , coefficient of determination

Taxon	LS		Y		r^2
	N	slope	SE	intercept	
Cercopithecines	62	0.26	0.01	1.56	0.93
Colobines	35	0.24	0.03	1.80	0.79

Step 4. STANDARDIZE RESIDUALS FROM SUBFAMILIAL LINES AND PRINT THEM FOR EACH SPECIES AND SEX

SAS Statements:

```
proc standard data=work.resid out=work.resid mean=0 std=1; by sflabel;
var r2; run; proc print data=work.resid noobs round;
var ordernu sex r2; run;
```

Output:

Table D. Standardized residuals for species from respective subfamilial lines. 1, female. 2, male. R2, residuals of standardized metatarsal 2 length. * variates which fall outside of 95% confidence interval.

SPECIES	SEX	R2	SPECIES	SEX	R2	SPECIES	SEX	R2
Htalapo	1	-1.69	Hfascic	1	-1.50	Cverus	1	-1.04
Htalapo	2	-0.49	Hfascic	2	-1.22	Cverus	2	-1.32
Cpogoni	1	-0.14	Hmaura	1	-1.08	Cbadius	1	0.53
Cpogoni	2	0.69	Hmaura	2	1.58	Cbadius	2	-1.22
Ccampb	1	0.06	Hnigra	1	-0.07	Csatana	1	-0.20
Ccampb	2	0.76	Hnigra	2	0.58	Csatana	2	0.54
Cnona	1	-0.94	Htonkea	1	-1.06	Cpolyko	1	1.32
Cnona	2	2.54*	Htonkea	2	0.70	Cpolyko	2	0.41
Cascani	1	-1.45	Hfascat	2	-2.52*	Cveller	2	0.32
Cascani	2	0.86	Hnulat	1	0.43	Cangole	1	0.01
Ccephus	1	0.06	Hnulat	2	0.72	Cangole	2	-0.95
Ccephus	2	1.05	Hnenest	1	-0.58	Cguerez	1	-1.00
Cpetau	1	-0.30	Hnenest	2	0.17	Cguerez	2	-1.07
Cpetau	2	1.02	Hsylvan	1	-0.86	Phosei	1	0.57
Caethio	1	-0.65	Hsylvan	2	0.70	Phosei	2	2.44*
Caethio	2	-0.24	Harco	2	-1.02	Prubicu	1	1.04
Cnitis	1	0.15	Hassan	2	0.17	Prubicu	2	1.38
Cnitis	2	0.37	Hthibet	2	-2.94*	Paygula	1	0.70
Cnictit	1	0.94	Ccalbig	1	-0.65	Paygula	2	0.09
Cnictit	2	1.31	Ccalbig	2	0.76	Pnelalo	1	0.77
Calbogu	1	-0.76	Ccgaler	1	1.07	Pnelalo	2	0.69
Calbogu	2	-0.16	Ccgaler	2	0.35	Pfronta	1	0.16
Epatas	1	0.28	Cctorqu	1	0.50	Pfronta	2	0.21
Epatas	2	2.28*	Cctorqu	2	0.94	Pcrista	1	-1.27
			Theroge	1	-0.85	Pcrista	2	-1.18
			Theroge	2	-0.38	Pobscur	1	-1.70
			Pcynoce	1	0.50	Pobscur	2	-1.00
			Pcynoco	2	-0.18	Pentell	1	1.17
			Phanadr	1	0.39	Pentell	2	1.43
			Phanadr	2	-0.20	Prozell	1	-1.00
			Panubis	1	-0.14	Prozell	2	-1.25
			Panubis	2	-0.08	Pnenaen	1	-0.11
			Pursinu	1	0.01	Pnenaen	2	0.02
			Pursinu	2	-0.44	Hlarvat	1	0.52
			Pleucop	1	-0.19	Hlarvat	2	-0.02
			Pleucop	2	0.50			
			Paphinx	1	-0.89			
			Paphinx	2	1.23			

Table 20. SAS statements and modified output for a G-test.

```
proc freq data=c.ray2_5;
tables trilabel*nuform / chisq nopercnt norow nocol nocum; run;
```

*Formulas 423>225 and 423>522 treated together for test

TABLE OF TRILABEL BY DIGIT RAY LENGTH FORMULA

423>522			
Frequency	324>225	324>522	423>225
Total			
Cercopithi	52	16	5
Papionins	49	28	37
Colobines	0	3	101
Total	101	47	143

Statistic	DF	Value	Prob
All groups	4	205.8	0.000
Subfamilies	2	183.0	0.000
Tribes	2	21.9	0.000

Table 21. Comparison of narrow and broad sample statistics for lengths of femur, tibia and calcaneus, and body mass. N, sample size; Mean, arithmetic mean; SD, one standard deviation of the mean. Note: for the broad sample, variable mass, no sample sizes nor standard deviations are given.

Species	Sex	Narrow			Broad		
		N	Mean	SD	N	Mean	SD
Femur							
Cpetau	F	1	135.50	.	3	133.50	4.82
Cnictit	M	1	179.00	.	14	179.21	8.10
Calbogu	F	1	150.50	.	11	143.77	6.18
	M	4	182.00	19.41	8	178.94	13.44
Mfascic	F	7	123.79	3.60	10	125.70	4.70
	M	2	139.75	1.77	10	145.10	6.98
Hnulat	M	6	184.50	8.93	10	185.55	7.78
Mnenest	F	3	169.50	8.41	7	166.50	12.36
	M	1	205.00	.	5	207.60	10.66
Harcro	M	1	166.00	.	2	172.75	9.55
Hassan	M	1	176.00	.	1	176.00	.
Cctorqu	M	1	223.50	.	11	218.14	11.17
Theroge	F	1	197.00	.	1	197.00	.
	M	1	216.00	.	2	215.00	1.41
Phanadr	F	2	207.75	10.96	2	207.75	10.96
	M	4	234.38	13.36	5	236.90	12.88
Panubis	F	3	228.67	2.75	5	226.80	10.41
	M	6	255.83	12.00	13	257.27	9.93
Pursinu	F	1	210.50	.	3	214.17	7.69
	M	1	251.00	.	4	270.00	23.19
Cverus	F	0	.	.	2	147.00	4.24
	M	2	148.25	6.72	5	150.20	4.13
Cpolyko	F	0	.	.	1	204.00	.
	M	0	.	.	2	205.50	5.66
Cguerez	M	1	197.00	.	16	199.09	9.46
Phosei	F	1	182.50	.	1	182.50	.
Prubicu	F	7	194.29	4.04	9	195.39	4.22
	M	7	199.43	4.77	10	201.25	5.40
Pcrista	F	4	169.63	2.10	13	170.08	6.07
	M	7	177.43	7.36	12	177.08	8.77
Pobscur	F	5	172.90	8.71	7	176.07	9.24
	M	4	186.38	11.12	8	184.69	8.40
Phenacu	M	2	226.00	4.24	5	233.10	8.49
Hlarvat	M	3	234.67	3.06	8	243.13	10.02

Table 21. (cont.)

		Narrow			Broad		
Species	Sex	N	Mean	SD	N	Mean	SD
Tibia							
Cpetan	F	1	133.00	.	3	129.67	4.16
Cnictit	H	1	173.50	.	14	173.11	8.64
Calbogu	F	1	160.00	.	11	141.27	9.55
	H	4	176.50	22.05	9	172.89	14.93
Hfascic	F	6	117.00	1.87	9	118.72	3.69
	H	2	129.75	0.35	10	134.80	6.43
Hnulatt	H	6	168.58	8.34	10	169.15	6.54
Hnenest	F	3	156.33	6.21	7	153.36	9.24
	H	1	184.50	.	5	186.60	7.79
Harcto	H	1	152.50	.	2	154.75	3.18
Hassan	H	1	163.50	.	1	163.50	.
Cetorqu	H	1	211.00	.	11	201.32	9.04
Theroge	F	1	191.00	.	1	191.00	.
	H	1	217.00	.	2	214.50	3.54
Phanadr	F	2	183.50	9.19	2	183.50	9.19
	H	4	203.63	10.80	5	206.40	11.23
Panubis	F	3	196.00	1.32	5	189.20	9.78
	H	7	222.21	9.18	15	225.47	11.05
Pursinu	F	1	184.50	.	3	193.50	20.07
	H	1	220.00	.	4	232.00	22.64
Cverus	F	0	.	.	2	139.25	1.06
	H	2	141.25	8.84	4	141.88	5.30
Cpolyko	F	0	.	.	1	191.00	.
	H	0	.	.	2	190.75	1.06
Cquerez	H	1	186.00	.	16	184.56	9.96
Phosei	F	1	162.50	.	2	169.75	10.25
Prubicu	F	7	176.93	4.43	11	178.50	4.40
	H	7	183.14	5.11	10	185.25	5.43
Pcrista	F	4	151.50	2.68	13	151.08	4.90
	H	7	161.71	5.25	12	160.63	6.19
Pobscur	F	5	150.60	5.94	7	157.43	7.06
	H	4	165.63	11.95	8	165.13	8.80
Pnenaou	H	2	203.25	0.35	5	207.10	4.55
Hlarvat	H	3	211.67	4.19	8	217.44	6.07

Table 21. (cont.)

			Narrow			Broad	
Species	Sex	N	Mean	SD	N	Mean	SD

Calcanens							

Cpetau	F	2	24.06	0.21	4	24.16	0.29
Cnictit	H	1	34.62	.	14	33.41	1.56
Calbogu	F	1	29.96	.	11	27.07	2.06
	H	4	33.42	2.03	9	33.27	1.58
Hfascic	F	7	23.29	0.81	10	23.62	1.01
	H	2	26.20	1.46	10	27.46	1.74
Mnulatt	H	6	36.28	1.27	10	35.99	1.13
Mnenest	F	3	30.50	1.22	7	30.23	1.84
	H	1	36.89	.	5	36.48	0.76
Harco	H	1	35.34	.	2	36.43	1.54
Hassan	H	1	32.79	.	1	32.79	.
Cctorqu	H	1	40.26	.	11	38.93	1.93
Theroge	F	1	39.29	.	1	39.29	.
	H	1	45.95	.	4	44.14	3.03
Phanadr	F	2	38.22	2.52	2	38.22	2.52
	H	4	43.51	2.41	5	43.51	2.08
Panubis	F	3	43.28	2.59	5	42.91	1.99
	H	7	48.84	2.16	15	49.86	3.03
Pursinu	F	1	41.53	.	4	43.14	3.04
	H	1	46.56	.	4	49.69	3.40
Cverus	F	1	25.90	.	3	26.36	0.75
	H	3	27.98	0.43	6	27.94	0.29
Cpolyko	F	1	36.35	.	2	35.35	1.41
	H	1	38.13	.	3	38.41	1.27
Cguerez	H	1	35.45	.	16	35.52	2.17
Phosei	F	1	29.51	.	2	30.80	1.82
Prubicu	F	7	31.27	0.69	11	31.32	0.71
	H	7	32.18	0.94	11	32.34	0.95
Perista	F	4	27.54	0.54	13	28.28	1.16
	H	7	30.70	1.31	12	30.56	1.32
Pobscur	F	5	29.77	1.24	7	30.11	1.17
	H	4	32.22	0.73	8	32.27	0.86
Pnenaen	H	2	37.51	0.31	5	38.66	1.35
Hlarvat	H	3	43.22	0.76	8	43.75	1.58

Table 21. (cont.)

		Harrov			Broad		
Species	Sex	N	Mean	SD	N	Mean	SD
Hass							

Cpetau	F	2	3157.50	222.74		3059	
Cnictit	H	1	7491.00	.		5765	
Calbogu	F	1	9194.00	.		4878	
	H	4	8654.50	1939.47		8795	
Mfascic	F	7	3145.71	484.80		3430	
	H	2	4767.00	321.03		5055	
Mnulatt	H	6	7220.67	1131.47		7502	
Mnenest	F	3	5826.33	472.54		6155	
	H	1	9988.00	.		9974	
Harcto	H	1	10200.00	.		10200	
Hassan	H	1	8700.00	.		8700	
Cctorqu	H	1	17706.00	.		12351	
Theroge	F	1	13800.00	.		13167	
	H	1	16500.00	.		18833	
Phanadr	F	2	10225.00	2156.68		9980	
	H	4	19300.00	3462.18		19585	
Panubis	F	3	17619.33	1160.73		13451	
	H	7	27729.86	3861.50		26435	
Pursinu	F	1	14755.00	.		14525	
	H	1	28602.00	.		29173	
Cverus	F	1	4200.00	.		3717	
	H	3	4583.33	246.64		4131	
Cpolyko	F	1	9700.00	.		7500	
	H	1	8000.00	.		8970	
Cquerez	H	1	9750.00	.		10158	
Phosei	F	1	5562.00	.		5566	
Prubicu	F	7	5999.29	538.09		6326	
	H	7	5707.43	332.29		6247	
Pcrista	F	4	5504.75	217.34		5772	
	H	7	6420.86	408.48		6656	
Pobscor	F	5	7352.80	549.19		6731	
	H	4	7945.00	945.08		7487	
Pnenacu	H	2	10896.00	642.05		10839	
Hlarvat	H	3	13975.00	2208.46		18649	

Table 22. Comparison of values from ancovas between narrow and broad samples, as defined in text. N, sample size; slope, LS slope, SE, standard error of the slope; Y-int, y-intercept; CD, coefficient of determination.

	Narrow						Broad				
Taxon	N	slope	SE	Y-int	CD		N	slope	SE	Y-int	CD
lxfenlen*lxmass											
Cercopithecines	20	0.31	0.03	2.40	0.88		20	0.32	0.02	2.30	0.91
Colobines	11	0.32	0.07	2.44	0.68		14	0.32	0.04	2.41	0.82
		Pr > F slope		Pr > F mean			Pr > F slope		Pr > F mean		
Subfamilies		0.8381		0.0007			0.8625		0.0003		
Tribes		0.2539		0.4975			0.7694		0.6059		
lxtiblen*lxmass											
Cercopithecines	20	0.27	0.02	2.68	0.88		20	0.28	0.02	2.59	0.89
Colobines	11	0.30	0.07	2.46	0.68		14	0.29	0.05	2.58	0.77
		Pr > F slope		Pr > F mean			Pr > F slope		Pr > F mean		
Subfamilies		0.7466		0.0061			0.7959		0.0013		
Tribes		0.5423		0.2533			0.9355		0.0842		
lxlencal*lxmass											
Cercopithecines	20	0.33	0.02	0.57	0.91		20	0.34	0.02	0.46	0.95
Colobines	14	0.39	0.05	0.05	0.85		14	0.33	0.03	0.57	0.89
		Pr > F slope		Pr > F mean			Pr > F slope		Pr > F mean		
Subfamilies		0.2253		0.3353			0.7376		0.5350		
Tribes		0.6186		0.4559			0.8215		0.8539		

Figure 7. Illustration of Measurements as defined in Table 14. A. Left femur, anterior view. B. Left tibia, anterior view. C. Left foot, dorsal view. D. Left calcaneus, dorsal view. Measurements defined in Table 14.

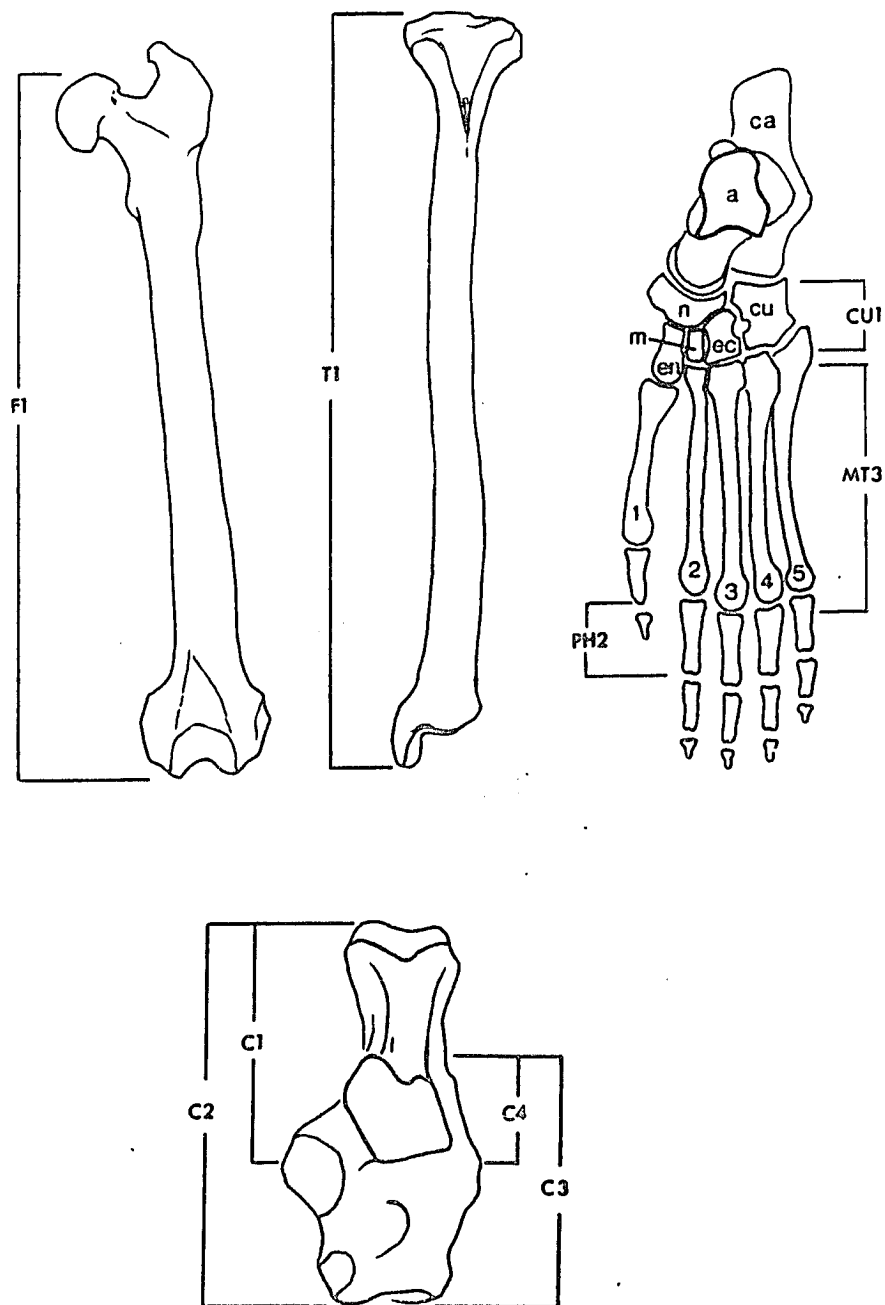


Figure 8. Identification of variates in bivariate plots. A. Colobine females. B. Colobine males.

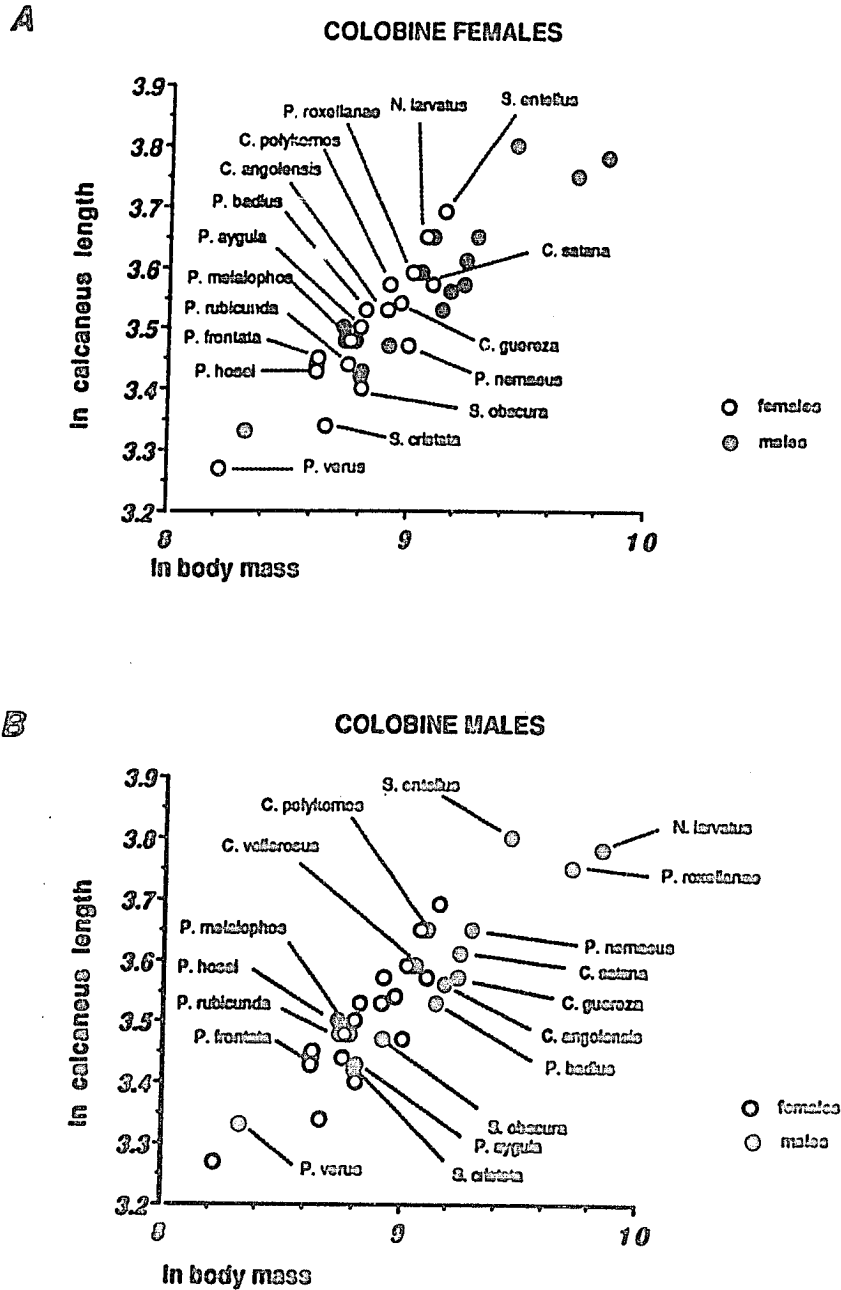
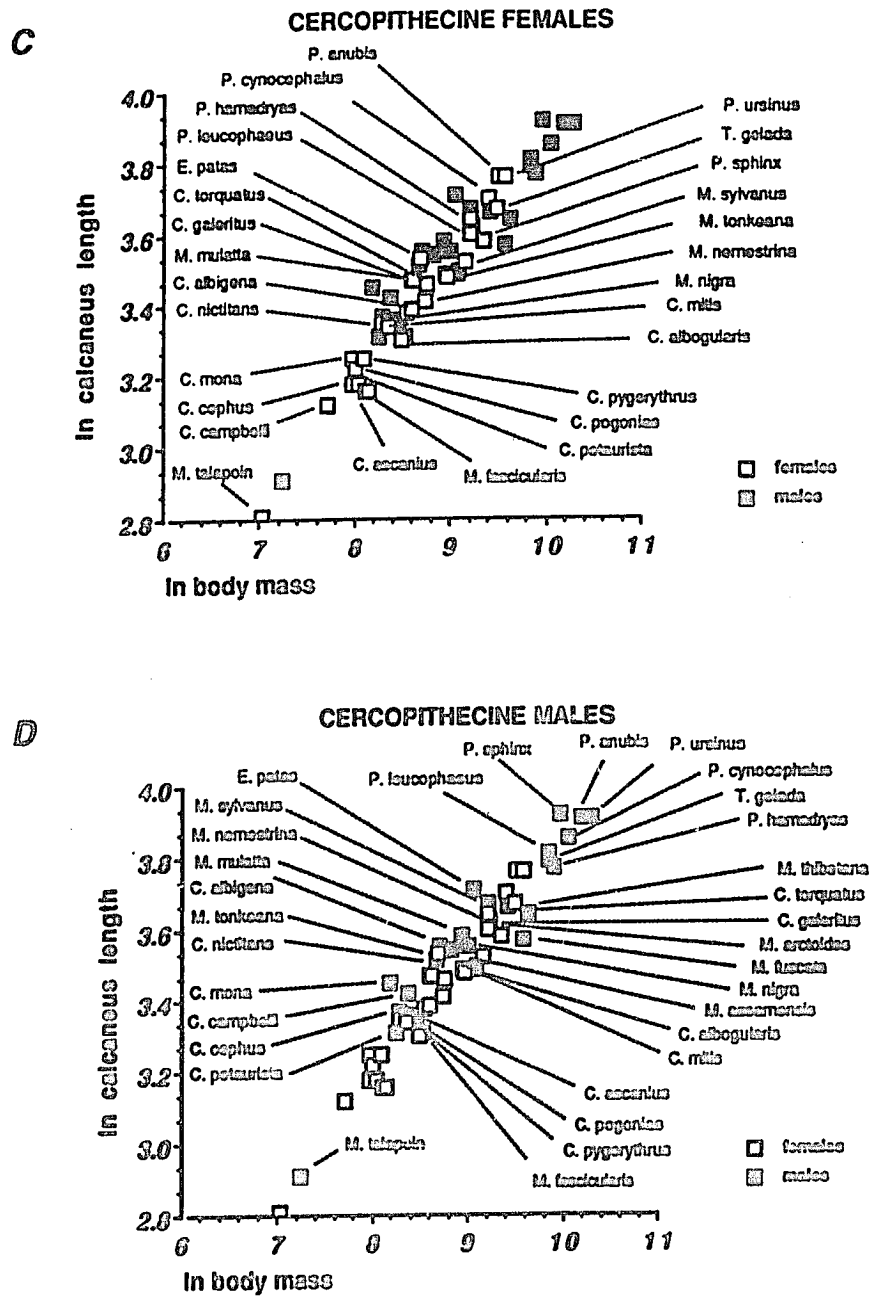


Figure 8. (cont.) C. Cercopithecine females. D. Cercopithecine males.



Chapter 7. RESULTS

Introduction

The results presented below are organized into four sections, coincident with the segmental arrangement of the hindlimb. Three sections cover indices, with the first section dealing with the main segments of the hindlimb, the second section dealing with the main segments of the foot excluding the hallux, and the third section dealing with the hallux. Within each of these three sections, the indices are presented first and these are followed by analyses of the scaling relationships of the indices' components with body mass. The fourth section deals with digit length and robusticity formulas. The summary at the conclusion of this chapter synthesizes the allometric basis for the correlations of indices with mass, synthesizes the main distinctions between the subfamilies for their scaling patterns and digit formulas, and synthesizes the data for particular species which depart from their respective subfamilial patterns.

Hindlimb Segments

Indices

Tibia/Femur. The average mean crural index for cercopithecine species is 98 with a range from 95-100 (Tables 23-24). Miopithecus has the highest average index value while C. pygerythrus has the smallest. The average mean crural index for papionin species is 91 with a range of mean values from 84-100 (Table 24). Female P. (Papio) anubis has the

lowest mean value for the tribe, but this is due to one female (KNM OM 3144) having an unusually low value for the length of the tibia. Within papionins, T. gelada has the highest average values for the crural index while P. (Papio) has the lowest average values. The average mean crural index for colobine species is 91 with a range of mean values from 87-95 (Table 24). P. (Procolobus) verus has the highest mean value while S. (Semnopithecus) entellus and P. (Rhinopithecus) roxellanae have the lowest values.

Figure 9A is a box-and-whisker plot of the mean crural index values within the cercopithecine tribes and colobines. This illustration clearly shows that the index discriminates most cercopithecins from most papionins, but not papionin species from colobines. The fact that the smallest colobine and cercopithecine species have the highest value for the index, and that the larger colobine and cercopithecine species have the lowest value for the index, suggests that the distinction in average crural index values between cercopithecins and papionins is a function of body mass. Indeed, a bivariate plot of the average species value for the crural index against body mass (Fig. 10A) illustrates a negative linear relationship for these variables (colobines $r = -0.539$; cercopithecines $r = -0.730$). There is complete overlap in index values between colobines and cercopithecines at comparable body masses, suggesting no fundamental difference between the two subfamilies. Three variates depart from the general familial trend. The female P. (Papio) anubis variate is an outlier in the plot, for the reason given above. It is more notable that T. gelada and male E. patas have rather high values

for the crural index given their body masses.

Foot/Femtib. In all three groups the average mean value for this index is between 35 and 36 with a range of 32-39 (Tables 23-24). Reference to Figure 9B further demonstrates that there is no major difference between the cercopithecoid groups for this index. However, in cercopithecines the average mean value, and the range of values, is higher than in papionins and colobines. Furthermore, within each cercopithecoid group, the smallest species have the highest values for the index and the larger species the lowest values. This suggests that, as with the tibia/femur index, the value of the foot/femtib index may be a function of body mass. Figure 10B is a bivariate plot of the foot/femtib index against body mass. The correlation between the values of the index and body mass is weakly negative in cercopithecines ($r = -0.486$) and virtually absent in colobines ($r = 0.005$) than was the case for the crural index and mass. The macaques, and especially M. thibetana, have higher values for this index than do other papionins at comparable body masses. It is also noteworthy that the African colobines have higher values for this index than do most Asian langurs, in particular the Presbytis species and Pygathrix nemaeus.

Foot/Tibia. The average mean value for the index is between 72 and 74 for all cercopithecoids with a range of 68-83 (Tables 23-24). Within cercopithecines the small-bodied M. talapoin has the highest mean values while the large-bodied E. patas has the lowest. Within papionins, the

macaques have a higher range of values (74-83) than do African papionins (69-75), although some overlap is evident. It is noteworthy that M. thibetana has an exceptionally high value for the foot/tibia index. Among the colobines there is no clear taxonomic pattern in the distribution of values for the foot/tibia index.

Reference to Fig. 9C illustrates the lack of a significant difference among the groups in this index. While some association of index values with body mass is suggested by the fact that cercopithecins have the lowest values for the mean and range, this is not supported by the distribution of values in papionins or colobines. Indeed, Figure 10C shows that there is no significant correlation between the value of the index and body mass for the subfamilies (colobines $r = 0.119$; cercopithecines $r = -0.129$). As with the foot/femur index, macaques have higher values for the foot/tibia index than do other papionins at comparable body masses.

Femur/Hind. The average mean value for the index is between 37 and 39 for all cercopithecids with a range of 36-41 (Tables 23-24). Within cercopithecins, the small-bodied M. talapoin has the lowest values for this index while E. patas has the largest value. Within papionins, the P. (Papio) species are noteworthy for consistently having the largest values of this index in the subfamily. Among the colobines, the African species have values for the index at the lower end of the range while the Asian forms have values at the upper end of the range. Reference to Figure 11A illustrates that cercopithecins have the lowest mean value

and range of smaller values for this index within the family.

Figure 12A shows that there is a significant positive linear correlation between the value of the index and body mass in the family, although this is stronger in cercopithecines than in colobines (colobines $r = 0.241$; cercopithecines $r = 0.742$). Two variates within the sample depart strongly from the familial linear trend. The first, female P. (Papio) anubis, has a larger average index than expected for its body mass because of the influence of KNM OM 3144, and thus does not represent a significant deviation. The second deviant variate comprises male T. gelada. Because only one individual makes up the sample, this too may be due to sampling error.

Tibia/Hind. The average mean value for the index is between 35 and 36 for all cercopithecids with a range of mean values of 34-37 (Tables 23-24). Within cercopithecins, no one species or species group has an apparently noteworthy value for this index. However, within papionins, T. gelada does stand out for having the highest value of the index. Colobines are similar to cercopithecins in the consistency of values among the species. Reference to Figure 11B illustrates that cercopithecins have the highest mean value and a range of higher values for this index than the other groups within the family.

The bivariate plot of the species mean values for the tibia/hind index against body mass (Fig. 12B) shows that there is a weak negative linear correlation between the value of the index and body mass in the family (colobines $r = -0.320$; cercopithecines $r = -0.483$). Six variates

within the sample depart strongly from the familial linear trend. The first, female P. (Papio) anubis, has a smaller average index than other variates at its body mass, again because of the influence of KNM OM 3144. The second deviant variate is M. thibetana, which also has a lower value for the tibia/hind index than might be expected for its body mass. Both sexes of T. gelada and E. patas make up the remaining deviant variates. In particular, the males of all four of these outlying species have higher values for this index than do other species at comparable body masses.

Foot/Hind. The average mean value for the index is 26 for all cercopithecoid species with a range of mean values of 24-28 (Tables 23-24). Within cercopithecins, the small-bodied M. talapoin and C. mona group species have the highest values for this index while the larger-bodied C. mitis group species and E. patas have the lowest values for the index. Similarly, in papionins the small-bodied M. fascicularis has the highest value for the index while the larger-bodied species have lower values. Within colobines, the Presbytis species and P. (Pygathrix) have the lowest values for the foot/hind index. Reference to Figure 11C illustrates that cercopithecins have the highest mean value, and a total range of higher values, for this index than the other groups within the family.

The bivariate plot of the species mean values for the foot/hind index against body mass (Fig. 12C) shows that there is a very weak negative linear correlation between the value of the index and body mass

in cercopithecines ($r = -0.490$) and no correlation within colobines ($r = 0.005$). While the weak correlation between body mass and the values of the index precludes much discussion of outliers, it is noteworthy that the macaque species, and in particular M. thibetana, have higher values for the foot/hind index than do other papionin species at comparable body masses.

Ancova of LS Regressions: Hindlimb Segment Measurements vs Body Mass

Hindlimb Length vs Mass. A test for the homogeneity of slopes indicated a significant difference between the cercopithecine tribes at the 0.01 level but no difference between the cercopithecoid subfamilies ($\text{Pr} > F 0.57$) (Table 25). Estimation of the slopes for cercopithecine tribes revealed that cercopithecins had a higher value (0.35) than did papionins (0.26). Reference to Figure 13A suggests that the higher slope in cercopithecins was due to the effect of two outlying variates: the female M. talapoin and male E. patas. The combined effect of a very small value for hindlimb length relative to body mass in female M. talapoin and a high value in male E. patas resulted in a steeper cercopithecine LS slope. When the female M. talapoin and male E. patas variates were dropped from the sample, and the cercopithecine slope re-estimated (0.31) and tested, there was no significant difference between the tribes ($\text{Pr} > F 0.26$) (Table 25). Furthermore, the probability of a greater F value for the difference between the cercopithecoid subfamilies became even less likely ($\text{Pr} > F 0.96$).

The 95% confidence interval around the cercopithecine line(s)

(slope 0.28 or 0.27) does not include the predicted geometric similarity coefficient while that around the colobine line (slope 0.27) does. However, both subfamilies exponents are close to the predicted elastic similarity coefficient. Because there is no significant difference between the slopes of the two subfamilies, it is reasonable to conclude that the hindlimb has a negative allometric relationship, if not elastic relationship, with body mass in both subfamilies. Therefore, species with a larger body mass have a relatively shorter hindlimb than those at smaller body mass.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F$ 0.31) but a highly significant difference between the two subfamilies ($Pr > F$ 0.0001). At any given body mass, the average colobine has a longer hindlimb than does the average cercopithecine. Reference to Figure 13A, and the species residual values in Table 26, indicates that five variates fall outside of the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas have longer hindlimbs than expected for their body masses and male M. thibetana and M. fuscata have shorter hindlimbs than expected for their body mass. Within colobines, male P. hosei has a significantly longer hindlimb than expected for its body mass. It is also of interest that, with the exception of female P. hosei, all the Presbytis variates lie above the colobine LS line while the S. (Trachypithecus) variates lie below the line.

Fentib Length vs Mass. A test for the homogeneity of slopes indicated no significant difference between the cercopithecine tribes ($Pr > F 0.14$) nor the cercopithecoid subfamilies ($Pr > F 0.38$) in the values of their estimated slopes (Table 25).

The upper 95% confidence limit in both subfamilies is coincident with the predicted value of the geometric similarity coefficient. However, both subfamilies exponents are close to the predicted coefficient for elastic similarity (colobines 0.27; cercopithecines 0.29). Because the LS slopes in both subfamilies lie well below the isometric coefficient, it is reasonable to conclude that fentib length has a negative allometric relationship, if not elastic relationship, with body mass. Therefore, species with a larger body mass have relatively shorter fentib lengths than those at smaller body mass.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.38$) but a highly significant difference between the two subfamilies ($Pr > F 0.0001$). At comparable body masses, the average colobine has a longer fentib than does the average cercopithecine. Reference to Figure 13B and Table 26 indicates that six variates fall just within, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and P. (Mandrillus) have longer fentibs than expected for their body masses while male M. thibetana and M. fuscata have shorter fentibs than expected for their body mass. Within colobines, male P. hosei has a significantly longer fentib than expected for its body mass. It is also of interest that, as

with hindlimb length, all the Presbytis variates lie above the colobine LS line while the S. (Trachypithecus) variates lie below the line.

Femur Length vs Mass. A test for the homogeneity of slopes indicated no significant difference between the cercopithecine tribes ($Pr > F 0.22$) nor the cercopithecoid subfamilies ($Pr > F 0.36$) in the values of their estimated slopes (Table 25).

The 95% confidence interval in both subfamilies includes the predicted value of the geometric similarity coefficient. Furthermore, the estimated LS coefficient in cercopithecines (0.32) is closer to the predicted geometric similarity coefficient than is the LS coefficient in colobines (0.28), which is closer to the predicted elastic similarity coefficient. However, because there is no significant difference between the subfamilies in their values of the LS coefficient, and because the predicted isometric coefficient is well within the 95% confidence interval of both subfamilial lines, it is reasonable to conclude that femur length scales isometrically with body mass. Therefore, species with a larger body mass have a relatively equivalent femur length as do species at smaller body mass.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.95$) but a highly significant difference between the two subfamilies ($Pr > F 0.0001$). At comparable body masses, the average colobine has a longer femur than does the average cercopithecine. Reference to Figure 13C and Table 26 indicates that seven variates

fall just within, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona, C. albigena, and P. (Mandrillus) have longer femora than expected for their body masses while male M. thibetana and M. fuscata have shorter femora than expected for their body mass. Within colobines, male P. (Piliocolous) badius has a significantly shorter femur than expected for its body mass. Again, as with hindlimb and femur lengths, all the Presbytis variates lie above the colobine LS line while the S. (Trachypithecus) variates lie below the line.

Tibia Length vs Mass. A test for the homogeneity of slopes indicated no significant difference between the cercopithecine tribes ($Pr > F 0.10$) nor the cercopithecoid subfamilies ($Pr > F 0.21$) in the values of their estimated slopes (Table 25).

In both subfamilies, the predicted value for the geometric similarity coefficient lies well above the upper 95% confidence limit of the LS estimated slope (cercopithecines 0.27; colobines 0.24). Therefore, it is reasonable to conclude that tibia length has a negative allometric relationship with body mass. As a result, species with larger body mass have a relatively shorter tibia than do species with a smaller body mass. Indeed, the LS slopes for both subfamilies are close to the predicted elastic similarity coefficient.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.08$) but a significant difference between the

two subfamilies ($Pr > F 0.002$). At comparable body masses, the average colobine has a longer tibia than does the average cercopithecine. Reference to Figure 13D and Table 26 indicates that nine variates fall just within, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona, E. patas and P.

(Mandrillus) have longer tibiae than expected for their body masses while male M. thibetana, M. arctoides and M. fuscata have shorter tibiae than expected for their body mass. Within colobines, male P.

(Piliocolobus) badius has a significantly shorter tibia than expected for its body mass and male P. hosei has a longer one. Again, as with hindlimb, femtib and femur lengths, all the Presbytis variates lie above the colobine LS line while the S. (Trachypithecus) variates lie below the line.

Foot Length vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes indicated a significant difference ($Pr > F 0.004$) while that between the cercopithecoid subfamilies was not significant ($Pr > F 0.90$) (Table 25). Estimation of the slopes for cercopithecine tribes revealed that cercopithecins (0.33) had a higher value than did papionins (0.23). Reference to Figure 13E suggested that, again, the higher slope in cercopithecins was due to the effect of two outlying variates: the female M. talapoin and male E. patas. The combined effect of a very small value for foot length in female M. talapoin and a high value in male E. patas was to rotate the cercopithecine LS slope counterclockwise. When the female M. talapoin and male E. patas

variates were dropped from the sample, and the cercopithecine tribal slopes re-estimated, there was no significant difference between the tribes ($Pr > F 0.14$) (Table 25).

The predicted geometric similarity coefficient is above the upper 95% confidence limit of the cercopithecine line (slope 0.26 or 0.25) but coincident with the upper 95% confidence limit of the colobine line (slope 0.27). However, because there is no significant difference between the slopes of the two subfamilies, and because the estimated slopes are well below the predicted isometric coefficient, it is reasonable to conclude that the foot has a negative allometric relationship with body mass in both subfamilies. Therefore, species with a larger body mass have a relatively shorter foot than those at smaller body mass. Furthermore, the LS exponents in both subfamilies are close to the predicted elastic similarity coefficient.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.4322$) but a highly significant difference between the two subfamilies ($Pr > F 0.0001$). At comparable body masses, the average colobine has a longer foot than does the average cercopithecine. Reference to Figure 13E and Table 26 indicates that six variates fell near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas have longer feet than expected for their body masses and male M. fuscata and female M. talapoin shorter feet than expected for their body mass. Within colobines, female C. polykomos has a significantly longer foot

than expected for its body mass and female S. (Trachypithecus) cristata has a shorter foot than expected for its body mass.

Foot Segments

Indices: Non-hallucal Segments

Tarsus/Foot. The average mean index for cercopithecine species is 37 with a range of 35-43 (Tables 27-28). Miopithecus has the lowest average index value while E. patas has the highest. C. pygerythrus is most similar to E. patas in having a relatively high average value for this index. The average mean tarsus/foot index for papionin species is 39 with a range of mean values of 36-42 (Table 28). Most macaques, Cercocebus and P. (Mandrillus) species have mean values in the range of 36-39. P. (Papio), T. gelada, M. fuscata and M. thibetana have higher values for the tarsus/foot index, in the range of 40-42. The average mean tarsus/foot index for colobine species is 35 with a range of mean values of 33-37 (Table 28). Among colobines, the Presbytis species generally have low average values in the range of 33-34, while the S. (Trachypithecus) species have higher values in the range of 35-36. The average values for African colobines completely overlap the Asian langur range.

Figure 14A is a box-and-whisker plot of the mean tarsus/foot index values within the cercopithecine tribes and colobines. This index clearly discriminates most papionins from colobines but cercopithecins bridge the gap between those two groups. A bivariate plot of the average species value for the tarsal/foot index against body mass (Fig. 15A)

demonstrates a moderately positive linear relationship for these variables, especially within cercopithecines (colobines $r = 0.553$; cercopithecines $r = 0.760$). There is very little overlap in index values between colobines and cercopithecines at comparable body masses, suggesting a fundamental difference between the two subfamilies for this index. Thus, at comparable body masses, colobines have a lower value for the tarsus/foot index than do cercopithecines. Furthermore, E. patas, and especially female E. patas, has rather high values for the tarsus/foot index given its body mass.

Metatarsal 3/Foot. The average mean index for cercopithecine species is 42 with a range of 40-43 (Tables 27-28). Given this narrow range in values, no one cercopithecine species or species group stands out as particularly noteworthy. The average mean metatarsal 3/foot index for papionin species is 40 with a range of mean values of 37-43 (Tables 27-28). The two most noteworthy species in this tribe are M. thibetana, which has a low average value for the metatarsal 3/foot index, and T. gelada, with a high average value. The average mean metatarsal 3/foot index for colobine species is 42 with a range of mean values of 40-44 (Tables 27-28). Among colobines, the Presbytis species are noteworthy for having average values at the upper end of the range.

Figure 14B is a box-and-whisker plot of the mean metatarsal 3/foot index values within the cercopithecine tribes and colobines. This plot shows that there is a large overlap in the range of values for the metatarsal 3/foot index among colobines and cercopithecines. Because

cercopithecins have values at the upper end of the papionin range, a mass affect is indicated. A bivariate plot of the average species value for the metatarsal 3/foot index against body mass (Fig. 15B) also demonstrates a weak negative correlation for these variables (colobines $r = -0.424$; cercopithecines $r = -0.399$). The only noteworthy outliers are M. thibetana, with an extremely low value for the metatarsal 3/foot index for its body mass, and T. gelada, with a large value for this index for its body mass.

Phalanx 3/Foot. The average mean index for cercopithecine species is 21 with a range of 18-23 (Tables 27-28). M. talapoin is noteworthy for having a large value for the phalanx 3/foot index while E. patas has the smallest value in the tribe. The average mean phalanx 3/foot index for papionin species is 21 with a range of mean values of 16-23 (Tables 27-28). The P. (Papio) species have average values at the lower end of the range of the tribe while T. gelada has the absolutely lowest values in the tribe. The average mean phalanx 3/foot index for colobine species is 24 with a range of mean values of 22-25 (Tables 27-28). Among colobines, the Presbytis species and Nasalis are noteworthy for having average values at the lower end of the range.

Figure 14C is a box-and-whisker plot of the mean phalanx 3/foot index values within the two cercopithecine tribes and colobines. This plot shows that there is a clear separation of colobines from cercopithecines in the mean and range of mean values for the phalanx 3/foot index. Furthermore, there is no distinction between the cercopithecine

tribes. A bivariate plot of the average species value for the phalanx 3/foot index against body mass (Fig. 15C) demonstrates that there is no correlation of these variables in colobines ($r = -0.078$) and depending upon the species composition of the sample, no correlation within cercopithecines. When P. (Papio), E. patas and T. gelada are included in the cercopithecine sample, the correlation coefficient is -0.570 , but when the terrestrial species are dropped from the sample the correlation coefficient drops to -0.197 . This is because P. (Papio), E. patas and T. gelada are quite distinct from other cercopithecines in having low average values for the phalanx 3/foot index for their body masses. Figure 15C also confirms that colobines have higher values for this index than do cercopithecines, even at comparable body masses.

Tarsus/Sole. The average mean index for cercopithecine species is 47 with a range of 45-51 (Tables 27-28). Only two species account for the extension of the range of mean values above the tribal mean. Erythrocebus patas has the highest values for the tarsal/sole index in the tribe and C. pygerythrus the second highest values. The average mean tarsus/sole index for papionin species is approximately 49 with a range of mean values of 47-53 (Table 28). Most macaques, Cercocebus and P. (Mandrillus) species have mean values in the range of 47-49. The P. (Papio) species, T. gelada, M. fuscata, nigra, tonkeana and M. thibetana have higher values for the tarsus/sole index, in the range of 50-53 (Table 27). The average mean tarsus/sole index for colobine species is about 46 with a range of mean values of 43-50 (Table 28). Among colobi-

nes, the Presbytis species generally have low average values, in the range of 43-45, while most of the S. (Trachypithecus) variates have higher values, in the range of 46-48. The average values for African colobines are similar to those of S. (Trachypithecus). P.

(Rhinopithecus) is noteworthy for having the highest values for this index in the subfamily.

Figure 16A is a box-and-whisker plot of the mean tarsus/sole index values within the cercopithecine tribes and colobines. This index clearly discriminates most papionins from colobines but cercopithecins bridge the gap between those two groups. A bivariate plot of the average species value for the tarsal/sole index against body mass (Fig. 17A) demonstrates a moderately positive linear relationship for these variables (colobines $r = 0.588$; cercopithecines $r = 0.717$). There is some separation of colobines from cercopithecines in this plot, but there is also some overlap.

Metatarsal 3/Sole. The average mean index for cercopithecine species is 53 with a range of 49-55 (Tables 27-28). Most species have average values in the range of 53-55, but C. pygerythrus, and especially E. patas, have low values for the metatarsal 3/sole index. The average mean metatarsal 3/sole index for papionin species is 51 with a range of mean values of 47-53 (Table 28). The P. (Papio) species, H. thibetana, arctoides, fuscata and H. tonkeana have values for the metatarsal 3/sole index at the lower end of the range. The average mean metatarsal 3/sole index for colobine species is 54 with a range of mean values of 50-57

(Table 28). Among colobines, the Presbytis species, in particular P. hosei and P. rubicunda, are noteworthy for having average values at the upper end of the range. P. (Rhinopithecus) is also exceptional for its low values for this index.

Figure 16B is a box-and-whisker plot of the mean metatarsal 3/sole index values within the cercopithecine tribes and colobines. This plot shows that there is practically a complete separation of colobines and papionins in their range of values for the metatarsal 3/sole index, but that the cercopithecins bridge the two groups by overlapping with them. A bivariate plot of the average species value for the metatarsal 3/sole index against body mass (Fig. 17B) illustrates a moderately linear negative relationships between the two variables (colobines $r = -0.588$; cercopithecines $r = -0.717$). The degree of separation, and overlap, between the two subfamilies is the same as for the preceding index, as is expected since the two indices are complementary to each other.

Phalanx 3/Sole. The average mean index for cercopithecine species is 27 with a range of 21-31 (Tables 27-28). M. talapoin is noteworthy for having a large value for the phalanx 3/sole index while E. patas has the smallest value in the tribe. The average mean phalanx 3/sole index for papionin species is 26 with a range of mean values of 19-30 (Table 28). The P. (Papio) species have average values at the lower end of the range of the tribe while T. gelada has the absolutely lowest values in the tribe. The average mean phalanx 3/sole index for colobine species is 31 with a range of mean values of 29-34 (Table 28). Among colobines, the

Presbytis species and N. larvatus are noteworthy for having average values at the lower end of the range.

Figure 16C is a box-and-whisker plot of the mean phalanx 3/sole index values within the cercopithecine tribes and colobines. This plot shows that there is a clear separation of colobines from cercopithecines in the mean and range of mean values for the phalanx 3/sole index. Furthermore, there is no distinction between the cercopithecine tribes. A bivariate plot of the average species value for the phalanx 3/sole index against body mass (Fig. 17C) indicates no correlation between the variables for colobines ($r = -0.077$) and, excluding the P. (Papio), E. patas and T. gelada, no correlation for cercopithecines ($r = -0.199$). When the three terrestrial genera are included within the cercopithecine sample the correlation coefficient is stronger at -0.572 . This is because P. (Papio), E. patas and T. gelada are quite distinct from other cercopithecines in having low average values for the phalanx 3/sole index for their body masses. Figure 17C also indicates that colobines have higher values for this index than do cercopithecines at comparable body masses.

Metatarsal 3/tarsus. The average mean index for cercopithecine species is 114 with a range of 94-120 (Tables 29-30). Most species have average values in the range of 112-120 but C. pygerythrus, and especially E. patas, have low values for the metatarsal 3/tarsus index. The average mean metatarsal 3/tarsus index for papionin species is 105 with a range of mean values of 90-114 (Table 30). P. (Papio), Macaca

thibetana, M. arctoides, M. fuscata and M. tonkeana have values for the metatarsal 3/tarsus index at the lower end of the range. The average mean metatarsal 3/tarsus index for colobine species is 119 with a range of mean values of 102-134 (Table 30). Among colobines, the Presbytis species, in particular P. hosei and P. rubicunda, are noteworthy for having average values at the upper end of the range. P. (Rhinopithecus) is also exceptional for its low values for this index.

Figure 18A is a box-and-whisker plot of the mean metatarsal 3/tarsus index values within the cercopithecine tribes and colobines. This plot shows that there is practically a complete separation of colobines and papionins in their range of values for the metatarsal 3/tarsus index, but that the cercopithecins bridge the two groups by overlapping with them. A bivariate plot of the average species value for the metatarsal 3/tarsus index against body mass (Fig. 19A) demonstrates a moderately linear negative relationships between the two variables (colobines $r = -0.585$; cercopithecines $r = -0.726$). The degree of separation, and overlap, between the two subfamilies is the same as for the index metatarsal 3/sole.

Power Arm/Load Arm. The average mean index for cercopithecine species is 25 with a range of 22-29 (Tables 29-30). M. talapoin is noteworthy for having a small value for the power arm/load arm index while E. patas has the largest value in the tribe. The average mean power arm/load arm index for papionin species is 28 with a range of mean values of 24-32 (Table 30). No one species or species group is par-

ticularly noteworthy for their value of this index. The average mean power arm/load arm index for colobine species is 25 with a range of mean values of 22-27 (Table 30). Among colobines, S. (Semnopithecus) entellus and P. (Rhinopithecus) are noteworthy for having the largest average values for this index.

Figure 18B is a box-and-whisker plot of the mean power arm/load arm index values within the cercopithecine tribes and colobines. This plot shows that there is a clear separation of colobines from papionins in the mean and range of mean values for the power arm/load arm index. Cercopithecins are similar to colobines in the mean value for this index. However, the cercopithecine range is more extensive than the colobine one, and overlaps with that of papionins. Because cercopithecins, in general, have lower values for the power arm/load arm index than do papionins it is likely that there is a mass effect in operation. This is also theoretically expected on biomechanical grounds. A bivariate plot of the average species value for the power arm/load arm index against body mass (Fig. 19B) shows a positive linear relationship between the values of this index and body mass (colobines $r = 0.638$; cercopithecines $r = 0.875$). Additionally, while there is some overlap between the two subfamilies, colobines, in general, have a lower value for the power arm/load arm index than do cercopithecines at comparable body mass.

Phalanx 3/tarsus. The average mean index for cercopithecine species is 58 with a range of 41-67 (Tables 29-30). M. talapoin is noteworthy

for having a large value for the phalanx 3/tarsus index while E. patas has the smallest value in the tribe. C. pygerythrus has the next smallest value for this index in the tribe. The average mean phalanx 3/tarsus index for papionin species is 54 with a range of mean values of 39-63 (Table 30). The P. (Papio) species have average values at the lower end of the range of the tribe while T. gelada has the absolutely lowest values in the tribe. The average mean phalanx 3/tarsus index for colobine species is 68 with a range of mean values of 64-76 (Table 30). Nasalis larvatus is noteworthy for having the lowest average values for this index.

Figure 18C is a box-and-whisker plot of the mean phalanx 3/tarsus index values within the cercopithecine tribes and colobines. This plot shows that there is a clear separation of colobines from cercopithecines in the mean and range of mean values for the phalanx 3/tarsus index. Furthermore, there is little distinction between the cercopithecine tribes. A bivariate plot of the average species value for the phalanx 3/tarsus index against body mass (Fig. 19C) demonstrates a negative correlation (colobines $r = -0.432$; all cercopithecines $r = -0.687$; cercopithecines without terrestrial genera $r = -0.584$). Figure 19C demonstrates that the P. (Papio) species, E. patas and T. gelada are quite distinct from other cercopithecines in having low average values for the phalanx 3/tarsus index for their body masses. Figure 19C also indicates that colobines have higher values for this index than do cercopithecines at any given body mass.

Phalanx 3/Metatarsal 3. The average mean phalanx 3/metatarsal 3 index for cercopithecine species is 52 with a range of 42-56 (Tables 29-30). E. patas is noteworthy for the low value of its index and M. talapoin for the high value of its index. The average mean phalanx 3/metatarsal 3 index for papionin species is 52 with a range of mean values of 39-63 (Table 30). Again, T. gelada is distinctive for its low value for this index. The P. (Papio) species are also noteworthy for differing from other papionins in having a relatively low value for this index. Macaca thibetana also stands out for its high value for this index. The average mean phalanx 3/metatarsal 3 index for colobine species is 57 with a range of mean values of 51-63 (Table 30). The Presbytis species are most noteworthy for their low values for this index.

Figure 18D is a box-and-whisker plot of the mean phalanx 3/metatarsal 3 index values within the cercopithecine tribes and colobines. This plot clearly shows that there is a distinction between colobines and most cercopithecines in the mean and range of values for this index, with colobines having higher values. A bivariate plot of the phalanx 3/metatarsal 3 index against body mass (Fig. 19D) demonstrates that there is a weak negative correlation for colobines ($r = -0.380$) and no linear correlation between body mass and the value of the index in cercopithecines (all species $r = 0.196$; without terrestrial genera $r = 0.236$). Figure 19D also clearly demonstrates that T. gelada has an extremely low value for the phalanx 3/metatarsal 3 index for its body mass. Similarly, E. patas and the P. (Papio) species have relatively low

values for their body masses. Macaca thibetana, on the other hand, has an extremely high index value for its body mass. While colobines have higher values for this index compared to many cercopithecines, there is a great deal of overlap between the macaques and colobine species at comparable body masses.

Bivariate Relationships of Lengths and Cross-sectional Dimensions of Metatarsal 3 and Proximal Phalanx 3. A bivariate plot of the length of the third metatarsal against its cross-sectional area at mid-shaft indicates that there is a positive correlation between these dimensions in both subfamilies (colobines $r = 0.833$; cercopithecines $r = 0.961$). While there is a great deal of overlap between the subfamilies, colobines, and especially Presbytis species, tend to have longer metatarsals at comparable cross-sectional areas than do cercopithecines (Fig. 20A). This is further indicated by a comparison of the RMA coefficients, wherein colobines have a higher value for the y-intercept (colobines 2.89; cercopithecines 2.78) (Fig. 20A). The 95% confidence intervals around the RMA lines (cercopithecine slope 0.39; colobine slope 0.43) for both subfamilies do not include the predicted elastic similarity exponent. In the case of cercopithecines neither is the predicted geometric similarity exponent included within the 95% confidence interval, but the geometric similarity exponent is included within the upper 95% confidence limit in colobines. Thus, for both subfamilies the allometric relationship is negative but not elastic.

The difference between the subfamilies is even more pronounced for

the bivariate plot of the length of proximal phalanx 3 against its mid-shaft breadth (Fig. 20B). (The data are logged because transforming them yielded a higher correlation coefficient). Both subfamilies again have a relatively strong positive correlation between the variables (colobines $r = 0.839$; cercopithecines $r = 0.796$). For both subfamilies the predicted elastic similarity exponent falls within the 95% confidence interval of the RMA lines (colobine slope 0.79; cercopithecine slope 0.70) and the predicted geometric similarity exponent is well above the upper 95% confidence limit. Thus, phalangeal length scales elastically with phalangeal breadth. Colobines clearly have a narrower proximal phalanx than do cercopithecines, as indicated by the difference in the RMA y-intercepts for the groups (colobines 2.44; cercopithecines 2.42). P. (Papio), M. thibetana, M. fuscata, T. gelada and E. patas have relatively short phalanges, given their mid-shaft breadths.

Ancova of LS Regressions: Non-hallucal Foot Segment Measurements vs Body Mass

Sole Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes and the cercopithecoid subfamilies were not significant at the 0.01 level (Table 31). However, the probability of a greater F value for a difference in slopes between the two cercopithecine tribes was significant at the 0.04 level, which is a much smaller value than is typical for this contrast. As was the case in previous comparisons (e.g., hindlimb and foot lengths on mass), the large value for male E. patas, and small value for female M. talapoin, resulted in a

steeper slope for cercopithecins (0.33) than papionins (0.27) (Fig 21A). When the outlying variates were removed from the sample and the test re-run, the difference between the tribes disappeared ($Pr > F$ 0.48) (Table 31).

The 95% confidence interval around the colobine LS line (slope 0.28) includes the predicted geometric similarity coefficient while the 95% confidence interval around the cercopithecine line (slope 0.28 or 0.29) does not. However, because both subfamilies have identical values for the LS slope, and are not significantly different from each other, it is reasonable to conclude that sole length has a negative allometric relationship with body mass. Larger cercopithecoid species have relatively shorter soles than do smaller species.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F$ 0.14) but a significant difference between the two subfamilies ($Pr > F$ 0.0001). Therefore, at comparable body masses, the average colobine has a longer sole than the average cercopithecine. Reference to Figure 21A and Table 32 indicate that five variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas have longer soles than expected for their body masses and male M. fuscata and M. thibetana have shorter soles than expected for their body masses. Within colobines, male P. hosei has a longer sole than expected for its body mass.

Tarsus Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.06$) and the cercopithecoid subfamilies ($Pr > F 0.69$) were not significant at the 0.01 level (Table 31).

The 95% confidence interval around both subfamilial LS lines (colobines 0.34; cercopithecines 0.32) includes the predicted geometric similarity coefficient. Furthermore, both subfamilial estimated slopes are extremely close to the predicted value of isometry. As a consequence, it is reasonable to conclude that tarsus length scales isometrically with body mass in cercopithecoids.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.27$) nor between the two subfamilies ($Pr > F 0.85$). Therefore, at comparable body masses, the average colobine has a tarsus which is equivalent in length to that of the average cercopithecine. Reference to Figure 21B and Table 32 indicates that six variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona, E. patas and M. tonkeana have a longer tarsus than expected for their body masses and male M. fuscata has a shorter tarsus than expected for its body mass. Within colobines, both male and female S. (Semnopithecus) entellus have a significantly longer tarsus than expected for their body masses.

Calcaneus Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.04$) and the cercopithecoid

subfamilies ($Pr > F 0.99$) were not significant at the 0.01 level (Table 31). However, the probability of a greater F value for a difference in slopes between the two cercopithecine tribes fell just short of being significantly different at the 0.01 level. This was due to the large value for male E. patas, which effected a counterclockwise rotation of the slope for cercopithecins (Fig. 21C). When the male E. patas value was removed, the degree of difference between the tribes disappeared ($Pr > F 0.13$).

The 95% confidence interval around both subfamilial LS (colobines 0.34; cercopithecines 0.32) lines includes the predicted geometric similarity coefficient. Furthermore, both subfamilial estimated slopes are extremely close to the predicted value of isometry. As a consequence, it is reasonable to conclude that calcaneus length scales isometrically in cercopithecids.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.10$) nor between the two subfamilies ($Pr > F 0.63$). Therefore, at comparable body masses, the average colobine has a calcaneus which is equivalent in length to that of the average cercopithecine. Reference to Figure 21C and Table 32 indicates that five variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas have a longer calcaneus than expected for their body masses and male M. fuscata has a shorter calcaneus than expected for its body mass. Within colobines, S. (Semnopithecus) has a significantly longer

calcaneus than expected for its body mass.

Calcaneal Load Arm Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.10$) and the cercopithecoid subfamilies ($Pr > F 0.34$) were not significant at the 0.01 level (Table 31).

The 95% confidence interval around the colobine LS line (slope 0.29) includes the predicted geometric similarity coefficient whereas the predicted geometric similarity coefficient fell well above the upper 95% confidence interval of the cercopithecine line (slope 0.25). Because both subfamilial estimated slopes are below the predicted value of isometry, it is reasonable to conclude that the calcaneal load arm has a negative allometric relationship with body mass. As a consequence, large cercopithecoid species have a shorter calcaneal load arm than do smaller-bodied species.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.07$) nor between the two subfamilies ($Pr > F 0.06$) at the 0.01 level. Therefore, at comparable body masses, the average colobine has a calcaneal load arm which is equivalent in length to that of the average cercopithecine. Reference to Figure 21D and Table 32 indicates that four variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona has a longer calcaneal load arm than expected for its body mass while M. fuscata and female M. talapoin have shorter

calcaneal load arms than expected for their body masses. Among colobines, female N. larvatus has a longer calcaneal load arm than expected for its body mass.

Cuboid Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F$ 0.28) and the cercopithecoid subfamilies ($Pr > F$ 0.21) were not significant at the 0.01 level (Table 31).

The colobine estimated slope (0.35) is greater than isometry, but the 95% confidence interval around the slope includes the predicted geometric similarity coefficient. However, the cercopithecine estimated slope (0.30) is less than the predicted value of isometry and the 95% confidence interval does not include the isometric coefficient. Therefore, it appears that cuboid length scales isometrically in colobines but has a negative allometric relationship with body mass in cercopithecines. On the other hand, because the subfamilies do not differ from each other in the values of their slopes, it is also reasonable to conclude that cuboid length scales isometrically in the family as a whole.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F$ 0.81) nor between the two subfamilies ($Pr > F$ 0.10) at the 0.01 level. Therefore, at comparable body masses, the average colobine has a cuboid which is equivalent in length to that of the average cercopithecine. Reference to Figure 21E and Table 32 indi-

cates that six variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona, both sexes of E. patas and male M. tonkeana have a longer cuboid than expected for their body masses. Within colobines, female S. (Semnopithecus) entellus has a significantly longer cuboid than expected for its body mass while male P. (Ptilocolobus) badius has a shorter cuboid than expected for its body mass.

Power Arm Length vs Mass. Tests for the homogeneity of slopes showed a significant between the cercopithecine tribes ($Pr > F 0.01$) while there was no significant difference between the cercopithecoid subfamilies ($Pr > F 0.74$) (Table 31). Examination of Figure 22A and Table 32 indicates that the likely reason for the significant difference between the tribes is that the low values for M. talapoin and high values for E. patas caused the cercopithecine line to rotate in a counterclockwise direction. When the Erythrocebus and Miopithecus variates were removed from the sample, and the test re-run, the probability for a greater F value rose to a non-significant level ($Pr > F 0.13$) (Table 31).

The predicted geometric similarity coefficient fell well below the lower 95% confidence limit of the original and modified cercopithecine LS lines (slope 0.38) and within the 95% confidence interval of the colobine line (slope 0.37). Nevertheless, it is reasonable to conclude that power arm length has a positive allometric relationship with body mass in cercopithecids: large cercopithecoid species have relatively

longer power arms than do smaller members of the family.

The results of ancovas for the both the original and modified LS lines showed no difference between the adjusted group means of the cercopithecine tribes ($Pr > F$ 0.37 or 0.85) but a significant difference between the two subfamilies ($Pr > F$ 0.0034) at the 0.01 level. However, this difference is so slight that it seems more reasonable to consider the subfamilies as having a power arm which is the same length at comparable body masses. Reference to Figure 22A confirms that this difference is not great, even though it is statistically significant at the 0.01 level. Reference to Figure 22A and Table 32 indicate that four variates fell outside of the 95% confidence intervals of the original subfamilial lines. Within cercopithecines, male C. mona and E. patas have longer power arms than expected for their body masses while male M. fuscata has a shorter power arm than expected for its body mass. Within colobines, S. (Semnopithecus) entellus, especially the males, has a longer power arm than expected for its body mass.

Load Arm Length vs Mass. Tests for the homogeneity of slopes showed no significant difference between the cercopithecine tribes ($Pr > F$ 0.05) at the 0.01 level nor between the cercopithecoid subfamilies ($Pr > F$ 0.64) (Table 31).

The predicted geometric similarity coefficient fell well above the upper 95% confidence limit of the cercopithecine LS line (slope 0.25) and above the upper 95% confidence limit of the colobine line (slope 0.26). Therefore, it is reasonable to conclude that load arm length has

a negative allometric relationship with body mass in cercopithecids: large cercopithecoid species have relatively shorter load arms than do smaller members of the family. Furthermore, the LS coefficients for both subfamilies are similar to the predicted elastic similarity coefficient.

The results of ancovas for the LS lines showed no difference between the adjusted group means of the cercopithecine tribes ($Pr > F$ 0.15) but a significant difference between the two subfamilies ($Pr > F$ 0.0001). At comparable body masses, the average colobine has a load arm which is longer than that of the average cercopithecine. Reference to Figure 22B and Table 32 indicate that five variates fell near the limits of, or outside of, the 95% confidence intervals of the original subfamilial lines. Within cercopithecines, male C. mona and E. patas have longer load arms than expected for their body masses while male M. fuscata and M. thibetana have shorter load arms than expected for their body masses. Within colobines, male P. hosei has a longer load arm than expected for its body mass.

Ray 3 Length vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F$ 0.003) was significant at the 0.01 level while that for the cercopithecoid subfamilies ($Pr > F$ 0.71) was not significant (Table 31). The difference in slopes between the cercopithecine tribes (cercopithecins 0.29; papionins 0.19) was likely due to the small value for the female M. talapoin variate and large value for the male E. patas variate, which effected a counterclockwise rotation of the slope for cercopithecins (Fig. 23A). When these variates were removed

from the sample, and the test re-run, the probability for a greater F value rose to a non-significant level ($Pr > F$ 0.08) (Table 31).

The predicted geometric similarity coefficient fell above the upper 95% confidence limit of both subfamilial LS lines (colobine slope 0.25; cercopithecine slope 0.23 or 0.21). Therefore, it is reasonable to conclude that ray 3 length has a negative allometric relationship with body mass in cercopithecids. As a consequence, large cercopithecoid species have relatively shorter third digit rays than smaller members of the family. Furthermore, the LS exponents for both subfamilies are coincident with or close to the predicted elastic similarity coefficient.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F$ 0.6869) but a significant difference between the two subfamilies ($Pr > F$ 0.0001). Therefore, at comparable body masses, the average colobine has a ray 3 which is longer than that of the average cercopithecine. Reference to Figure 23A and Table 33 indicates that five variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona has a longer ray 3 than expected for its body mass while male M. fuscata and female M. talapoin have a shorter ray 3 than expected for their body masses. Within colobines, female C. polykomos and male P. hosei have significantly longer third digit rays than expected for their body masses.

Metatarsal 3 Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.06$) and the cercopithecoid subfamilies ($Pr > F 0.71$) were not significant at the 0.01 level (Table 31).

The predicted geometric similarity coefficient fell well above the upper 95% confidence limit of both subfamilial LS lines (colobine slope 0.22; cercopithecine slope 0.24). Therefore, it is reasonable to conclude that metatarsal 3 length has a negative allometric relationship with body mass in cercopithecoids. As a consequence, large cercopithecoid species have relatively shorter third metatarsals than smaller members of the family. Furthermore, the LS exponents for both subfamilies are close to, albeit below, the predicted elastic similarity coefficient.

The results of an ancova for the difference between the adjusted group means indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.12$) but a significant difference between the two subfamilies ($Pr > F 0.0001$). Therefore, at comparable body masses, the average colobine has a metatarsal 3 which is longer than that of the average cercopithecine. Reference to Figure 23B and Table 33 indicates that five variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona has a longer metatarsal 3 than expected for its body mass while male H. fuscata and H. thibetana and female H. talapoin have a shorter metatarsal 3 than expected for their body masses. Within colobines, male P. hosei has a significantly longer third metatarsal than expected for its body mass.

Proximal Phalanx 3 Length vs Mass. Tests for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.002$) and the cercopithecoid subfamilies ($Pr > F 0.05$) were significant at the 0.01 and 0.05 levels, respectively (Table 31). Examination of Figure 23C indicates that the likely reason for the significant difference between the tribes is that the low values for the P. (Papio) species caused the papionin line to rotate in a clockwise direction, while the low value for M. talapoin caused the cercopithecine line to rotate in the opposite direction. Similarly, the low values for the P. (Papio) species and T. gelada caused the cercopithecine slope to be significantly different from the colobine slope. When the P. (Papio), Theropithecus and Miopithecus variates were removed from the sample, and the test re-run, the probability for greater F values rose to non-significant levels ($Pr > F 0.60$ for tribes, 0.30 for subfamilies) (Table 31).

The predicted geometric similarity coefficient fell well above the upper 95% confidence limit of the original and modified cercopithecine LS lines (slopes 0.19 and 0.25 respectively) and was coincident with the upper 95% confidence limit of the colobine line (slope 0.27). Therefore, it is reasonable to conclude that proximal phalanx 3 length has a negative allometric relationship with body mass in cercopithecids: large cercopithecoid species have relatively shorter third proximal phalanges than do smaller members of the family. Furthermore, in cercopithecines the modified LS exponent is identical to the predicted elastic similarity coefficient while the colobine exponent is close to it.

The results of ancovas for the both the original and modified LS

lines showed no difference between the adjusted group means of the cercopithecine tribes ($Pr > F$ 0.17 or 0.05) at the 0.01 level but a significant difference between the two subfamilies ($Pr > F$ 0.0001). Therefore, at comparable body masses, the average colobine has a proximal phalanx 3 which is longer than that of the average cercopithecine. Reference to Figure 23C and Table 33 indicates that three variates fell outside of the 95% confidence intervals of the original subfamilial lines. Within cercopithecines, both sexes of T. gelada have a shorter proximal phalanx 3 than expected for their body masses. Within colobines, female C. polykomos has a significantly longer third proximal phalanx than expected for its body mass. The residuals of species from the modified cercopithecine LS line were calculated by forcing a slope of 0.25 through the data (Table 33). Again, only T. gelada fell outside of the 95% confidence interval for the modified line.

Metatarsal 3 Area vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F$ 0.02) and between the cercopithecine subfamilies ($Pr > F$ 0.61) showed no significant differences at the 0.01 level (Table 31). However, the slopes of the cercopithecine tribes were significantly different at the 0.02 level, a value low enough to warrant further investigation. Reference to Figure 23D and Table 33 suggests that the small values for M. talapoin and large values for E. patas effected a counterclockwise rotation to the cercopithecine line and thus were the cause of the difference between cercopithecine tribes. When these variates were removed from the sample and the tribal

slopes re-estimated and tested, there was no significant difference between the tribes ($Pr > F 0.69$) (Table 31).

The predicted value of geometric similarity lay well within the 95% confidence intervals of both the colobine and modified cercopithecine lines (colobine slope 0.60; cercopithecine modified slope 0.63). Because there is no significant difference between the slopes of the two subfamilies it is reasonable to conclude that metatarsal 3 cross-sectional area scales isometrically in both subfamilies. Therefore, species with a larger body mass have a similarly proportioned third metatarsal as those at smaller body mass.

The results of an ancova for the difference between the adjusted group means of the modified cercopithecine and original colobine lines indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.07$) but a significant difference between the subfamilies ($Pr > F 0.0001$). Thus, at comparable body masses, colobines on average have a larger cross-sectional area to their third metatarsal than do cercopithecines. Reference to Figure 23D and Table 33 indicate that five variates fall outside of the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas and female M. nigra have larger cross-sectional areas than expected for their body masses. Among colobines, male S. (Semnopithecus) entellus has a larger cross-sectional area than expected for its body mass while female S. (Trachypithecus) cristata has a smaller cross-sectional area than expected for its body mass.

Phalanx 3 Breadth vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F$ 0.07) and between the cercopithecoid subfamilies ($Pr > F$ 0.52) showed no significant differences at the 0.01 level (Table 31).

The predicted value of geometric similarity lay well within the 95% confidence intervals of both the colobine and cercopithecine lines (colobine slope 0.35; cercopithecine slope 0.32). Because there is no significant difference between the slopes of the two subfamilies it is reasonable to conclude that phalanx 3 breadth scales isometrically with body mass in both subfamilies. Therefore, species with a larger body mass have a similarly broad third phalanx as those at smaller body mass.

The results of an ancova for the difference between the adjusted group means of the cercopithecine and colobine lines indicated that there was no difference between the cercopithecine tribes ($Pr > F$ 0.99) nor the subfamilies ($Pr > F$ 0.02) at the 0.01 level of significance. Thus, at comparable body masses, colobines on average have the same breadth to their third proximal phalanx as do cercopithecines. Reference to Figure 23E and Table 33 indicate that seven variates fell near the limit of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona and E. patas and female M. nigra have larger breadths than expected for their body masses while male M. nigra and female M. sphinx have smaller breadths than expected for their body masses. Among colobines, male P. (Procolobus) verus has a larger breadth than expected for its body mass while male C. vellerosus has a smaller cross-sectional area than expected for its body mass.

Hallucal Segments

Hallucal Indices

Ray 1/Foot. The average mean ray 1/foot index for cercopithecine species is 38 with a range of 31-42 (Tables 34-35). E. patas is noteworthy for having the lowest average index. The average mean ray 1/foot index for papionin species is 39 with a range of mean values of 33-44 (Table 35). M. thibetana and T. gelada have the lowest indices in the tribe with the P. (Papio) species ranking second lowest (Table 34). The average mean ray 1/foot index for colobine species is 37 with a range of mean values of 35-41 (Table 35). Among colobines, S. (Trachypithecus) obscura has the largest index and C. guereza the lowest value.

Figure 24A is a box-and-whisker plot of the mean ray 1/foot index values within the cercopithecine tribes and colobines. This plot clearly shows that there is little difference among cercopithecids in the average mean value or range of mean values for the ray 1/foot index. Furthermore, a bivariate plot of the average species value for the ray 1/foot index against body mass (Fig. 25A) demonstrates that there is a poor correlation between body mass and the value of the index (colobines $r = 0.095$; cercopithecines $r = -0.261$). However, it is also apparent that three groups of variates lie at the periphery of the cercopithecid distribution. E. patas and T. gelada have relatively short indices for their body masses while female P. (Mandrillus) leucophaeus has a relatively large index for its body mass. It can also be seen that the P. (Papio) species and M. thibetana have the relatively small indices which are typical of African colobines at the middle range of body masses.

Ray 1/Sole. The average mean ray 1/sole index for cercopithecine species is 48 with a range of 38-54 (Tables 34-35). E. patas is noteworthy for having the lowest average index. The average mean ray 1/sole index for papionin species is 49 with a range of mean values of 40-57 (Table 35). T. gelada has the lowest index in the tribe with the P. (Papio) species and M. thibetana ranking second lowest (Table 34). The average mean ray 1/sole index for colobine species is 49 with a range of mean values of 43-55 (Table 35). Among colobines, the S. (Trachypithecus) species and N. larvatus have the highest values for the ray 1/sole index and S. (Semnopithecus) entellus the lowest value.

Figure 24B is a box-and-whisker plot of the mean ray 1/sole index values within the cercopithecine tribes and colobines. This plot clearly shows that there is little difference among cercopithecids in the average mean value or range of mean values for the ray 1/sole index. Furthermore, a bivariate plot of the average species value for the ray 1/sole index against body mass (Fig. 25B) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = -0.145$; cercopithecines $r = -0.298$). As with the ray 1/foot index, it is also apparent that three groups of variates lie at the periphery of the cercopithecoid distribution. The P. (Papio) species and especially E. patas and T. gelada have relatively low indices for their body masses.

Ray 1/Metatarsal 3. The average mean ray 1/metatarsal 3 index for cercopithecine species is 91 with a range of 79-100 (Tables 34-35). E.

patas is again noteworthy for having the lowest average index. The average mean ray 1/metatarsal 3 index for papionin species is 96 with a range of mean values of 77-111 (Table 35). T. gelada has the lowest index in the tribe with the P. (Papio) species ranking second lowest. The P. (Mandrillus) species, M. nigra, M. tonkeana and M. nemestrina have the largest values for this index in the tribe. The average mean ray 1/metatarsal 3 index for colobine species is 89 with a range of mean values of 82-100 (Table 35). Among colobines, the S. (Trachypithecus) species, N. larvatus and P. (Pygathrix) nemaeus have the highest values for the ray 1/metatarsal 3 index and S. (Semnopithecus) entellus the lowest value.

Figure 24C is a box-and-whisker plot of the mean ray 1/metatarsal 3 index values within the cercopithecine tribes and colobines. This plot clearly shows that there is little difference between colobines and cercopithecines in the average mean value or range of mean values for the ray 1/metatarsal 3 index. The papionins, which extensively overlap the range of values of the other two groups, nevertheless have a higher mean value and a range which extends into much higher values. A bivariate plot of the average species value for the ray 1/metatarsal 3 index against body mass (Fig. 25C) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = 0.151$; cercopithecines $r = -0.028$). However, E. patas and T. gelada have relatively low indices for their body masses.

Ray 1/Ray 3. The average mean ray 1/ray 3 index for cercopithecine

species is 60 with a range of 55-66 (Tables 34-35). E. patas is noteworthy for having the lowest average index. The average mean ray 1/ray 3 index for papionin species is 63 with a range of mean values of 56-71 (Table 35). T. gelada has the lowest value with M. thibetana the second lowest in the tribe. The average mean ray 1/ray 3 index for colobine species is 57 with a range of mean values of 53-63 (Table 35). Among colobines, the S. (Trachypithecus) species, N. larvatus and P. (Pygathrix) nemaeus have the highest values for the ray 1/ray 3 index.

Figure 26A is a box-and-whisker plot of the mean ray 1/ray 3 index values within the cercopithecine tribes and colobines. This plot shows that there is a distinction between papionins and colobines in the mean value and range of values for the ray 1/ray 3 index. Cercopithecins, however, overlap those two groups. A bivariate plot of the average species value for the ray 1/ray 3 index against body mass (Fig. 27A) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = 0.283$; cercopithecines $r = 0.131$). Figure 27A also demonstrates that there is some distinction between the two subfamilies, although E. patas and T. gelada lie within the colobine range and S. (Trachypithecus) and P. (Pygathrix) within the cercopithecine range.

Metatarsal 1/Metatarsal 3. The average mean metatarsal 1/metatarsal 3 index for cercopithecine species is 61 with a range of 54-65 (Tables 36-37). E. patas is noteworthy for having the lowest average index. The average mean metatarsal 1/metatarsal 3 index for papionin species is 66

with a range of mean values of 57-77 (Table 37). T. gelada has the lowest value and the P. (Mandrillus) species the highest values in the tribe for this index. The average mean metatarsal 1/metatarsal 3 index for colobine species is 61 with a range of mean values of 59-69 (Table 37). Among colobines, S. (Semnopithecus) entellus has the lowest value for this index with C. guereza and P. badius both ranking second to it.

Figure 26B is a box-and-whisker plot of the mean metatarsal 1/metatarsal 3 index values within the cercopithecine tribes and colobines. This plot shows that colobines and cercopithecins are similar to each other in the mean and range of values for the metatarsal 1/metatarsal 3 index. Papionins have a higher mean and range of higher values than do colobines and cercopithecins. A bivariate plot of the species average metatarsal 1/metatarsal 3 index against body mass (Fig. 27B) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = 0.163$; cercopithecines $r = 0.180$). Figure 27 also demonstrates that there is extensive overlap between the two subfamilies. It is also noteworthy that the P. (Mandrillus) species, especially female P. (Mandrillus) leucophaeus, lie at the top of the plot and E. patas at the bottom.

Phalanx 1/Phalanx 3. The average mean phalanx 1/phalanx 3 index for cercopithecine species is 57 with a range of 52-63 (Tables 36-37). No species is distinctive in its value for this index. The average mean phalanx 1/phalanx 3 index for papionin species is 58 with a range of mean values of 51-66 (Table 37). Like cercopithecins, no species is

distinctive in its value for this index. The average mean phalanx 1/phalanx 3 index for colobine species is 51 with a range of mean values of 46-59 (Table 37). Among colobines, the S. (Trachypithecus) species and N. larvatus are noteworthy for their high values in this index.

Figure 26C is a box-and-whisker plot of the mean phalanx 1/phalanx 3 index values within the cercopithecine tribes and colobines. This plot clearly shows that colobines are distinctive from cercopithecins and papionins, in having a lower mean value and range of means. A bivariate plot of the species average phalanx 1/phalanx 3 index against body mass (Fig. 27C) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = 0.394$; cercopithecines $r = 0.108$). Figure 27C also demonstrates that there is a clear distinction between the two subfamilies in the average value of the index for any particular body mass. With the exception of N. larvatus and P. nemaeus, colobines tend to have a lower value for the phalanx 1/phalanx 3 index than do cercopithecines at comparable body mass. Female M. tonkeana has a moderately high value for this index given its body mass.

Phalanx 1/Metatarsal 1. The average mean phalanx 1/metatarsal 1 index for cercopithecine species is 48 with a range of 43-52 (Tables 36-37). E. patas is noteworthy for the low value of its index. The average mean phalanx 1/metatarsal 1 index for papionin species is 46 with a range of mean values of 35-53 (Table 37). Papioninans and macacins are distinguished from each by the mean values of this index: the range of mean values in papioninans is, with the exception of T. gelada, 41-47

and in macacins is 47-52. Theropithecus gelada is particularly noteworthy for having an extremely low value for this index. The average mean phalanx 1/metatarsal 1 index for colobine species is 47 with a range of mean values of 40-55 (Table 37). Although the sample mass is small, P. (Pygathrix) nemaus stands out for its high value for this index.

Figure 26D is a box-and-whisker plot of the mean phalanx 1/metatarsal 1 index values within the cercopithecine tribes and colobines. This plot shows that there is extensive overlap in the ranges of mean values for this index in cercopithecids. A bivariate plot of the species average phalanx 1/metatarsal 1 index against body mass (Fig. 27D) demonstrates that there is little correlation between body mass and the value of the index (colobines $r = 0.412$; cercopithecines $r = -0.484$). Figure 27D also demonstrates that T. gelada has an extremely low value for the phalanx 1/metatarsal 1 index for its body mass.

Ancova of LS Regressions: Hallucal Segment Measurements vs Body Mass

Ray 1 Length vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.07$) and cercopithecid subfamilies ($Pr > F 0.23$) showed no significant differences at the 0.01 level (Table 38). However, the slopes of the cercopithecine tribes (cercopithecins 0.26; papionins 0.17) were significantly different at the 0.07 level, a value low enough to warrant further investigation. Reference to Figure 28A and Table 39 shows that the P. (Papio) species, T. gelada, M. thibetana and E. patas have relatively short halluces for their body

masses, and were likely the cause of the significant difference between the tribal slopes. Therefore, these variates were removed from the sample and the ancova was re-run. Indeed, with the outlying variates removed, the probability values for a greater F value increased dramatically to a level where the differences between the tribes were insignificant ($Pr > F 0.50$) (Table 38).

The modified cercopithecine estimated LS slope (0.32) is close to the predicted value of geometric similarity while the upper 95% confidence limit of the colobine line (slope 0.27) is coincident with the predicted isometric coefficient. Because there is no significant difference between the slopes of the two subfamilies it is reasonable to conclude that ray 1 length scales isometrically in both subfamilies. Therefore, species with a larger body mass have a similarly proportioned hallux as do those at smaller body mass.

The results of an ancova for the difference between the adjusted group means of the modified cercopithecine and original colobine lines indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.13$) nor between the subfamilies ($Pr > F 0.37$). This is also apparent by inspection of Figure 28A. Reference to Figure 28A and Table 39 indicates that five variates fall near the limits of or outside of the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male M. thibetana, T. gelada and P. (Papio) ursinus have shorter halluces than expected for their body masses. All the other P. (Papio) variates also fall well below the modified subfamilial line, but not to the same extreme as the above mentioned ones. Within colobines,

male P. hosei has a significantly longer hallux than expected for its body mass.

Metatarsal 1 Length vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F$ 0.06) and cercopithecoid subfamilies ($Pr > F$ 0.76) showed no significant differences at the 0.01 level (Table 38). However, as in the preceding case, the slopes of the cercopithecine tribes (cercopithecins 0.29; papionins 0.20) were significantly different at the 0.06 level and for the same reason. Therefore, the P. (Papio) species, T. gelada, M. thibetana and E. patas were removed from the sample and the ancova was re-run. Again, with the outlying variates removed, the probability values for a greater F value increased dramatically to a level where the differences between the tribes were insignificant ($Pr > F$ 0.84) (Table 38).

The modified cercopithecine estimated LS slope (0.33) is coincident with the predicted value of geometric similarity. However, the predicted value for isometry lies above the upper 95% confidence limit of the colobine line (slope 0.25). Indeed, the colobine line is coincident with that predicted by the elastic similarity model. Nevertheless, because there is no significant difference between the slopes of the two subfamilies it is reasonable to conclude that metatarsal 1 length scales isometrically in both subfamilies. Therefore, species with a larger body mass have a similarly proportioned metatarsal as those at smaller body mass.

The results of an ancova for the difference between the adjusted

group means of the modified cercopithecine and original colobine lines indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.19$) nor between the subfamilies ($Pr > F 0.35$). This is also apparent by inspection of Figure 28B. Reference to Figure 28B and Table 39 indicates that five variates fall near the limits of, or outside of, the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male C. mona has a metatarsal 1 longer than expected for its body mass while M. fuscata and M. thibetana have first metatarsals shorter than expected for their body masses. Within colobines, male P. hosei has a significantly longer metatarsal than expected for its body mass while male P. (Piliocolobus) badius has a shorter one than expected for its body mass.

Phalanx 1 Length vs Mass. A test for the homogeneity of slopes between the cercopithecine tribes ($Pr > F 0.08$) and cercopithecoid subfamilies ($Pr > F 0.02$) showed no significant differences at the 0.01 level. However, the slopes of the cercopithecine tribes and the cercopithecoid subfamilies were significantly different enough to warrant further investigation. Reference to Figure 28C and Table 39 shows that the P. (Papio) species, T. gelada, M. thibetana and E. patas have relatively short phalanges for their body masses, and were likely the cause of the significant difference between the tribal slopes (cercopithecine slope 0.22; papionin slope 0.12), as was the case for the regressions of the complete hallux and body mass. Therefore, these variates were removed from the sample and the ancova was re-run. With the outlying variates

removed, the probability values for a greater F value increased to a level where the differences between the tribes and subfamilies were insignificant ($Pr > F 0.45$) (Table 38).

The predicted value of geometric similarity lay well within the 95% confidence intervals of both the colobine (slope 0.32) and modified cercopithecine (slope 0.30) lines. Because there is no significant difference between the slopes of the two subfamilies it is reasonable to conclude that phalanx 1 length scales isometrically in both subfamilies. Therefore, species with a larger body mass have a similarly proportioned phalanx 1 as those at smaller body mass.

The results of an ancova for the difference between the adjusted group means of the modified cercopithecine and original colobine lines indicated that there was no difference between the cercopithecine tribes ($Pr > F 0.18$) nor between the subfamilies ($Pr > F 0.59$). This is also apparent by inspection of Figure 28C. Reference to Figure 28C and Table 39 indicate that six variates fall outside of the 95% confidence intervals of the subfamilial lines. Within cercopithecines, male P. (Papio) ursinus and both sexes of T. gelada have shorter hallucal phalanges than expected for their body masses. All the other P. (Papio) variates also fall well below the subfamilial line, but not to the same extreme as the above mentioned ones. Within colobines, female P. (Pygathrix) nemaeus has a significantly longer hallux than expected for its body mass and male C. quereza and P. aygula a shorter hallux than expected for their body masses.

Digit Length and Robusticity Formulas

Length Formulas

Digit Rays. There are fifteen permutations of the formulas for the length of the digit rays (Table 40). Of these fifteen permutations, eight account for the highest frequencies among the groups. The fifteen formulas are collapsed into four, of which two account for the majority of the specimens.

In cercopithecins, the most common (71%) ray length formula is $3 \geq 4 > 2 \geq 5$ and the second most common (22%) permutation is $3 \geq 4 > 5 \geq 2$ (Tables 41-42). Thus, the third digit ray is generally the longest while the second and fifth vie for last place. In papionins, the most common (43%) digit ray length formula is, as in cercopithecins, $3 \geq 4 > 2 \geq 5$ (Table 42). Two formulas vie for second place: $3 \geq 4 > 5 \geq 2$ (25%) and $4 \geq 3 > 5 \geq 2$ (26%). Formula $4 \geq 3 \geq 2 \geq 5$ accounted for the remaining 6% of the papionin sample. Examination of Table 41 reveals that it is primarily the P. (Papio) species and C. albigena which present the formula $4 \geq 3 > 5 \geq 2$. In colobines, the digit ray length formula $4 \geq 3 > 5 \geq 2$ is the most common (96%) within the sample (Table 42). With only three exceptions, the fourth digit ray is consistently the longest in colobines. Similarly, the fifth digit ray is consistently the third longest and the second is the shortest.

A G-test of the frequencies of digit ray formulas among the three cercopithecoid clades indicates that the cercopithecine tribes are significantly different from each other ($p < 0.0001$) as are the cercopithecoid subfamilies ($p < 0.0001$) (Table 42). However, the relative proportion of the G values indicates that the difference between the sub-

families was more significant than that between the tribes. Furthermore, it can be demonstrated that the reason the two cercopithecine tribes are significantly different is due to the effect of the P. (Papio) and C. albigena specimens with a formula of $4 \geq 3 > 5 \geq 2$. When these specimens were removed from the sample, and the test re-run, the probability for the G value comparing the cercopithecine tribes was increased to a non-significant level ($p < 0.174$).

Within cercopithecins, the difference in length between the central pair of rays, 3 and 4, and between the flanking pair of rays, 2 and 5, is on average less than 1% (Tables 43-44). The difference in length between the medial and lateral pairs of rays is larger, on average 5%. Papionins are similar to cercopithecins. In colobines, on average, the third ray is shorter than the fourth and the second ray is 3% shorter than the fifth. Comparison of the medial and lateral pairs of rays indicates that the third ray is 7% longer than the second and the fourth ray is 5% longer than the fifth.

Analysis of variance and multiple a posteriori t-tests were performed on the differences in length between pairs of rays among cercopithecids (Table 44). These revealed that for all comparisons there was no difference between the cercopithecine tribes at the 0.01 experimentwise level but a significant difference between colobines and cercopithecines for the comparisons of central, flanking and medial pairs of rays. Colobines had a shorter third ray compared to the fourth and a shorter second ray compared to the fifth than did cercopithecines. Similarly, colobines had a shorter second ray compared to the third than did cerco-

pithecines.

The average proportions of each ray to their summed total is presented in Table 45 and illustrated as a box-and-whisker plot in Figure 29. In cercopithecins and papionins, the flanking rays are typically approximately 24% of the summed lengths while the central rays approximately comprise 26% each. The distinctive length formula of the P. (Papio) species and C. albigena, relative to the other papionins, is also highlighted in the average proportion of the ray lengths (Table 45). P. (Papio) and C. albigena both have small values for the relative proportion of the third ray and a large value for that of the fifth ray. In colobines, the second ray is typically 23% of the summed lengths, the third ray is 26%, the fourth ray is 27% and the fifth ray is 24% of the summed lengths.

Figure 29 illustrates what is already clear from the foregoing: that, on average, colobines have a proportionally shorter second digit ray and longer fourth and fifth digit rays than do cercopithecines. The subfamilies are otherwise similar to each other in the proportionate length of the third digit ray. Thus, colobines are distinguished from cercopithecines in that the third and fourth digits project substantially beyond the flanking fifth and second. In most cercopithecines, there is a moderately steep gradient between digits, although nothing of the sort as between the central and flanking digits in colobines. The strongly terrestrial P. (Papio) species and arboreal C. albigena depart from this plan in moderating the degree of the gradient: the third digit ray is reduced in length and the fifth increased.

Metatarsals. There are thirty-one permutations of the formulas for the length of the metatarsals (Table 46). Of these thirty-one permutations, ten account for 85% of the specimens and of those ten, five account for 60% of the specimens. Thus, the majority of permutations represent only a few individuals. The thirty-one permutations were collapsed into six formulas, of which two account for the majority of specimens.

In cercopithecins, the most common (64%) metatarsal length formula is $4 \geq 3 \geq 5 \geq 2$ and the second most common (21%) permutation is $3 \geq 4 \geq 5 \geq 2$ (Tables 47-48). Thus, the fourth metatarsal is usually the longest and the second is the shortest. In papionins, the most common (55%) metatarsal length formula is $4 \geq 3 \geq 5 \geq 2$ (Table 48). The remaining 45% of the sample is divided among four other permutations. Of these, 27% of the sample has the fourth metatarsal shorter than the third ($3 \geq 4 \geq 5 \geq 2$ and $3 \geq 4 \geq 2 \geq 5$). The P. (Papio) species differ from other papionins in having a large number of individuals with the metatarsal length formula $4 \geq 5 \geq 3 \geq 2$. In colobines, the most common (53%) metatarsal length formula is, like cercopithecines, $4 \geq 3 \geq 5 \geq 2$ (Table 48). The second most common (44%) formula is $4 \geq 5 \geq 3 \geq 2$. Only six individuals are distributed among two other formulas.

A G-test of the frequency of metatarsal length formulas among cercopithecids yielded highly significant differences between the subfamilies ($p < 0.0001$) and between the cercopithecine tribes ($p < 0.002$) (Table 48). However, the G value for the difference between subfamilies is much greater than that between the cercopithecine tribes. Examination

of Table 48 indicates that while all cercopithecids have in common the metatarsal length formula $4 \geq 3 \geq 5 \geq 2$, colobines are distinguished from cercopithecines in having a greater proportion of its sample with the formula $4 \geq 5 \geq 3 \geq 2$. Furthermore, in colobines there are only two common metatarsal formulas whereas in cercopithecines there is one common pattern, four which are less frequent but still significant, and one rarer formula. Thus, it appears that colobines are more conservative than cercopithecines in the number of permutations of the metatarsal formula. Colobines are also distinctive in that in no instance does any specimen have a third metatarsal longer than the fourth. The reason that the cercopithecine tribes statistically differ from each other in metatarsal formulas is that the P. (Papio) species have a large number of individuals with the formula $4 \geq 5 \geq 3 \geq 2$ (Table 47). When a G-test is performed on the sample with these P. (Papio) individuals removed, the probability of a greater difference between the subtribes drops to 0.05 (Table 48). At the experimentwise-rate used in this study this is a non-significant result. However, it is suggestive that the tribes do differ from each other.

Within cercopithecins and papionins, the fourth metatarsal is, on average, less than 1% longer than the third, the fifth metatarsal is greater than 1% longer than the second, and the difference between the medial pair of metatarsals is greater than the lateral pair (Tables 49-50). In colobines, the average difference in length between the fourth and third metatarsals is practically 2%. The difference between the second and fifth metatarsals is 5%. As in cercopithecines, the dif-

ference in length between the medial pair of metatarsals is greater than the lateral pair.

Differences between the subfamilies and the cercopithecine tribes are further highlighted by anovas and multiple a posteriori t-tests of the average differences in length between pairs of metatarsals (Table 50). Colobines are significantly different from cercopithecines in having a shorter third metatarsal relative to the fourth and a much shorter second metatarsal relative to the fifth. Colobines differ only from papionins in having a shorter second metatarsal relative to the third.

The average proportions of each metatarsal to their summed total is presented in Table 51 and illustrated in Figure 30. In cercopithecins and papionins, the central metatarsals both comprise approximately 26% of the total metatarsal length. The fifth metatarsal is slightly larger than the second, as expected given the metatarsal length formulas. Within cercopithecins, E. patas is noteworthy for having a relatively long second metatarsal and proportionately short third, fourth and especially fifth metatarsals (Table 51). The values for the average proportion of individual metatarsals relative to their sum also highlight P. (Papio) and C. albigena (Table 51). In P. (Papio), the third metatarsal is proportionately shorter and the fifth longer compared to the other papionins. Cercocebus albigena, on the other hand, has a proportionately much shorter second metatarsal and longer fourth and fifth metatarsals. In colobines, the fourth metatarsal is the proportionately longest in the array of lateral metatarsals. Metatarsals three

and five both contribute approximately equally to the summed length of the metatarsals while the second metatarsal is by far the shortest. Thus, in colobines, compared to cercopithecines, the medial metatarsals (two and three) are relatively shorter while the lateral metatarsals (four and five) are relatively longer. These differences are clearly illustrated in Figure 30.

Proximal Phalanges. There are twenty-one permutations of the formulas for proximal phalangeal length (Table 52). Of these permutations, seven account for 86% of the specimens and, of those seven, three account for 67% of the sample. Thus, the majority of phalangeal permutations, as with the metatarsals, represent only a few individuals. The twenty-one permutations were collapsed into four formulas, of which one accounts for the majority of specimens.

In all cercopithecids, the most common (79%) phalangeal formula is $3 \geq 4 \geq 2 \geq 5$ (Tables 53-54). However, in colobines, this formula accounts for only 52% of the sample. The majority of the remainder of the specimens are distributed over three other formulas, in which phalanges three and four, or two and five, switch places (Table 54).

A G-test of the frequencies of the phalangeal length formulas among cercopithecids reveals that there is a highly significant difference between the subfamilies (Table 54). Indeed, the highest G value is for the comparison of the subfamilies, because colobines are much more variable than cercopithecines in their phalangeal formulas. In order to compare the cercopithecine tribes, individuals with the formula $3 \geq 4 \geq 5 \geq 2$

were combined with the other rarer variants, resulting in a two-by-two frequency table. A two-tailed Fisher's Exact Test of the distribution of phalangeal formulas in cercopithecines indicated no significant difference between the tribes ($p < 1.00$).

Within both cercopithecines and papionins, the average difference in length between the central pair of phalanges is on the order of 2%, whereas that between the flanking pair of phalanges is somewhat greater (Tables 55-56). The disparity between the lateral pair of phalanges is greater than the medial pair. Theropithecus gelada is distinctive because there is little difference between the flanking pair of phalanges. In colobines, the great variety in phalangeal formulas leads to an average difference in length between the pairs of central phalanges and the pairs of flanking phalanges of less than 1%. On the other hand, the difference between the medial and lateral pairs is on the order of 10-11% (Tables 55-56).

Anovas and multiple t-tests for the significance of differences between pairs of digits among cercopithecids revealed that, for most contrasts, colobines are significantly different from cercopithecines (Table 56). Colobines show a smaller difference between the members of the central or flanking pairs of phalanges than do cercopithecines and a greater disparity between the medial pair of phalanges. For the tests of the differences in the lateral pairs, colobines differ only from papionins and not cercopithecines.

The average proportions of each phalanx to their summed total is presented in Table 57 and illustrated in Figure 31. In cercopithecines,

the second phalanx comprises approximately 24% of the summed phalangeal length, the third phalanx 28%, the fourth phalanx 27% and the fifth 21%. No one cercopithecine species stands out from the rest, thus the sample is relatively homogeneous or invariant for this, and the other two descriptions of relative lateral phalangeal lengths. In papionins, the relative proportions are similar to those in cercopithecines, except that the average third phalanx is slightly shorter and the fifth slightly longer. Theropithecus gelada stands out for the proportions of its second and fifth phalanges. The second phalanx is proportionately smaller in T. gelada than in other papionins, while its fifth is relatively larger (Table 57). Furthermore, both the second and fifth phalanges make up the same relative proportion (23% each) of the summed phalangeal lengths. Colobines differ significantly from cercopithecines in having a relatively short second phalanx and a relatively long fourth phalanx (Table 57 and Figure 31). This suggests that the reason colobines consistently differ from cercopithecines in the disparity in differences between phalangeal pairs is because each comparison involves either the second or fifth phalanx.

Robusticity Formulas

Metatarsal Cross-sectional Area. There are forty-three metatarsal cross-sectional area formulas in cercopithecids (Table 58). These were collapsed into four categories.

Within cercopithecines, two collapsed formulas are equally common, $3 \geq 4 \geq 2 \geq 5$ and $3 \geq 2 \geq 4 \geq 5$ (Tables 59-60). These formulas are similar in that

the third metatarsal consistently has the largest cross-sectional area while the fifth has the smallest. The formulas differ in the relative positions of metatarsals two and four. Papionins are similar to cercopithecins in that the two formulas, $3 \geq 4 \geq 2 \geq 5$ and $3 \geq 2 \geq 4 \geq 5$, account for the majority (83%) of the specimens (Table 60). Moreover, there is more variability in papionins than cercopithecins. However, there is no apparent taxonomic pattern to the distribution of these alternative formulas. In colobines, the majority (68%) of specimens have the formula $3 \geq 4 \geq 2 \geq 5$. The next most common (19%) formula, $3 \geq 4 \geq 5 \geq 2$, differs in the order of the flanking metatarsals. The formula $3 \geq 2 \geq 4 \geq 5$, which is so common in cercopithecines, is found in only 14% of colobines.

A G-test of the frequencies of metatarsal cross-sectional area formulas in cercopithecids reveals that there are significant differences between the subfamilies ($p < 0.0001$) and between the tribes (0.0001) (Table 60). Examination of Table 60 shows that colobines differ from cercopithecines in having fewer specimens with the formula $3 \geq 2 \geq 4 \geq 5$ and more than six times as many specimens with the formula $3 \geq 4 \geq 5 \geq 2$. It may be important that, with only one exception, no African colobine, Presbytis or P. (Pygathrix) species has the common cercopithecine formula $3 \geq 2 \geq 4 \geq 5$. Among cercopithecines, the tribes differ in that papionins are more variable than cercopithecins.

Within cercopithecins, on average, the central metatarsals differ by 10% while the flanking metatarsals differ in area by 12% (Tables 61-62). The disparity between the lateral pair of metatarsals is greater than the medial pair. Erythrocebus patas is noteworthy for the average

differences between pairs of metatarsals (Table 61). The differences between the pairs of central and flanking metatarsals are quite small compared to other cercopithecins. In papionins, the disparity between the members of the central pair of metatarsals and the flanking pair is similar to the pattern in cercopithecins (Tables 62). The difference in cross-sectional area between the lateral pair of metatarsals is greater than the medial pair. In colobines, the difference in cross-sectional area between the central pair of metatarsals is slightly greater than that between the flanking metatarsals (Table 62). Furthermore, the difference in area between the medial pair (15%) is greater than that between the lateral pair (13%). In *P. (Rhinopithecus)* the relative differences in cross-sectional area between the central, flanking and lateral pairs of metatarsals are large compared to other colobines while the difference in area between the medial pair of metatarsals is smaller (Table 61).

Analyses of variance and multiple a posteriori t-tests of the differences in area between pairs of metatarsals among cercopithecids shows that colobines differ from cercopithecins, but not papionins in having a smaller value for the difference in area between the central pair of metatarsals (Table 62). Colobines and papionins occupy opposite poles of a cline of values for the difference in area between the medial and lateral pair of metatarsals. Neither colobines, nor papionins, differ significantly from the intermediately positioned cercopithecins, but they do differ significantly from each other. The average value in colobines is larger than that in either group of cercopithecines.

The average proportions of each metatarsal cross-sectional area to the summed total of all lateral metatarsals is presented in Table 63 and illustrated in Figure 32. Within cercopithecins, the second metatarsal cross-sectional area comprises about 25% of the summed areas, the third metatarsal 30%, the fourth metatarsal 25% and the fifth metatarsal 20%. Erythrocebus patas is noteworthy for the relative proportions of individual metatarsal cross-sectional area (Table 63). In E. patas, the second and third metatarsal cross-sectional areas are smaller relative to those in other cercopithecins whereas the fourth and fifth metatarsal areas are larger. In papionins, the second and fourth metatarsals each comprise approximately 25% of the summed cross-sectional areas, while the third metatarsal comprises approximately 30% and the fifth 20%. In colobines, the average proportions of the cross-sectional areas present the same pattern as seen in the cross-sectional area formulas and average differences between pairs of metatarsals. The second metatarsal comprises approximately 23% of the summed total area, the third metatarsal comprises approximately 31%, the fourth 26% and the fifth 20%. The two colobine species, P. (Rhinopithecus) and N. larvatus, are noteworthy for their departures from the general colobine pattern (Table 63). P. (Rhinopithecus) is particularly distinctive in that the second metatarsal comprises a large proportion of the summed areas while the fifth comprises a small proportion (Table 63). The value for its fourth metatarsal is on the lower end of the range for colobines, thus yielding the moderately large difference between the third and fourth metatarsals described above. Figure 32 illustrates how in colobines the second

metatarsal is proportionately smaller in cross-sectional area than in cercopithecines and the fourth larger. It also illustrates how in papionins the third metatarsal cross-sectional area is, on average, smaller than in cercopithecins or colobines.

Phalangeal Breadth. There are thirty-two permutations of the phalangeal breadth formulas in cercopithecids (Table 64). These were collapsed into five formulas.

In cercopithecids, the two phalangeal breadth formulas, $3 \geq 4 \geq 2 \geq 5$ and $3 \geq 4 \geq 5 \geq 2$, account for 69-89% of the sample (Tables 65-66). Thus, in the majority of cercopithecids, the third phalanx is the broadest, the fourth is second to it and the second and fifth phalanges vie for last place. A G-test of the frequencies of formulas in cercopithecids indicate that the subfamilies are significantly different from each other ($p < 0.000$) whereas the cercopithecine tribes are not significantly different at the 0.01 level. Colobines are essentially more conservative than cercopithecines in terms of the number of breadth formula permutations present in the sample.

In cercopithecins and papionins, the central phalanges differ by, on average, about 2-3% while the flanking phalanges differ, on average, by 1-2%. The difference between the lateral pair of phalanges is less than that of the medial pair in cercopithecins and the two pairs are equal in papionins (Tables 67-68). Colobines are similar to cercopithecines in the contrasts of the central or flanking pairs but differ in the degree of difference between the medial and lateral pairs. The only

statistically significant difference which emerged from the anova and a posteriori tests was between colobines and papionins for the difference in breadth between the medial pair of phalanges; colobines had a greater difference.

The average proportion of each phalanx to the summed total of phalangeal breadths is presented in Table 69 and illustrated in Figure 33. Examination of both the Table and Figure show that there is no difference between cercopithecins and colobines in the relative proportions of the phalanges but that papionins differ slightly from both groups, in having broader flanking phalanges and narrower central ones.

Summary

Table 70 summarizes the correlation of indices to mass in cercopithecids and of the lengths of the third metatarsal and proximal phalanges to their cross-sectional dimensions. Eight indices were negatively correlated with body mass (tibia/hind, tibia/femur, foot/hind, foot/femtib, mt3/foot, mt3/sole and mt3/tarsus) and four indices were positively correlated with body mass (femur/hind, tarsus/foot, tarsus/sole and power/load). In the case of the tibia/femur index, and more indirectly for the others, these correlations conform to predictions about the effect of increasing body mass on lever mechanics. Certainly for the tibia/femur index and presumably for the others, mechanical similarity among animals is maintained by the change in value of these indices with increase in body mass. There is no a priori reason to have expected the majority of the eleven indices which were not

correlated with body mass to have shown such a correlation. This is because most of these indices involved comparisons between elements which were not lever arms of one system. The foot/tibia could be construed as comparing related lever arms. However, because foot length is a composite measure, of the foot lever length plus phalangeal length, its allometric signal was muted.

Table 71 adds to the information of Table 70 the scaling exponents for the components of each index for each subfamily. The scaling exponents clearly indicate the mathematical reasons for the correlations of the indices with body mass. Indices which had a positive correlation with body mass did so because the numerator of each index had a much larger allometric exponent than did the denominator of the index (Table 71). The opposite explanation prevailed for indices which had a negative correlation with body mass: the numerator had a smaller allometric exponent than did the denominator. There is no clear pattern for the values of the allometric exponents and those indices which showed no correlation with body mass. This is probably due to the confounding of a number of factors, such as the strength of the allometric relations and, in many cases, the lack of disparity between the exponents for the numerator and denominator of the indices.

Table 72 summarizes the differences between the subfamilies in the correlation of indices with body mass. There are clear differences in the values of nine indices between the subfamilies at comparable body masses. Five indices which distinguish the subfamilies (tarsus/foot, tarsus/sole, mt3/sole, mt3/tarsus, power arm/load arm) are all expres-

sions of the same phenomenon, which is most effectively described by the fifth index: power arm/load arm. That colobines have smaller values than cercopithecines for three of these indices (tarsus/foot, tarsus/sole, power arm/load arm) and larger values than cercopithecines for two others (mt3/sole, mt3/tarsus) is due to the inverse relationship between the indices. Four indices and one of the bivariate relationships for which the subfamilies differ (ph3/foot, ph3/sole, ph3/tarsus, ph1/ph3, lenph3*brdph3) are all expressions of another phenomenon: the relative length of the phalanges. Similarly, the difference between the subfamilies in the bivariate relationship lenmt3*areamt3 is related to the relative length of the metatarsals.

The striking contrast between the subfamilies in their values for these nine indices and two bivariate relationships are explicable by reference to Table 73, which lists the differences in the subfamilial adjusted group means next to the components of the indices. The reason that colobines have larger indices at comparable body masses to cercopithecines for five indices and two bivariate relationships is that the difference in adjusted group means between the subfamilies for the denominators of the indices was small or non-existent compared to that for the numerators. Similarly, for those indices in which colobines have smaller values at comparable body masses to cercopithecines, the adjusted group means in colobines was much greater than in cercopithecines for the denominators of the indices, whereas there was little difference between the subfamilies for the numerators. Again, there is no clear pattern between the values of the adjusted group means for those indices

in which the two subfamilies were the same.

Table 74 summarizes the species which are noteworthy for their departures from familial or subfamilial patterns in the values of indices. Within cercopithecines, the macaques are distinguished from the rest of Papionini by their values for eight indices. Macaques have particularly high values compared to other papionins of similar body mass for three indices (foot/femtib, foot/tibia, foot/hind), all of which are expressions of the relative length of the foot within the hindlimb. They are also distinguished from other papionins by having high values for the tarsus/sole index and, inversely, low values for the mt3/sole and mt3/tarsus indices. Finally, macaques are distinctive for their high values for the ray1/mt3 and ph1/mt1 indices. The values for indices are reflected and partially explained by reference to the residual values of each macaque variate from the cercopithecine regression lines. High values for indices are due to the residual values for the numerator being higher than those for the denominator and the converse is true for the low values for indices.

Macaca thibetana has values for four indices which appear to be extreme variants of the macaque pattern. Its values for the indices describing the relative length of the foot to the hindlimb (foot/femtib, foot/tibia, foot/hind) are extremely high. Conversely, M. thibetana's value for the index describing the relative length of the third metatarsal (mt3/foot) is extremely low. In these values, then, M. thibetana lies along the trajectory described by the values of other macaques. But, M. thibetana is distinguished from other macaques by five other

indices. It has an extremely low value for the tibia/hind index as well as very low values for the indices describing the relative length of the hallux to the foot (ray1/foot, ray1/sole). Finally, M. thibetana is distinguished from other macaques by its high value for the ph3/mt3 index and low value for the length of its third phalanx given its breadth. It will be shown in the next chapter that the distinctiveness of M. thibetana from other macaques in these indices is interpretable in terms of its latitudinal distribution.

Macaca fuscata departs from the typical macaque pattern, and is similar to M. thibetana, in one regard: it has a low value for the length of the third phalanx given its breadth. This, too, may be a consequence of the thermal conditions in which M. fuscata lives.

The P. (Papio) species are distinguished from most other cercopithecines by their low values, relative to body mass, for indices which describe the relative lengths of the phalanges (ph3/foot, ph3/sole, ph3/tarsus, ph3/mt3, length ph3*breadth ph3) and hallux (ray1/foot, ray1/sole). These departures from the more typical cercopithecine pattern are interpretable in light of their habitat preferences, as described in Chapter 3 and discussed in the next chapter.

The P. (Mandrillus) species are similar to typical cercopithecines in their values for most indices. However, they are distinguished by their very high values for indices describing the length of the hallux (ray1/foot, mt1/mt3). This is likely due to the combined effect of their body mass and degree of arboreality, as described in Chapter 3.

Theropithecus gelada carries the trend seen in the P. (Papio)

species to an extreme. It has very low values for the indices describing phalangeal length (ph3/foot, ph3/sole, ph3/tarsus, ph3/mt3, length ph3*breath ph3) and hallucal length (ray1/foot, ray1/sole, ray1/mt3, ph1/mt1). However, T. gelada is also distinguished from other papionins by its values describing the proportions of the the third metatarsal and hindlimb long bones. It has very high values for the mt3/foot index, which is probably a function of its short phalanges. More important are its high values for the tibia/femur and tibia/hind indices and a low value for the femur/hind index. The values of these long bone indices are due to the fact that Theropithecus has an extremely short femur for its body mass and a tibia of expected length. The exact scaling relationships of the bones to body mass is less important than the effect of these proportions on the mechanics of the hindlimb during locomotion.

The last cercopithecine which stands out from other species, is E. patas. Erythrocebus patas is similar to T. gelada in its extreme values for indices describing phalangeal length, hallucal length, and the proportions of the hindlimb long bones. It differs from T. gelada and P. (Papio), however, in its extremely high values for two indices which directly or indirectly describe the ratio of the foot lever arms: tarsus/foot and power/load. Special explanations are required to explain why a cursorial specialist such as E. patas would have such an unexpectedly high value for the power/load index.

Within colobines, Semnopithecus and Presbytis are noteworthy for their index values relative to body mass. S. (Semnopithecus) entellus is

noteworthy for its low values, relative to body mass, for indices describing the relative length of the hallux. In Presbytis, the values for nine indices, relating to one distinctive aspect of the foot, serve to distinguish this genus from other colobines, and especially S. (Trachypithecus). Presbytis is distinctive because of its relatively long metatarsus which affects the values of nine indices. Thus, Presbytis has high values for the mt3/foot, mt3/sole, and mt3/tarsus indices and the length of mt3 against its cross-sectional area. Conversely, it has low values for the tarsus/foot, tarsus/sole, ph3/foot, ph3/sole and ph3/mt3 indices. S. (Trachypithecus) is distinguished from other colobines by its high values, relative to body mass, for the indices describing the relative lengths of the hallux. S. (Trachypithecus) has high values not so much because the hallux is elongated but because the values for the denominators of the indices are small. In particular, S. (Trachypithecus) species have a shorter third digit ray than expected for their body masses.

Table 75 summarizes the scaling of measurements with body mass. As discussed in Chapter 5, a large animal is expected to increase the length of the in-lever around a joint, and to decrease the length of the out-lever, in order to maintain mechanical similarity with smaller-bodied animals. Furthermore, to reduce bending moments in long bones with an increase in body mass, the proportion of the diameter to the length of the bones must change so that bones become stouter or more robust. The scaling of measurements in this study conforms to these expectations with an increase in body mass. There is no a priori reason

to expect one or the other lever arms to increase or decrease in mass. Obviously a number of factors will constrain the direction in which one or both lever arms change. Similarly, a bone could theoretically become broader in diameter as easily as shorter in length, all other things being equal. Therefore, it is necessary to empirically determine the scaling relationships of the relevant dimensions for any group.

Two sets of lever arms around two joints were examined in this study: the lever arms around the knee joint and the lever arms around the upper ankle joint. In cercopithecids, the power arm or in-lever of the knee joint (the femur) scales isometrically. As a consequence, it is the tibia which has a negative allometric relationship with body mass. The reason(s) for the isometric scaling of the femur is beyond the scope of this study, but may relate to the more complex movements of the femur around the hip joint. In any case, the two lever arms around the knee joint are changing in a predictable fashion with body mass. The negative allometric scaling of the tibia contributes to the negative allometric scaling of the composite measurements of which it is a part, hind and femtib.

The power arm (in-lever) of the foot around the upper ankle joint has a moderately positive allometric relationship with body mass and the load arm (out-lever) has a strongly negative allometric relationship with body mass. There are three components to the load arm of the foot: the length of the calcaneus distal to the midpoint of the proximal astragalar facet, the length of the cuboid and the length of the third metatarsal. This analysis revealed that the composite tarsus measure-

ment, as well as its constituent parts, the calcaneus and cuboid, scale isometrically with body mass. However, because the power arm component of the calcaneus has a positive allometric relationship with body mass, it is not surprising that the load arm of the calcaneus has a negative allometric relationship with body mass. Additionally, the length of the third metatarsal has a negative allometric relationship with mass. As a consequence, changes in the ratio of the power arm to the load arm in the foot affect the proportions of the calcaneus and metatarsus but not the cuboid.

In terms of the relationship of the dimensions of importance to bending stresses in the metatarsus, it has already been shown that the third metatarsal has a negative allometric relationship with mass. Therefore, it is not unexpected that the cross-sectional area at the midshaft of the third metatarsal scales isometrically with body mass. This same pattern also holds for the third proximal phalanx: its breadth scales isometrically while its length has a negative allometric relationship with body mass.

Finally, the length of the hallux and its constituent lengths, metatarsal and phalangeal, scale isometrically with body mass. This, again, is not unexpected given that on theoretical grounds there is no reason to expect the proportions of the hallux, or its parts, to change with body mass in cercopithecids.

Table 76 summarizes the differences between the subfamilies in the adjusted group means of the regression lines. There is a clear difference between the subfamilies in the elevations of the lines, for the

regressions of eleven measurements with body mass, and no difference for the regressions of nine measurements with mass. When colobines differ from cercopithecines in their adjusted group means, they consistently have higher values at comparable body masses. In each case, as discussed in the next chapter, the higher values in colobines compared to cercopithecines, can be related to fundamental differences in their locomotor repertoire.

Table 77 summarizes the dimensions for which twenty-six variates deviate from their respective subfamilial regression lines. For the majority of these outliers, the variates represent only one sex of a species, and the deviation from subfamilial lines is for a few measurements at the most. In several cases (male P. hosei, male C. mona, male P. (Piliocolobus) badius), a large number of measurements are affected so that a pattern is apparent. Nevertheless, an explanation for their deviation is not clear, given what is known about the locomotion of these species in the wild. However, for five species, either both sexes are outliers to the subfamilial lines, or in the cases of M. fuscata and M. thibetana, where only one sex represents the species, the deviations are so strong that a pattern emerges which is consistent with known behavioral specializations and/or geographical distributions.

Erythrocebus patas is an outlier from the cercopithecine line for the regression of ten measurements with body mass. Given its body mass, it has an extremely long tibia, calcaneus and cuboid. In turn, these elongated bones contribute to E. patas being an outlier for the regressions of the composite measurements on mass: hind, foot, sole and tar-

sus. As well, E. patas has a long power arm and, because of the elongation of the calcaneus and cuboid, a long load arm in the foot.

Macaca thibetana is an outlier from the cercopithecine line for the regressions of nine measurements on body mass. Given its estimated body mass, it has an extremely short femur, tibia, mt3 and mt1. These short bones contribute to M. thibetana being an outlier for the regressions of four composite measurements on mass: hind, femtib, sole and ray1. The short metatarsus also causes M. thibetana's load arm in the foot to be shorter than expected.

Macaca fuscata is an outlier from the cercopithecine line for the regressions of fifteen measurements on body mass. Macaca fuscata has an extremely short femur, tibia, calcaneus, mt3 and mt1 for its body mass. These short bones contribute to M. fuscata being an outlier for the regressions of the composite measurements hind, femtib, foot, sole, tarsus, ray3 and ray1. Macaca fuscata also has a short power arm and short load arm for its body mass.

Theropithecus gelada is an outlier from the cercopithecine line for the regressions of three measurements on mass. Its first and third phalanges are extremely short for its body mass. The short first phalanx contributes to T. gelada being an outlier for the regression of ray1 on mass.

Semnopithecus entellus is an outlier from the colobine line for the regressions of four measurements on body mass. Semnopithecus entellus has a long calcaneus and a long cuboid given its body mass. These elongated bones contribute to S. entellus being an outlier for the regres-

sion of the composite measurements tarsus and load arm on mass.

Table 78 summarizes the digit formulas in the subfamilies and identifies species which differ from their typical subfamilial patterns. The two subfamilies are very different from each other in their ray length formulas. In cercopithecines, the third ray is consistently the longest and is always followed by the fourth ray, but there is variation in the ranking of the fifth and second rays. The gradient in length of the series, from the medial to the lateral side of the foot, is not great in cercopithecines. The cercopithecine pattern is in strong contrast to the colobine condition, wherein the lateral rays are longer than the medial, and the central rays project substantially beyond the flanking rays. Intriguingly, the P. (Papio) species and C. albigena have a large number of specimens with a ray length formula like the colobines. However, P. (Papio) and C. albigena differ from colobines in that the gradient along the series is not marked.

Both subfamilies are characterized by the majority of specimens having a metatarsal length formula in which the lateral metatarsals of a pair (central, flanking) are longer than the medial. For the remainder of the specimens the subfamilies differ from each other. Cercopithecines are very variable with five other permutations represented among the specimens. The remainder of the specimens in colobines, on the other hand, are characterized by only one other permutation. Furthermore, the subfamilies differ in that the gradient along the series is slight in cercopithecines but great in colobines. It is also of interest that a large number of specimens in the P. (Papio) species are similar to

colobines in their alternative metatarsal length formula.

The subfamilial pattern of distribution in the phalangeal length formulas is the opposite to that seen with the metatarsal length formulas. The majority of specimens in both subfamilies are characterized by a formula in which the medial phalanges of a pair are longer than the lateral. However, colobines tend to be more variable than cercopithecines in the frequency of alternative permutations. As with the preceding length formulas, colobines show a greater gradient along the series than do cercopithecines.

The majority of specimens in both subfamilies have a metatarsal cross-sectional area formula in which the medial metatarsals of a pair are larger than the lateral. As was the case with the metatarsal length formulas, cercopithecines are more variable than colobines in the number of alternative permutations present. The subfamilies differ strongly in that the central metatarsals in colobines are much larger than the flanking, whereas in cercopithecines the difference is not so great. Papionins are distinguished from cercopithecins in that the medial metatarsals are relatively large.

In both subfamilies the most common phalangeal breadth formulas, as with the phalangeal length formulas, features the medial phalanges of a pair being larger than the lateral. However, there is a great deal of variability in phalangeal breadth formulas, with cercopithecines being even more variable than colobines. Therefore, the utility of this formula for functional interpretation is limited.

Table 23. Means and ranges of variation (in parentheses) of values for indices describing relative lengths of hindlimb segments. N, number of specimens per species by sex.

Species	Sex	N	Tibia/Femur	N	Foot/Pentib	Foot/Tibia	Femur/Hind	Tibia/Hind	Foot/Hind
<i>H. talapoin</i>	F	7	100 (97-101)	5	38 (36-38)	75 (72-77)	36 (36-37)	36 (36-37)	27 (27-28)
<i>H. talapoin</i>	M	4	100 (97-102)	4	37 (35-40)	74 (69-80)	37 (35-37)	37 (36-37)	27 (26-29)
<i>C. pogonias</i>	F	5	99 (97-100)	0					
<i>C. pogonias</i>	M	13	98 (95-103)	2	36 (36-36)	74 (73-75)	37 (37-38)	36 (36-36)	27 (26-27)
<i>C. campbelli</i>	F	2	97 (96-99)	1	37	73	37	37	26
<i>C. campbelli</i>	M	2	98 (98-99)	2	37 (36-38)	74 (73-76)	37 (37-37)	36 (36-36)	27 (27-27)
<i>C. mona</i>	F	2	98 (97-99)	2	36 (36-37)	73 (72-75)	37 (37-37)	36 (36-37)	27 (26-27)
<i>C. mona</i>	M	11	98 (94-99)	8	37 (36-38)	74 (72-77)	37 (37-38)	36 (35-37)	27 (26-28)
<i>C. ascanius</i>	F	8	97 (94-100)	8	35 (35-36)	72 (70-74)	38 (37-38)	36 (36-37)	26 (26-26)
<i>C. ascanius</i>	M	10	97 (95-102)	10	35 (34-37)	72 (68-75)	37 (36-38)	37 (36-37)	26 (25-27)
<i>C. cephus</i>	F	4	98 (97-99)	1	36	72	37	37	26
<i>C. cephus</i>	M	17	98 (96-101)	2	35 (34-37)	71 (69-74)	37 (37-38)	37 (37-37)	26 (25-27)
<i>C. petaurista</i>	F	3	97 (96-98)	1	36	72	37	37	26
<i>C. petaurista</i>	M	1	98	1	37	74	37	36	27
<i>C. pygerythrus</i>	F	12	95 (94-96)	8	37 (35-39)	75 (73-80)	38 (37-38)	36 (35-36)	27 (26-28)
<i>C. pygerythrus</i>	M	15	95 (92-96)	9	35 (34-36)	73 (70-76)	38 (38-39)	36 (35-36)	26 (26-27)
<i>C. nitis</i>	F	12	97 (95-100)	11	36 (35-38)	74 (72-75)	37 (36-38)	36 (36-37)	27 (26-27)
<i>C. nitis</i>	M	8	97 (94-100)	7	36 (34-37)	73 (69-75)	37 (37-38)	36 (36-37)	26 (25-27)
<i>C. nictitans</i>	F	5	99 (95-102)	0					
<i>C. nictitans</i>	M	14	97 (94-99)	1	35	71	38	37	26
<i>C. albogularis</i>	F	11	98 (94-106)	9	36 (34-37)	72 (68-74)	37 (37-38)	36 (36-37)	26 (25-27)
<i>C. albogularis</i>	M	8	96 (93-99)	6	35 (33-36)	71 (67-74)	38 (37-38)	36 (36-37)	26 (25-27)
<i>E. patas</i>	F	2	98 (98-98)	1	34	69	39	37	25
<i>E. patas</i>	M	3	99 (95-101)	1	34	68	37	37	25
Total		179		98					

Table 23. (cont.)

Species	Sex	N	Tibia/Femur	N	Foot/Pentib	Foot/Tibia	Femur/Hind	Tibia/Hind	Foot/Hind
<i>H. fascicularis</i>	F	9	94 (92-95)	6	37 (36-38)	77 (75-79)	38 (37-38)	35 (35-36)	27 (27-28)
<i>H. fascicularis</i>	H	10	93 (92-94)	10	37 (35-41)	77 (72-84)	38 (37-38)	35 (34-36)	27 (26-29)
<i>H. fuscata</i>	H	3	93 (92-94)	2	38 (37-38)	78 (77-79)	38 (37-38)	35 (35-35)	27 (27-28)
<i>H. nulatta</i>	F	10	92 (90-95)	0					
<i>H. nulatta</i>	H	10	91 (89-94)	2	38 (37-39)	80 (77-83)	38 (38-38)	35 (34-35)	28 (27-28)
<i>H. nigra</i>	F	1	92	1	36	76	38	35	27
<i>H. nigra</i>	H	3	91 (90-93)	2	35 (35-36)	74 (74-74)	39 (39-39)	35 (35-35)	26 (26-26)
<i>H. tonkeana</i>	F	1	91	1	37	77	38	35	27
<i>H. tonkeana</i>	H	2	92 (91-93)	1	37	77	38	35	27
<i>H. nemestrina</i>	F	7	92 (91-96)	5	36 (34-38)	75 (72-78)	38 (37-39)	35 (35-36)	26 (26-28)
<i>H. nemestrina</i>	H	5	90 (88-91)	4	35 (34-37)	74 (71-78)	39 (38-39)	35 (35-36)	26 (25-27)
<i>H. sylvanus</i>	F	1	89	1	36	77	39	35	27
<i>H. sylvanus</i>	H	4	91 (89-94)	2	38 (37-38)	79 (79-79)	38 (37-39)	35 (34-35)	27 (27-28)
<i>H. arctoides</i>	H	2	90 (88-92)	0					
<i>H. assanensis</i>	H	1	93	0					
<i>H. thibetana</i>	H	4	90 (87-95)	3	39 (38-40)	83 (81-84)	38 (38-38)	34 (34-34)	28 (28-28)
<i>C. albigena</i>	F	10	93 (88-96)	9	34 (33-34)	70 (67-73)	39 (38-40)	36 (35-37)	25 (25-25)
<i>C. albigena</i>	H	14	93 (90-98)	11	33 (32-36)	69 (66-72)	39 (37-40)	36 (36-37)	25 (24-26)
<i>C. galeritus</i>	F	4	91 (85-96)	1	37	75	37	36	27
<i>C. galeritus</i>	H	8	92 (88-95)	5	33 (32-35)	69 (66-73)	40 (39-40)	36 (35-36)	25 (24-26)
<i>C. torquatus</i>	F	7	93 (91-97)	4	35 (35-36)	73 (72-75)	38 (37-39)	36 (35-36)	26 (26-27)
<i>C. torquatus</i>	H	11	92 (89-99)	7	35 (34-36)	72 (70-73)	39 (37-39)	36 (35-37)	26 (25-27)
<i>T. gelada</i>	F	1	97	1	35	70	38	37	26
<i>T. gelada</i>	H	2	100 (99-101)	1	35	69	37	37	26
<i>P. cynocephalus</i>	F	4	90 (89-91)	3	33 (31-34)	69 (66-72)	40 (40-40)	36 (35-36)	25 (24-25)
<i>P. cynocephalus</i>	H	9	88 (87-89)	8	33 (32-34)	70 (67-73)	40 (40-41)	35 (35-36)	25 (24-25)
<i>P. hanadryas</i>	F	2	88 (88-89)	2	34 (34-34)	72 (71-72)	40 (40-40)	35 (35-35)	25 (25-25)
<i>P. hanadryas</i>	H	5	87 (86-88)	4	33 (33-33)	71 (70-72)	40 (40-40)	35 (35-35)	25 (25-25)
<i>P. anubis</i>	F	5	84 (77-86)	2	34 (33-34)	75 (74-76)	41 (40-43)	34 (33-34)	25 (25-26)
<i>P. anubis</i>	H	13	87 (84-90)	5	35 (34-35)	74 (73-76)	40 (39-40)	35 (34-35)	26 (25-26)
<i>P. ursinus</i>	F	2	87 (86-88)	2	35 (35-35)	73 (71-74)	40 (40-40)	35 (35-35)	26 (26-26)
<i>P. ursinus</i>	H	4	86 (84-88)	2	32 (32-32)	69 (68-69)	40 (40-40)	35 (35-35)	24 (24-25)
<i>P. leucophaeus</i>	F	2	90 (87-92)	2	34 (33-35)	72 (71-73)	39 (39-40)	35 (35-36)	25 (25-26)
<i>P. leucophaeus</i>	H	1	90	0					
<i>P. sphinx</i>	F	4	91 (89-93)	4	34 (33-37)	70 (62-78)	39 (39-40)	35 (34-36)	25 (25-27)
<i>P. sphinx</i>	H	2	90 (88-91)	0					
Total		83		111					

Table 23. (cont.)

Species	Sex	N	Tibia/Femur	N	Foot/Femur	Foot/Tibia	Femur/Hind	Tibia/Hind	Foot/Hind
<i>P. verus</i>	F	2	95 (93-96)	2	38 (38-38)	78 (78-78)	37 (37-38)	35 (35-36)	28 (27-28)
<i>P. verus</i>	M	4	95 (92-97)	3	37 (36-37)	75 (74-78)	38 (37-38)	36 (35-36)	27 (27-27)
<i>P. badius</i>	F	13	90 (83-94)	10	38 (37-40)	80 (77-86)	38 (37-39)	35 (33-35)	28 (27-29)
<i>P. badius</i>	M	12	90 (87-94)	6	38 (37-39)	80 (76-83)	38 (37-39)	34 (34-35)	28 (27-28)
<i>C. satana</i>	F	1	89	1	35	74	39	35	26
<i>C. satana</i>	M	2	68 (87-89)	0					
<i>C. polykonos</i>	F	1	94	0					
<i>C. polykonos</i>	M	2	93 (91-94)	2	36 (36-36)	75 (74-76)	38 (38-38)	35 (35-36)	27 (26-27)
<i>C. vellerosus</i>	M	1	94	1	36	74	38	36	27
<i>C. angolensis</i>	F	4	92 (91-94)	2	36 (36-37)	75 (74-76)	38 (38-38)	36 (35-36)	27 (26-27)
<i>C. angolensis</i>	M	2	92 (89-95)	1	36	74	38	36	27
<i>C. guereza</i>	F	13	92 (86-97)	7	36 (35-37)	75 (73-78)	38 (38-39)	35 (35-36)	27 (26-27)
<i>C. guereza</i>	M	16	93 (89-96)	9	36 (35-37)	74 (71-76)	38 (38-39)	36 (35-36)	26 (26-27)
<i>P. hosei</i>	F	1	89	1	34	72	40	35	25
<i>P. hosei</i>	M	2	93 (92-94)	2	34 (34-34)	70 (70-71)	39 (38-39)	36 (36-36)	25 (25-26)
<i>P. rubicunda</i>	F	9	91 (90-93)	6	34 (33-36)	72 (68-75)	39 (39-40)	36 (35-36)	26 (25-26)
<i>P. rubicunda</i>	M	10	92 (89-95)	8	34 (33-36)	72 (70-74)	39 (38-39)	36 (35-36)	26 (25-26)
<i>P. aygula</i>	F	3	92 (92-93)	3	36 (34-37)	74 (70-77)	38 (38-39)	35 (35-36)	26 (25-27)
<i>P. aygula</i>	M	3	91 (91-92)	3	32 (32-33)	68 (67-69)	40 (39-40)	36 (36-36)	25 (24-25)
<i>P. nelalophos</i>	F	4	92 (90-95)	3	34 (34-35)	71 (70-73)	39 (38-39)	36 (36-36)	26 (25-26)
<i>P. nelalophos</i>	M	3	92 (90-94)	3	35 (33-36)	73 (69-76)	39 (39-39)	35 (35-36)	26 (25-27)
<i>P. frontata</i>	M	2	93 (91-95)	1	35	71	38	36	26
<i>S. cristata</i>	F	13	89 (86-91)	7	36 (35-37)	75 (74-78)	39 (38-40)	35 (34-35)	26 (26-27)
<i>S. cristata</i>	M	12	91 (88-93)	6	35 (35-37)	75 (73-78)	39 (38-40)	35 (35-36)	26 (26-27)
<i>S. obscura</i>	F	7	89 (88-90)	2	36 (35-36)	75 (75-76)	39 (39-39)	35 (35-35)	26 (26-26)
<i>S. obscura</i>	M	8	89 (87-92)	3	36 (34-38)	76 (72-81)	39 (38-39)	35 (34-36)	27 (26-28)
<i>S. entellus</i>	F	6	88 (85-91)	0					
<i>S. entellus</i>	M	2	87 (85-88)	0					
<i>P. roxellanae</i>	F	5	87 (86-89)	0					
<i>P. roxellanae</i>	M	1	88	0					
<i>P. nanaeus</i>	F	2	91 (90-93)	1	33	70	40	36	25
<i>P. nanaeus</i>	M	5	89 (84-92)	1	33	70	40	35	25
<i>H. larvatus</i>	F	4	88 (86-90)	3	36 (36-36)	77 (77-79)	39 (39-39)	34 (34-35)	27 (27-27)
<i>H. larvatus</i>	M	8	90 (87-91)	6	37 (35-38)	78 (75-80)	39 (38-40)	35 (34-35)	27 (26-27)
Total		183		111					

Table 24. Means, ranges of variation (in parentheses) and standard deviations of values for indices describing relative lengths of hindlimb. N, number of species by sex.

Species	N	Mean (Range)	SD	Species	N	Mean (Range)	SD
Tibia/Femur				Femur/Hind			
Cercopithecins	24	97.6 (94.8-100.0)	1.3	Cercopithecins	22	37.3 (36.4-38.0)	0.4
Papionins	36	90.9 (83.5-99.8)	3.0	Papionins	31	38.8 (37.0-41.3)	1.0
Colobines	24	90.8 (86.7-94.6)	2.2	Colobines	28	38.6 (37.2-40.0)	0.7
Foot/Femur				Tibia/Hind			
Cercopithecins	22	35.8 (33.9-37.5)	0.9	Cercopithecins	22	36.4 (35.6-37.3)	0.3
Papionins	31	35.1 (32.1-39.0)	1.8	Papionins	31	35.3 (33.6-37.2)	0.7
Colobines	28	35.4 (32.4-38.0)	1.5	Colobines	28	35.3 (34.4-36.2)	0.5
Foot/Tibia				Foot/Hind			
Cercopithecins	22	72.4 (67.9-75.3)	1.9	Cercopithecins	22	26.3 (25.3-27.3)	0.5
Papionins	31	73.6 (68.8-83.0)	3.8	Papionins	31	26.0 (24.3-28.0)	1.0
Colobines	28	74.1 (68.0-80.1)	3.0	Colobines	28	26.1 (24.5-27.6)	0.8

Table 25. Least Squares coefficients and statistics for regressions of hindlimb segments on body mass. N, sample size; slope, LS slope; SE, standard error of the slope; y-int, y-intercept; r^2 , coefficient of determination. * female M. talapoin and male E. patas removed from sample.

Taxon	N	slope	SE	y-int	r^2	Taxon	N	slope	SE	y-int	r^2
<u>lxhind*lxmass</u>						<u>lxtiblen*lxmass</u>					
Cercopithecines	53	0.28	0.02	3.64	0.88	Cercopithecines	60	0.27	0.02	2.71	0.84
Cercopithecins	22	0.35	0.03	3.07	0.89	Cercopithecins	24	0.34	0.03	2.13	0.88
Papionins	31	0.26	0.03	3.84	0.77	Papionins	36	0.27	0.03	2.66	0.71
Cercopithecines	51	0.27	0.02	3.75	0.87 *	Colobines	34	0.24	0.03	3.02	0.61
Cercopithecins	20	0.31	0.03	3.43	0.86 *						
Colobines	28	0.27	0.04	3.83	0.69						
		Pr > F slope		Pr > F mean			Pr > F slope		Pr > F mean		
Subfamilies		0.5712		0.0001		Subfamilies		0.2074		0.0020	
Tribes		0.0133		0.3127		Tribes		0.0988		0.0787	
<u>lxfootlen*lxmass</u>						<u>lxfootlen*lxmass</u>					
Subfamilies		0.9568		0.0001 *		Cercopithecines	54	0.26	0.01	2.47	0.83
Tribes		0.2551		0.7771 *		Cercopithecins	22	0.33	0.03	1.95	0.88
						Papionins	32	0.23	0.02	2.73	0.81
<u>lxfentib*lxmass</u>						Cercopithecines	52	0.25	0.01	2.58	0.89 *
Cercopithecines	60	0.29	0.02	3.24	0.87	Cercopithecins	20	0.29	0.03	2.26	0.80 *
Cercopithecins	24	0.35	0.03	2.81	0.89	Colobines	29	0.27	0.03	2.44	0.76
Papionins	31	0.29	0.03	3.31	0.73						
Colobines	34	0.27	0.03	3.53	0.66						
		Pr > F slope		Pr > F mean			Pr > F slope		Pr > F mean		
Subfamilies		0.3778		0.0001		Subfamilies		0.8979		0.0001	
Tribes		0.1360		0.3834		Tribes		0.0042		0.4322	
						Subfamilies		0.5080		0.0001 *	
<u>lxfenlen*lxmass</u>						Tribes		0.1408		0.9382 *	
Cercopithecines	60	0.32	0.02	2.38	0.88						
Cercopithecins	24	0.35	0.02	2.09	0.90						
Papionins	36	0.30	0.03	2.52	0.74						
Colobines	35	0.28	0.03	2.81	0.67						
		Pr > F slope		Pr > F mean							
Subfamilies		0.3559		0.0001							
Tribes		0.2161		0.9507							

Table 26. Residuals of species by sex values from subfamilial
LS lines of hindlimb segments on body mass.

Species	Sex	Hind	Femur	Pæur	Tibia	Foot
<i>E. talapoin</i>	F	-1.88	-1.48	-1.34	-1.52	-2.04
<i>E. talapoin</i>	M	-0.82	-0.74	-0.69	-0.74	-0.91
<i>C. pogonias</i>	F	.	-0.02	-0.12	0.09	.
<i>C. pogonias</i>	M	0.29	0.29	0.11	0.46	0.41
<i>C. campbelli</i>	F	0.82	0.55	0.63	0.47	0.64
<i>C. campbelli</i>	M	0.51	0.31	0.14	0.46	0.87
<i>C. boza</i>	F	-0.20	-0.22	-0.23	-0.19	-0.22
<i>C. boza</i>	M	2.15	1.88	1.78	1.93	2.62
<i>C. ascanius</i>	F	-1.19	-0.99	-0.92	-0.97	-1.54
<i>C. ascanius</i>	M	0.62	0.55	0.44	0.64	0.51
<i>C. cephus</i>	F	-0.23	0.40	0.35	0.45	-0.49
<i>C. cephus</i>	M	0.34	0.93	0.77	1.05	0.16
<i>C. petaurista</i>	F	0.08	-0.16	-0.16	-0.14	0.01
<i>C. petaurista</i>	M	0.36	0.22	0.12	0.31	0.57
<i>C. pygerythrus</i>	F	-0.73	-0.64	-0.51	-0.74	-0.67
<i>C. pygerythrus</i>	M	-0.43	-0.28	-0.26	-0.30	-0.61
<i>C. mitis</i>	F	-0.06	-0.06	-0.16	0.04	0.04
<i>C. mitis</i>	M	0.02	-0.14	-0.41	0.11	0.18
<i>C. nictitans</i>	F	.	0.81	0.63	0.96	.
<i>C. nictitans</i>	M	1.31	1.16	1.01	1.27	1.20
<i>C. albogularis</i>	F	-1.10	-0.85	-1.06	-0.62	-1.31
<i>C. albogularis</i>	M	-0.26	-0.42	-0.65	-0.12	-0.25
<i>E. patas</i>	F	1.05	0.28	0.07	0.47	0.65
<i>E. patas</i>	M	2.10	1.43	1.05	1.86	1.93

Table 26. (cont.)

Species	Sex	Hind	Femur	Tibia	Foot	
<i>H. fascicularis</i>	F	-1.38	-1.43	-1.35	-1.57	-1.24
<i>H. fascicularis</i>	M	-1.13	-1.21	-1.08	-1.30	-0.86
<i>H. fuscata</i>	M	-2.98	-2.92	-3.08	-2.69	-2.49
<i>H. mulatta</i>	F	.	0.04	0.18	-0.11	.
<i>H. mulatta</i>	M	0.38	0.30	0.42	0.14	1.23
<i>H. nigra</i>	F	-0.23	-0.35	-0.20	-0.50	-0.05
<i>H. nigra</i>	M	0.45	0.27	0.36	0.14	0.47
<i>H. tonkeana</i>	F	-0.91	-1.03	-0.90	-1.16	-0.62
<i>H. tonkeana</i>	M	0.99	0.87	0.98	0.71	1.67
<i>H. nenestrina</i>	F	-0.42	-0.27	-0.15	-0.40	-0.40
<i>H. nenestrina</i>	M	0.53	0.58	0.70	0.39	0.54
<i>H. sylvanus</i>	F	-0.87	-1.00	-0.81	-1.22	-0.57
<i>H. sylvanus</i>	M	0.68	0.32	0.37	0.22	1.56
<i>H. arctoides</i>	M	.	-1.80	-1.66	-1.92	.
<i>H. assanensis</i>	M	.	-0.78	-0.81	-0.75	.
<i>H. thibetana</i>	M	-2.52	-2.76	-2.75	-2.72	-1.54
<i>C. albigena</i>	F	0.76	0.89	0.97	0.77	0.12
<i>C. albigena</i>	M	1.85	1.81	1.82	1.73	1.39
<i>C. galeritus</i>	F	0.38	1.18	1.40	0.89	0.70
<i>C. galeritus</i>	M	0.84	0.88	0.89	0.81	0.16
<i>C. torquatus</i>	F	0.67	0.56	0.63	0.46	0.64
<i>C. torquatus</i>	M	0.85	0.57	0.48	0.61	0.84
<i>T. gelada</i>	F	-0.57	-0.62	-1.03	-0.23	-0.71
<i>T. gelada</i>	M	-0.44	-0.66	-1.34	0.00	-1.06
<i>P. cynocephalus</i>	F	0.74	0.87	1.08	0.71	0.08
<i>P. cynocephalus</i>	M	-0.14	0.10	0.14	-0.01	-0.65
<i>P. hanadryas</i>	F	0.50	0.48	0.70	0.19	0.07
<i>P. hanadryas</i>	M	-0.27	-0.41	-0.30	-0.59	-0.79
<i>P. anubis</i>	F	0.44	0.16	0.63	-0.41	0.09
<i>P. anubis</i>	M	-0.45	-0.49	-0.44	-0.50	-0.34
<i>P. ursinus</i>	F	-0.71	-0.86	-0.38	-0.39	0.13
<i>P. ursinus</i>	M	0.10	-0.31	-0.23	-0.48	-0.57
<i>P. leucophaeus</i>	F	0.35	0.31	0.45	0.12	-0.01
<i>P. leucophaeus</i>	M	.	1.93	1.83	1.89	1.35
<i>P. sphinx</i>	F	-0.23	0.07	0.11	0.07	-0.87
<i>P. sphinx</i>	M	.	1.85	1.77	1.93	.

Table 26. (cont.)

Species	Sex	Hind	Pentib	Femur	Tibia	Foot
<i>P. verus</i>	F	-1.08	-1.23	-1.45	-1.17	-0.5
<i>P. verus</i>	M	-1.14	-1.38	-1.57	-1.27	-0.7
<i>P. badius</i>	F	0.12	-0.33	-0.26	-0.48	1.1
<i>P. badius</i>	M	-1.32	-1.94	-1.90	-1.91	-0.6
<i>C. satana</i>	F	0.39	0.42	0.49	0.29	0.2
<i>C. satana</i>	M	.	0.98	1.09	0.81	.
<i>C. polykonos</i>	F	.	0.90	0.60	1.10	1.9
<i>C. polykonos</i>	M	0.27	0.19	-0.05	0.40	0.6
<i>C. vellerosus</i>	M	0.16	0.10	-0.20	0.38	0.3
<i>C. angolensis</i>	F	0.40	-0.14	-0.31	-0.03	0.7
<i>C. angolensis</i>	M	-1.23	-1.26	-1.41	-1.05	-1.2
<i>C. guereza</i>	F	-0.80	-0.84	-0.97	-0.75	-0.6
<i>C. guereza</i>	M	-1.02	-0.85	-1.07	-0.58	-1.1
<i>P. hosei</i>	F	-0.18	0.02	0.16	0.39	-0.8
<i>P. hosei</i>	M	2.13	2.08	1.83	2.14	1.8
<i>P. rubicunda</i>	F	0.78	0.74	0.66	0.69	0.5
<i>P. rubicunda</i>	M	1.33	1.33	1.17	1.32	1.0
<i>P. aggula</i>	F	0.43	0.40	0.27	0.44	0.5
<i>P. aggula</i>	M	0.66	0.97	0.89	0.90	-0.6
<i>P. melalophos</i>	F	1.00	1.04	0.87	1.07	0.6
<i>P. melalophos</i>	M	0.81	0.80	0.74	0.78	0.5
<i>P. frontata</i>	F	.	.	1.51	.	.
<i>P. frontata</i>	M	0.86	0.94	0.73	0.98	0.6
<i>S. cristata</i>	F	-1.62	-1.27	-1.08	-1.56	-1.9
<i>S. cristata</i>	M	-1.09	-1.08	-1.07	-1.14	-1.3
<i>S. obscura</i>	F	-0.73	-1.33	-1.20	-1.50	-0.8
<i>S. obscura</i>	M	-1.37	-1.02	-0.92	-1.16	-1.3
<i>S. entellus</i>	F	.	0.51	0.65	0.29	.
<i>S. entellus</i>	M	.	0.84	1.04	0.63	.
<i>P. roxellanae</i>	F	.	-0.53	-0.29	-0.84	.
<i>P. roxellanae</i>	M	.	-0.99	-0.91	-0.93	.
<i>P. nanaeus</i>	F	0.71	0.83	0.70	0.82	-0.2
<i>P. nanaeus</i>	M	1.23	1.05	1.09	0.97	0.1
<i>H. larvatus</i>	F	0.86	0.62	0.77	0.31	1.3
<i>H. larvatus</i>	M	-0.53	-0.56	-0.58	-0.32	-0.2

Table 27. Means and ranges of variation (in parentheses) of values for indices describing the relative lengths of the major segments of the foot. Conventions as in Table 23.

Species	Sex	N	Tarsus/Foot	Ht3/Foot	Ph3/Foot	Ph3/Sole	N	Tarsus/Sole	Ht3/Sole
<i>H. talapoin</i>	F	5	35 (34-36)	42 (41-43)	23 (23-24)	31 (30-31)	7	46 (44-48)	54 (52-56)
<i>H. talapoin</i>	M	4	35 (34-36)	42 (41-44)	23 (22-23)	29 (28-30)	4	46 (44-47)	55 (53-57)
<i>C. pogonias</i>	F	0					4	46 (45-47)	54 (53-55)
<i>C. pogonias</i>	M	2	37 (36-37)	42 (41-42)	22 (21-22)	28 (27-29)	13	46 (45-47)	54 (53-55)
<i>C. campbelli</i>	F	1	36	42	22	29	2	46 (45-46)	54 (54-55)
<i>C. campbelli</i>	M	2	37 (37-37)	42 (41-42)	21 (21-22)	27 (27-28)	2	47 (47-48)	53 (52-54)
<i>C. nona</i>	F	2	36 (36-36)	42 (42-42)	22 (22-22)	28 (28-28)	2	46 (46-46)	54 (54-54)
<i>C. nona</i>	M	8	37 (36-37)	42 (41-43)	22 (21-23)	28 (26-29)	11	47 (45-48)	53 (52-55)
<i>C. ascanius</i>	F	9	37 (36-38)	42 (41-43)	22 (21-22)	27 (26-28)	10	47 (46-48)	53 (52-55)
<i>C. ascanius</i>	M	10	36 (34-38)	43 (40-45)	21 (20-22)	27 (25-29)	10	46 (43-49)	54 (51-57)
<i>C. cephus</i>	F	1	36	42	22	28	4	47 (46-47)	53 (53-54)
<i>C. cephus</i>	M	2	37 (35-39)	42 (42-43)	21 (20-22)	27 (24-29)	17	47 (45-48)	54 (52-55)
<i>C. petaurista</i>	F	2	35 (34-35)	43 (42-43)	23 (22-23)	29 (29-30)	4	46 (44-48)	54 (52-56)
<i>C. petaurista</i>	M	1	35	42	22	29	1	45	55
<i>C. pygerythrus</i>	F	8	39 (37-40)	40 (39-41)	21 (21-23)	27 (26-30)	12	49 (48-51)	51 (49-53)
<i>C. pygerythrus</i>	M	9	38 (37-40)	41 (40-42)	21 (20-22)	26 (25-28)	14	48 (47-50)	52 (51-54)
<i>C. nitis</i>	F	11	36 (35-37)	42 (41-43)	23 (22-23)	29 (28-30)	12	47 (45-48)	54 (52-55)
<i>C. nitis</i>	M	7	36 (35-37)	42 (41-44)	22 (21-23)	28 (27-30)	8	46 (45-47)	54 (53-55)
<i>C. nictitans</i>	F	0					5	46 (45-47)	54 (53-55)
<i>C. nictitans</i>	M	1	39	41	21	26	14	47 (45-49)	53 (51-55)
<i>C. albogularis</i>	F	9	36 (34-38)	42 (41-43)	22 (20-24)	28 (24-31)	11	47 (45-48)	54 (52-55)
<i>C. albogularis</i>	M	6	37 (36-38)	42 (40-43)	22 (21-22)	28 (27-28)	9	47 (46-49)	53 (52-54)
<i>E. patas</i>	F	1	43	40	18	21	2	51 (51-52)	49 (48-49)
<i>E. patas</i>	M	1	41	42	18	22	4	50 (49-51)	50 (49-51)
Total		102					182		

Table 27. (cont.)

Species	Sex	N	Tarsus/Foot	Ht3/Foot	Ph3/Foot	Ph3/Sole	N	Tarsus/Sole	Ht3/Sole
<i>H. fascicularis</i>	F	6	36 (35-38)	41 (40-42)	23 (22-24)	30 (28-31)	10	47 (46-49)	53 (51-54)
<i>H. fascicularis</i>	M	10	37 (35-38)	40 (39-42)	23 (21-24)	29 (27-31)	10	48 (46-50)	52 (51-54)
<i>H. fuscata</i>	M	2	40 (39-40)	39 (40-40)	21 (21-21)	27 (27-27)	3	50 (50-51)	50 (49-50)
<i>H. mulatta</i>	F	0					10	49 (47-51)	51 (49-53)
<i>H. mulatta</i>	M	2	38 (37-38)	41 (40-41)	22 (21-22)	28 (27-28)	10	48 (47-51)	52 (49-53)
<i>H. nigra</i>	F	1	37	40	23	30	1	48	52
<i>H. nigra</i>	M	2	38 (38-39)	40 (40-40)	22 (21-22)	27 (27-27)	3	48 (48-49)	52 (51-52)
<i>H. tonkeana</i>	F	1	39	39	22	28	1	50	50
<i>H. tonkeana</i>	M	1	38	39	23	30	2	50 (49-51)	50 (49-51)
<i>H. nenestrina</i>	F	5	37 (35-38)	40 (39-41)	23 (22-24)	30 (29-32)	7	48 (46-49)	52 (51-54)
<i>H. nenestrina</i>	M	4	38 (37-38)	40 (39-40)	23 (22-24)	30 (29-31)	5	48 (46-49)	52 (51-54)
<i>H. sylvanus</i>	F	1	38	41	22	28	1	48	52
<i>H. sylvanus</i>	M	2	39 (38-39)	40 (39-41)	22 (22-22)	28 (28-28)	4	49 (48-50)	51 (50-52)
<i>H. arctoides</i>	M	0					2	51 (50-51)	49 (49-50)
<i>H. assanensis</i>	M	0					1	47	53
<i>H. thibetana</i>	M	3	41 (40-41)	37 (36-37)	23 (23-23)	30 (30-30)	4	53 (52-53)	47 (47-48)
<i>C. albigena</i>	F	9	37 (35-38)	41 (40-43)	22 (22-23)	28 (28-29)	10	47 (45-49)	53 (52-55)
<i>C. albigena</i>	M	11	37 (36-38)	41 (41-43)	22 (21-23)	28 (27-29)	14	47 (46-48)	53 (52-54)
<i>C. galeritus</i>	F	1	37	42	21	27	4	47 (47-48)	53 (52-53)
<i>C. galeritus</i>	M	5	38 (38-40)	40 (39-42)	21 (20-22)	27 (26-29)	8	48 (47-51)	52 (50-53)
<i>C. torquatus</i>	F	4	37 (37-38)	42 (41-42)	21 (21-22)	27 (26-28)	7	47 (47-48)	53 (52-53)
<i>C. torquatus</i>	M	7	37 (36-37)	42 (41-43)	22 (21-22)	27 (27-28)	11	47 (46-49)	53 (51-54)
<i>T. gelada</i>	F	1	41	43	16	19	1	48	52
<i>T. gelada</i>	M	3	41 (41-42)	43 (43-43)	16 (15-17)	19 (18-20)	4	50 (49-51)	51 (50-51)
<i>P. cynocephalus</i>	F	4	40 (40-41)	41 (41-42)	19 (18-19)	23 (22-24)	8	49 (47-51)	51 (50-53)
<i>P. cynocephalus</i>	M	10	41 (40-42)	40 (39-42)	18 (18-19)	22 (22-24)	11	50 (48-52)	50 (48-52)
<i>P. hanadryas</i>	F	2	40 (40-41)	41 (41-41)	19 (19-19)	23 (23-23)	2	50 (49-50)	50 (50-51)
<i>P. hanadryas</i>	M	4	40 (40-41)	41 (41-42)	18 (18-19)	22 (22-23)	5	50 (49-52)	50 (48-51)
<i>P. anubis</i>	F	2	41 (40-42)	40 (40-40)	19 (19-19)	24 (24-24)	5	51 (50-53)	49 (47-50)
<i>P. anubis</i>	M	5	41 (40-42)	40 (39-41)	19 (18-20)	24 (22-25)	15	51 (49-52)	49 (48-51)
<i>P. ursinus</i>	F	2	42 (42-42)	40 (40-40)	18 (18-18)	22 (22-22)	4	51 (50-51)	49 (49-50)
<i>P. ursinus</i>	M	2	42 (41-43)	40 (40-40)	18 (17-19)	22 (20-23)	4	51 (51-52)	49 (48-49)
<i>P. leucophaeus</i>	F	2	38 (37-39)	40 (39-41)	22 (22-23)	29 (28-29)	2	49 (48-50)	51 (50-52)
<i>P. leucophaeus</i>	M	1	38	41	22	28	2	48 (48-49)	52 (52-52)
<i>P. sphinx</i>	F	4	38 (37-39)	40 (39-41)	22 (22-23)	29 (28-30)	5	48 (47-50)	52 (50-53)
<i>P. sphinx</i>	M	0					3	49 (47-50)	52 (50-53)
Total		119					199		

Table 27. (cont.)

Species	Sex	N	Tarsus/Foot	Ht3/Foot	Ph3/Foot	Ph3/Sole	N	Tarsus/Sole	Ht3/Sole
<i>P. verus</i>	F	3	34 (33-35)	42 (41-43)	24 (24-25)	32 (32-33)	3	45 (43-46)	55 (54-57)
<i>P. verus</i>	M	5	35 (35-36)	41 (40-42)	24 (23-25)	31 (30-33)	6	46 (45-48)	54 (52-55)
<i>P. badius</i>	F	10	34 (33-36)	42 (41-43)	24 (23-26)	32 (30-34)	13	45 (44-47)	55 (53-56)
<i>P. badius</i>	M	7	35 (34-37)	41 (40-43)	24 (23-25)	31 (30-33)	14	46 (43-48)	54 (52-57)
<i>C. satana</i>	F	1	35	40	25	34	1	46	54
<i>C. satana</i>	M	0					2	46 (45-46)	55 (54-55)
<i>C. polykonos</i>	F	1	34	42	24	31	2	45 (45-45)	55 (55-55)
<i>C. polykonos</i>	M	3	36 (35-37)	40 (40-41)	24 (23-24)	31 (30-31)	3	47 (46-48)	53 (52-54)
<i>C. vellerosus</i>	M	1	35	42	23	30	1	46	54
<i>C. angolensis</i>	F	2	36 (35-37)	41 (40-41)	24 (24-24)	32 (31-32)	4	46 (45-48)	54 (52-55)
<i>C. angolensis</i>	M	1	36	41	24	31	2	47 (46-47)	53 (53-54)
<i>C. guereza</i>	F	7	36 (35-37)	40 (39-42)	24 (23-25)	31 (29-33)	14	47 (46-49)	53 (51-55)
<i>C. guereza</i>	M	9	35 (35-37)	41 (39-42)	24 (23-24)	31 (29-32)	15	46 (45-48)	54 (52-55)
<i>P. hosei</i>	F	1	34	42	24	31	2	44 (44-45)	56 (55-57)
<i>P. hosei</i>	M	2	33 (33-34)	44 (44-44)	23 (23-23)	30 (30-30)	2	43 (43-43)	57 (57-57)
<i>P. rubicunda</i>	F	6	33 (32-34)	44 (43-45)	23 (23-24)	30 (30-31)	11	43 (42-43)	57 (57-58)
<i>P. rubicunda</i>	M	9	33 (32-34)	44 (43-45)	23 (23-24)	31 (30-31)	11	43 (42-44)	57 (56-58)
<i>P. aygula</i>	F	3	34 (33-35)	43 (42-44)	23 (23-24)	31 (30-31)	3	45 (43-46)	56 (54-57)
<i>P. aygula</i>	M	3	34 (34-34)	43 (43-44)	23 (22-24)	30 (28-31)	3	44 (44-44)	56 (56-56)
<i>P. melalophos</i>	F	3	35 (34-35)	42 (42-43)	23 (23-23)	30 (30-31)	4	45 (45-45)	55 (55-56)
<i>P. melalophos</i>	M	4	34 (33-36)	43 (42-43)	23 (22-24)	30 (28-31)	4	44 (43-47)	56 (54-58)
<i>P. frontata</i>	F	0					2	45 (45-46)	55 (54-55)
<i>P. frontata</i>	M	1	34	44	22	29	2	45 (44-46)	55 (54-56)
<i>T. cristata</i>	F	7	35 (33-36)	42 (41-43)	24 (22-25)	31 (28-34)	13	45 (44-47)	55 (53-56)
<i>S. cristata</i>	M	6	35 (34-37)	41 (41-42)	24 (23-24)	31 (30-32)	12	46 (45-47)	54 (53-55)
<i>S. obscura</i>	F	2	35 (34-36)	40 (40-41)	25 (25-25)	33 (33-33)	7	47 (46-49)	53 (51-54)
<i>S. obscura</i>	M	3	36 (34-37)	41 (39-42)	24 (23-24)	31 (30-31)	8	47 (44-49)	53 (51-56)
<i>S. entellus</i>	F	0					7	48 (45-49)	52 (51-55)
<i>S. entellus</i>	M	0					2	48 (48-49)	52 (52-53)
<i>P. roxellanae</i>	F	0					6	50 (48-50)	50 (50-52)
<i>P. roxellanae</i>	M	0					1	49 (49-49)	51 (51-51)
<i>P. nemeus</i>	F	1	34 (34-34)	41 (41-41)	25 (25-25)	34 (34-34)	2	45 (45-45)	55 (55-55)
<i>P. nemeus</i>	M	1	37 (37-37)	40 (40-40)	24 (24-24)	31 (31-31)	5	47 (46-48)	53 (52-54)
<i>H. larvatus</i>	F	3	36 (36-37)	41 (40-41)	23 (23-23)	30 (30-31)	5	47 (46-48)	53 (52-54)
<i>H. larvatus</i>	M	6	36 (35-37)	41 (40-43)	23 (23-24)	30 (29-31)	8	47 (45-48)	53 (52-55)
Total		111					200		

Table 28. Means, ranges of variation (in parentheses) and standard deviations of values for indices describing the relative lengths of the major segments of the foot. Conventions as in Table 24.

Species	N	Mean (Range)	SD	Species	N	Mean (Range)	SD
Tarsus/Foot				Tarsus/Sole			
Cercopithecins	22	36.9 (34.7-42.8)	1.9	Cercopithecins	24	46.8 (45.4-51.4)	1.4
Papionins	32	38.8 (36.1-42.3)	1.8	Papionins	36	48.9 (46.7-52.6)	1.5
Colobines	29	34.7 (32.7-36.7)	1.0	Colobines	35	45.8 (42.7-49.6)	1.6
Mt3/Foot				Mt3/Sole			
Cercopithecins	22	41.6 (39.8-42.7)	0.7	Cercopithecins	24	53.2 (48.6-54.6)	1.4
Papionins	32	40.4 (37.0-43.3)	1.2	Papionins	36	51.1 (47.4-53.3)	1.5
Colobines	29	41.7 (39.8-44.0)	1.2	Colobines	35	54.2 (50.4-57.3)	1.6
Ph3/Foot				Ph3/Sole			
Cercopithecins	22	21.4 (17.5-23.3)	1.4	Cercopithecins	22	27.3 (21.2-30.5)	2.2
Papionins	32	20.8 (15.9-23.3)	2.1	Papionins	32	26.4 (18.9-30.3)	3.3
Colobines	29	23.6 (22.3-25.4)	0.7	Colobines	29	31.0 (28.7-34.1)	1.2

Table 29. Means and ranges of variation (in parentheses) of values for indices describing the relative lengths of the major segments of the foot. Conventions as in Table 23.

Species	Sex	N	Ht3/Tarsus	Pover/Load	N	Ph3/Tarsus	Ph3/Ht3
M. talapoin	F	7	117 (109-127)	22 (20-24)	5	67 (64-70)	56 (55-57)
M. talapoin	M	4	120 (113-130)	22 (20-23)	4	64 (62-68)	54 (52-56)
C. pogonias	F	4	116 (112-122)	23 (22-24)	0		
C. pogonias	M	13	117 (112-123)	23 (23-25)	2	59 (57-61)	52 (51-54)
C. campbelli	F	2	118 (116-121)	23 (23-23)	1	62	54
C. campbelli	M	2	112 (109-115)	26 (26-26)	2	58 (58-58)	52 (50-53)
C. nona	F	2	118 (117-119)	24 (23-24)	2	62 (61-62)	52 (52-52)
C. nona	M	11	114 (109-120)	25 (24-26)	8	59 (55-61)	52 (49-55)
C. ascanius	F	10	115 (107-120)	24 (22-27)	9	59 (55-62)	51 (49-53)
C. ascanius	M	10	117 (105-131)	24 (23-26)	10	58 (54-61)	50 (46-54)
C. cephus	F	4	114 (111-117)	24 (23-25)	1	60 (60-60)	53
C. cephus	M	17	115 (109-123)	25 (22-28)	2	57 (51-63)	50 (47-52)
C. petaurista	F	4	117 (108-126)	22 (21-23)	2	65 (63-67)	53 (53-54)
C. petaurista	M	1	120	24	1	63	53
C. pygerythrus	F	12	105 (97-110)	25 (22-28)	8	55 (51-63)	52 (50-57)
C. pygerythrus	M	14	109 (102-115)	26 (24-28)	9	55 (51-58)	50 (49-52)
C. nitis	F	12	115 (108-122)	25 (24-27)	11	62 (59-65)	54 (52-56)
C. nitis	M	8	116 (111-123)	26 (24-28)	7	61 (58-63)	53 (49-56)
C. nictitans	F	5	118 (113-123)	24 (23-25)	0		
C. nictitans	M	14	114 (105-122)	25 (24-26)	1	54	51
C. albogularis	F	11	115 (109-123)	24 (23-26)	9	61 (53-69)	53 (45-56)
C. albogularis	M	9	113 (106-118)	26 (25-27)	6	59 (57-61)	52 (50-54)
B. patas	F	2	94 (93-96)	29 (28-30)	1	41	44
B. patas	M	4	100 (98-102)	29 (28-30)	1	43	42
Total		182			102		

Table 29. (cont.)

Species	Sex	N	Ht3/Tarsus	Power/Load	N	Ph3/Tarsus	Ph3/Ht3
<i>M. fascicularis</i>	F	10	113 (106-118)	25 (23-26)	6	63 (61-66)	56 (52-59)
<i>M. fascicularis</i>	M	10	109 (102-120)	26 (24-30)	10	61 (56-68)	56 (52-59)
<i>M. fuscata</i>	M	3	99 (98-101)	29 (28-29)	2	54 (53-54)	54 (53-55)
<i>M. nulatata</i>	F	10	106 (96-111)	27 (26-27)	0		
<i>M. nulatata</i>	M	10	107 (97-114)	27 (25-28)	2	58 (55-60)	53 (52-54)
<i>M. nigra</i>	F	1	107	27	1	63	59
<i>M. nigra</i>	M	3	107 (104-110)	28 (27-28)	2	56 (56-57)	53 (53-54)
<i>M. tonkeana</i>	F	1	99	28	1	56	57
<i>M. tonkeana</i>	M	2	100 (97-103)	28 (26-29)	1	60 (60-60)	59
<i>M. nemestrina</i>	F	7	108 (103-118)	25 (23-26)	5	62 (59-69)	58 (55-60)
<i>M. nemestrina</i>	M	5	108 (104-118)	27 (25-29)	4	61 (59-63)	58 (56-61)
<i>M. sylvanus</i>	F	1	109	26	1	57	53
<i>M. sylvanus</i>	M	4	105 (99-109)	27 (26-27)	2	56 (56-57)	55 (54-56)
<i>M. arctoides</i>	M	2	97 (95- 99)	29 (28-29)	0		
<i>M. assanensis</i>	M	1	114	28	0		
<i>M. thibetana</i>	M	4	90 (89- 91)	30 (28-32)	3	57 (56-58)	64 (63-64)
<i>C. albigena</i>	F	10	111 (106-120)	24 (23-25)	9	60 (58-63)	54 (52-56)
<i>C. albigena</i>	M	14	112 (108-118)	25 (24-26)	11	59 (56-61)	52 (50-55)
<i>C. galeritus</i>	F	4	111 (109-112)	26 (25-27)	1	57	51
<i>C. galeritus</i>	M	8	107 (98-114)	27 (25-29)	5	56 (51-58)	53 (50-56)
<i>C. torquatus</i>	F	7	112 (108-115)	25 (23-26)	4	58 (56-59)	52 (49-54)
<i>C. torquatus</i>	M	11	113 (104-118)	26 (25-26)	7	58 (57-60)	52 (51-52)
<i>T. gelada</i>	F	1	107	28	1	40	37
<i>T. gelada</i>	M	4	102 (98-106)	29 (28-30)	3	39 (37-41)	37 (36-39)
<i>P. cynocephalus</i>	F	8	104 (98-112)	28 (27-28)	4	47 (45-48)	46 (45-47)
<i>P. cynocephalus</i>	M	11	99 (93-108)	29 (26-31)	10	44 (42-47)	45 (43-48)
<i>P. hanadryas</i>	F	2	102 (100-104)	29 (29-29)	2	47 (46-47)	46 (45-47)
<i>P. hanadryas</i>	M	5	101 (94-106)	30 (28-31)	4	45 (44-47)	44 (43-45)
<i>P. anubis</i>	F	5	95 (89-101)	30 (29-32)	2	47 (46-48)	48 (48-48)
<i>P. anubis</i>	M	15	98 (91-103)	30 (28-32)	5	46 (43-49)	48 (46-51)
<i>P. ursinus</i>	F	4	96 (94- 99)	29 (28-30)	2	43 (42-43)	45 (45-46)
<i>P. ursinus</i>	M	4	96 (93- 97)	32 (30-33)	2	42 (39-45)	44 (42-47)
<i>P. leucophaeus</i>	F	2	106 (101-110)	26 (26-27)	2	59 (57-61)	56 (56-56)
<i>P. leucophaeus</i>	M	2	107 (106-108)	27 (27-28)	1	58	53
<i>P. sphinx</i>	F	5	107 (101-111)	28 (26-28)	4	59 (57-62)	56 (54-58)
<i>P. sphinx</i>	M	3	107 (101-112)	28 (26-30)	0		
Total		199			119		

Table 29. (cont.)

Species	Sex	N	Ht3/Tarsus	Power/Load	N	Ph3/Tarsus	Ph3/Ht3
<i>P. verus</i>	F	3	124 (119-133)	22 (21-23)	3	72 (70-75)	59 (56-61)
<i>P. verus</i>	M	6	117 (109-121)	25 (23-27)	5	69 (66-71)	58 (56-60)
<i>P. badius</i>	F	13	121 (113-126)	26 (23-28)	10	70 (64-75)	58 (55-63)
<i>P. badius</i>	M	14	117 (109-131)	25 (23-28)	7	69 (63-73)	58 (55-61)
<i>C. satana</i>	F	1	117	25	1	73	63
<i>C. satana</i>	M	2	120 (118-121)	24 (24-24)	0		
<i>C. polykonos</i>	F	2	123 (122-124)	25 (24-27)	1	71	57
<i>C. polykonos</i>	M	3	112 (108-116)	27 (26-27)	3	65 (64-68)	59 (57-60)
<i>C. vellerosus</i>	M	1	119	24	1	67	56
<i>C. angolensis</i>	F	4	117 (109-120)	24 (24-25)	2	68 (65-71)	59 (59-60)
<i>C. angolensis</i>	M	2	114 (113-116)	25 (25-25)	1	66	58
<i>C. guereza</i>	F	14	114 (105-120)	26 (24-29)	7	66 (63-70)	59 (54-61)
<i>C. guereza</i>	M	15	117 (106-121)	26 (23-27)	9	67 (63-70)	57 (55-60)
<i>P. hosei</i>	F	2	127 (123-130)	24 (24-24)	1	70	57
<i>P. hosei</i>	M	2	132 (131-133)	23 (23-23)	2	69 (68-70)	52 (52-53)
<i>P. rubicunda</i>	F	11	134 (131-140)	23 (21-24)	6	71 (68-74)	53 (52-54)
<i>P. rubicunda</i>	M	11	133 (128-141)	23 (22-24)	9	71 (69-74)	53 (52-55)
<i>P. aygula</i>	F	3	125 (119-133)	25 (23-27)	3	69 (67-69)	55 (52-57)
<i>P. aygula</i>	M	3	128 (126-128)	24 (23-24)	3	67 (65-70)	53 (51-56)
<i>P. nelalophos</i>	F	4	123 (121-125)	24 (23-25)	3	67 (66-68)	55 (54-56)
<i>P. nelalophos</i>	M	4	127 (115-135)	24 (23-25)	4	68 (61-73)	54 (51-56)
<i>P. frontata</i>	F	2	120 (118-122)	23 (23-24)	0		
<i>P. frontata</i>	M	2	123 (117-129)	23 (23-23)	1	67 (66-66)	51
<i>S. cristata</i>	F	13	121 (111-129)	23 (21-25)	7	69 (61-77)	57 (51-61)
<i>S. cristata</i>	M	12	117 (112-122)	24 (22-24)	6	67 (63-69)	57 (56-59)
<i>S. obscura</i>	F	7	113 (104-119)	24 (22-26)	2	71 (69-72)	61 (60-62)
<i>S. obscura</i>	M	8	114 (105-126)	25 (23-27)	3	66 (63-70)	58 (56-61)
<i>S. entellus</i>	F	7	110 (106-122)	27 (24-28)	0		
<i>S. entellus</i>	M	2	108 (106-110)	27 (26-28)	0		
<i>P. roxellanae</i>	F	6	102 (99-108)	27 (26-28)	0		
<i>P. roxellanae</i>	M	1	102	27	0		
<i>P. nanaeus</i>	F	2	123 (123-123)	24 (23-24)	1	76	62
<i>P. nanaeus</i>	M	5	112 (108-116)	25 (24-27)	1	64	59
<i>H. larvatus</i>	F	5	112 (109-116)	24 (23-26)	3	64 (62-65)	57 (56-58)
<i>H. larvatus</i>	M	8	115 (108-121)	26 (24-27)	6	64 (61-66)	55 (53-59)
Total		200			111		

Table 30. Means, ranges of variation (in parentheses) and standard deviations of values for indices describing the relative lengths of the major segments of the foot. Conventions as in Table 24.

Species	N	Mean (Range)	SD
Mt3/Tarsus			
Cercopithecins	24	113.8 (94.4-120.4)	6.2
Papionins	36	104.6 (90.0-114.3)	6.0
Colobines	35	118.6 (101.7-134.2)	7.7
Power/Load			
Cercopithecins	24	24.6 (21.5-29.2)	1.9
Papionins	36	27.5 (24.1-31.7)	3.5
Colobines	35	24.5 (22.2-27.0)	1.3
Ph3/Tarsus			
Cercopithecins	22	58.4 (40.8-66.6)	6.2
Papionins	32	54.0 (38.5-63.4)	7.4
Colobines	29	68.2 (63.6-76.0)	2.9
Ph3/Mt3			
Cercopithecins	22	51.5 (42.4-56.2)	3.1
Papionins	32	51.6 (38.5-63.4)	6.1
Colobines	29	56.9 (51.0-62.9)	2.9

Table 31. Least Squares coefficients and statistics for regressions of foot segments on body mass. Conventions as in Table 25. * male E. patas and female H. talapoin removed from sample. ** male E. patas removed from sample.

Taxon	N	slope	SE	y-int	r ²	Taxon	N	slope	SE	y-int	r ²
<u>lxsolc*lxmass</u>						<u>lxlncl*lxmass</u>					
Cercopithecines	60	0.28	0.01	2.09	0.91	Cercopithecines	60	0.32	0.01	0.67	0.93
Cercopithecins	24	0.33	0.03	1.63	0.88	Cercopithecins	24	0.38	0.03	0.20	0.89
Papionins	36	0.27	0.02	2.15	0.85	Papionins	36	0.31	0.02	0.73	0.89
Cercopithecines	58	0.29	0.01	2.17	0.90 *	Cercopithecines	59	0.32	0.01	0.68	0.93 **
Cercopithecins	22	0.30	0.03	1.95	0.81 *	Cercopithecins	23	0.36	0.03	0.34	0.88 **
Colobines	35	0.28	0.03	2.16	0.78	Colobines	35	0.34	0.03	0.53	0.84
Pr > F slope Pr > F mean Subfamilies 0.5766 0.0001 Tribes 0.0409 0.1390						Pr > F slope Pr > F mean Subfamilies 0.9886 0.6250 Tribes 0.0347 0.0999					
Subfamilies 0.9556 0.0001 * Tribes 0.4814 0.4086 *						Subfamilies 0.8196 0.4633 ** Tribes 0.1312 0.2977 **					
<u>lxtarsus*lxmass</u>											
Cercopithecines	60	0.32	0.01	1.03	0.93						
Cercopithecins	24	0.36	0.03	0.65	0.87						
Papionins	36	0.30	0.02	1.13	0.89						
Colobines	35	0.34	0.03	0.82	0.85						
Pr > F slope Pr > F mean Subfamilies 0.6890 0.8494 Tribes 0.0600 0.2645											

Table 31. (cont.) * male *H. patas* and female *H. talapoin* removed from sample.

Taxon	N	slope	SE	y-int	r ²	Taxon	N	slope	SE	y-int	r ²
lxlcal*lxmass						lxpower*lxmass					
Cercopithecines	60	0.25	0.01	0.59	0.92	Cercopithecines	60	0.38	0.02	-.57	0.93
Cercopithecins	24	0.31	0.02	0.31	0.90	Cercopithecins	24	0.45	0.03	-1.16	0.89
Papionins	36	0.26	0.02	0.71	0.89	Papionins	36	0.35	0.02	-.36	0.89
Colobines	35	0.29	0.03	0.24	0.79	Cercopithecines	58	0.38	0.01	-.56	0.94 *
		Pr > F slope		Pr > F mean		Cercopithecins	22	0.41	0.04	-.84	0.84 *
Subfamilies		0.3346		0.0561		Colobines	35	0.37	0.04	-.60	0.76
Tribes		0.0972		0.0730				Pr > F slope		Pr > F mean	
lxlcub*lxmass						Subfamilies		0.7391		0.0034	
Cercopithecines	60	0.30	0.01	-.16	0.90	Tribes		0.0123		0.3715	
Cercopithecins	24	0.32	0.04	-.31	0.79			Pr > F slope		Pr > F mean	
Papionins	36	0.28	0.02	0.05	0.83	Subfamilies		0.9560		0.0071 *	
Colobines	35	0.35	0.03	-.56	0.80	Tribes		0.1256		0.8515 *	
		Pr > F slope		Pr > F mean		lxload*lxmass					
Subfamilies		0.2131		0.0949		Cercopithecines	60	0.25	0.01	2.11	0.90
Tribes		0.2817		0.8052		Cercopithecins	24	0.31	0.03	1.68	0.87
lxload*lxmass						Papionins	36	0.25	0.02	2.16	0.83
Cercopithecines	60	0.25	0.01	2.11	0.90	Colobines	35	0.26	0.03	2.16	0.74
Cercopithecins	24	0.31	0.03	1.68	0.87			Pr > F slope		Pr > F mean	
Papionins	36	0.25	0.02	2.16	0.83	Subfamilies		0.6419		0.0001	
Colobines	35	0.26	0.03	2.16	0.74	Tribes		0.0511		0.1463	
		Pr > F slope		Pr > F mean							
Subfamilies		0.6419		0.0001							
Tribes		0.0511		0.1463							

Table 31. (cont.) * male *E. patas* and female *H. talapoin* removed from sample. ***Papio*, *Theropithecus* and *Miopithecus* removed from sample.

Taxon	N	slope	SE	y-int	r ²	Taxon	N	slope	SE	y-int	r ²
lxy3*lxnass						lxph3len*lxnass					
Cercopithecines	54	0.23	0.01	2.31	0.84	Cercopithecines	54	0.19	0.02	1.57	0.63
Cercopithecins	22	0.29	0.03	1.75	0.85	Cercopithecins	22	0.25	0.03	1.06	0.74
Papionins	32	0.19	0.02	2.65	0.68	Papionins	32	0.10	0.04	2.39	0.20
Cercopithecines	52	0.21	0.01	2.42	0.82 *	Cercopithecines	42	0.25	0.02	1.02	0.75 **
Cercopithecins	20	0.26	0.04	2.03	0.75	Cercopithecins	20	0.20	0.05	1.45	0.50 **
Colobines	29	0.25	0.03	2.28	0.66	Papionins	22	0.23	0.04	1.27	0.65 **
						Colobines	29	0.27	0.03	1.07	0.73
		Pr > F slope		Pr > F mean				Pr > F slope		Pr > F mean	
Subfamilies		0.7108		0.0001		Subfamilies		0.0511		0.0001	
Tribes		0.0030		0.6869		Tribes		0.0017		0.1692	
Subfamilies		0.3945		0.0001 *		Subfamilies		0.2952		0.0001 **	
Tribes		0.0804		0.8903 *		Tribes		0.6020		0.0454 **	
lxt3*lxnass											
Cercopithecines	60	0.24	0.01	1.74	0.85						
Cercopithecins	24	0.31	0.03	1.22	0.85						
Papionins	36	0.24	0.02	1.76	0.76						
Colobines	35	0.22	0.03	2.03	0.58						
		Pr > F slope		Pr > F mean							
Subfamilies		0.2714		0.0001							
Tribes		0.0582		0.1213							

Table 31. (cont.) *** male *E. patas* removed from sample.

Taxon	N	slope	SE	y-int	r ²
lxxreant3*lxnass					
Cercopithecines	60	0.65	0.02	-2.79	0.93
Cercopithecins	24	0.73	0.06	-3.47	0.89
Papionins	36	0.58	0.04	-2.17	0.88
Cercopithecines	56	0.63	0.03	-2.61	0.92 ***
Cercopithecins	23	0.69	0.05	-3.16	0.89 ***
Colobines	35	0.60	0.05	-2.28	0.81

	Pr > F slope	Pr > F mean
Subfamilies	0.6113	0.0001
Tribes	0.0159	0.4527
Subfamilies	0.8190	0.0001 ***
Tribes	0.6931	0.0721 ***

lxxrph3*lxnass

Cercopithecines	54	0.32	0.01	-1.41	0.91
Cercopithecins	22	0.36	0.03	-1.73	0.89
Papionins	32	0.29	0.03	-1.15	0.82
Colobines	29	0.35	0.04	-1.61	0.78

	Pr > F slope	Pr > F mean
Subfamilies	0.5171	0.0214
Tribes	0.0715	0.9925

Table 32. Residuals of species by sex values from subfamilial LS lines of foot segments on body mass.

Species	Sex	Sole	Parsus	Calc	LdCal	Cuboid	Power	Load
<i>M. talapoin</i>	F	-1.77	-1.36	-1.59	-1.91	-0.67	-1.30	-1.88
<i>M. talapoin</i>	M	-0.88	-0.80	-1.00	-1.26	-0.25	-1.41	-0.91
<i>C. pogonias</i>	F	0.01	0.11	0.02	0.29	0.29	-0.21	0.09
<i>C. pogonias</i>	M	0.46	0.06	0.12	0.90	-0.06	-0.70	0.68
<i>C. campbelli</i>	F	0.24	0.14	0.03	0.17	0.38	0.07	0.30
<i>C. campbelli</i>	M	0.91	0.85	1.27	1.42	-0.23	1.32	0.84
<i>C. mona</i>	F	-0.25	-0.46	-0.46	-0.34	-0.40	-0.38	-0.19
<i>C. mona</i>	M	2.73	2.62	2.74	2.37	2.01	2.32	2.65
<i>C. ascanius</i>	F	-1.54	-1.60	-1.42	-1.21	-1.77	-1.02	-1.52
<i>C. ascanius</i>	M	0.61	0.21	0.26	0.21	0.07	0.22	0.68
<i>C. cephus</i>	F	0.38	0.47	0.61	1.12	0.10	0.23	0.42
<i>C. cephus</i>	M	1.09	0.86	0.87	0.54	0.73	0.78	1.08
<i>C. petaurista</i>	F	-0.40	-0.59	-0.68	-0.10	-0.31	-1.31	-0.23
<i>C. petaurista</i>	M	0.43	-0.14	0.25	0.96	-1.03	0.48	0.60
<i>C. pygerythrus</i>	F	-0.52	0.17	0.06	-0.08	0.40	0.17	-0.69
<i>C. pygerythrus</i>	M	-0.32	-0.20	-0.24	-0.68	-0.08	-0.03	-0.44
<i>C. nitis</i>	F	-0.06	-0.31	0.04	0.14	-1.05	0.19	-0.06
<i>C. nitis</i>	M	-0.07	-0.74	-0.42	-0.64	-1.40	-0.40	-0.02
<i>C. nictitans</i>	F	0.81	0.36	0.51	0.39	-0.02	0.43	0.85
<i>C. nictitans</i>	M	1.41	1.06	1.25	1.45	0.48	0.90	1.49
<i>C. albogularis</i>	F	-1.17	-1.47	-1.24	-1.05	-1.78	-1.47	-1.11
<i>C. albogularis</i>	M	-0.71	-1.19	-0.95	-0.58	-1.58	-0.93	-0.57
<i>E. patas</i>	F	0.47	1.64	1.41	-0.20	1.92	1.68	-0.09
<i>E. patas</i>	M	2.18	2.69	2.54	1.91	2.65	2.95	1.96

Table 32. (cont.)

Species	Sex	Sole	Parsus	Calc	LdCal	Cuboid	Power	Load
<i>M. fascicularis</i>	F	-1.67	-1.59	-1.62	-1.78	-1.28	-0.99	-1.70
<i>M. fascicularis</i>	M	-1.18	-1.01	-1.19	-1.08	-0.47	-0.75	-1.15
<i>M. fuscata</i>	M	-2.62	-2.35	-2.43	-2.32	-1.83	-2.27	-2.64
<i>M. mulatta</i>	F	0.62	0.95	1.00	0.34	0.73	1.08	0.41
<i>M. mulatta</i>	M	1.03	1.08	1.10	0.76	0.88	0.98	0.95
<i>M. nigra</i>	F	-0.49	-0.22	-0.24	0.24	-0.12	0.51	-0.45
<i>M. nigra</i>	M	0.43	0.42	0.24	-0.27	0.77	0.54	0.38
<i>M. tonkeana</i>	F	-0.94	-0.28	-0.73	-1.63	0.75	-0.17	-1.16
<i>M. tonkeana</i>	M	1.37	2.08	1.69	1.46	2.64	1.83	1.25
<i>M. nemestrina</i>	F	-0.61	-0.49	-0.66	0.01	-0.02	-1.19	-0.46
<i>M. nemestrina</i>	M	0.18	-0.01	-0.12	0.05	0.25	-0.17	0.29
<i>M. sylvanus</i>	F	-0.84	-1.07	-1.08	-1.15	-0.87	-1.53	-0.78
<i>M. sylvanus</i>	M	1.30	1.34	1.05	1.55	1.80	0.64	1.45
<i>M. arctoides</i>	M	-0.78	-0.13	-0.26	-0.08	0.20	-0.39	-0.88
<i>M. assanensis</i>	M	-0.65	-1.25	-1.12	-1.81	-1.37	-0.14	-0.64
<i>M. thibetana</i>	M	-2.18	-1.18	-1.49	-0.88	-0.34	-1.83	-2.25
<i>C. albigena</i>	F	0.11	0.04	-0.19	0.31	0.55	-0.40	0.28
<i>C. albigena</i>	M	1.36	1.02	0.95	1.20	1.03	1.01	1.50
<i>C. galeritus</i>	F	0.91	0.80	0.81	0.25	0.69	1.28	0.84
<i>C. galeritus</i>	M	0.16	-0.01	0.18	0.20	-0.44	0.10	0.16
<i>C. torquatus</i>	F	0.21	-0.07	0.06	0.31	-0.33	-0.43	0.29
<i>C. torquatus</i>	M	0.46	-0.22	-0.18	-0.23	-0.28	-0.53	0.63
<i>T. gelada</i>	F	0.01	-0.27	-0.35	-1.37	-0.02	-0.33	-0.07
<i>T. gelada</i>	M	-0.18	-0.29	-0.32	-0.53	-0.16	-0.46	-0.18
<i>P. cynocephalus</i>	F	0.50	0.51	0.51	0.54	0.44	0.42	0.49
<i>P. cynocephalus</i>	M	-0.26	-0.24	-0.35	-0.41	0.05	-0.47	-0.25
<i>P. hanadryas</i>	F	0.37	0.64	0.61	-0.38	0.63	1.18	0.12
<i>P. hanadryas</i>	M	-0.69	-0.72	-0.74	-0.52	-0.55	-0.63	-0.64
<i>P. anubis</i>	F	0.30	0.97	0.94	1.26	0.91	0.85	0.18
<i>P. anubis</i>	M	-0.11	-0.08	-0.10	0.30	0.00	-0.12	-0.05
<i>P. ursinus</i>	F	0.16	0.69	0.63	0.81	0.75	0.44	0.06
<i>P. ursinus</i>	M	-0.70	-0.58	-0.65	-0.88	-0.32	0.01	-0.76
<i>P. leucophaeus</i>	F	-0.42	-0.45	-0.09	0.97	-1.23	-0.58	-0.30
<i>P. leucophaeus</i>	M	0.61	0.09	0.09	0.90	0.08	-0.21	0.90
<i>P. sphinx</i>	F	-1.09	-1.27	-1.09	-0.15	-1.51	-0.38	-0.91
<i>P. sphinx</i>	M	1.29	0.74	1.17	0.19	-0.37	0.52	1.14

Table 32. (cont.)

Species	Sex	Sole	Parsus	Calc	LdCal	Cuboid	Power	Load
<i>P. verus</i>	F	-0.71	-0.27	-0.26	-0.32	-0.21	-1.29	-0.79
<i>P. verus</i>	M	-0.97	-0.02	0.21	0.26	-0.51	0.19	-1.15
<i>P. badius</i>	F	0.67	0.64	0.92	0.08	-0.19	1.31	0.44
<i>P. badius</i>	M	-1.59	-1.72	-1.36	-1.33	-2.04	-1.10	-1.59
<i>C. satana</i>	F	-0.26	-0.29	-0.15	-0.07	-0.51	-0.55	-0.25
<i>C. satana</i>	M	0.45	-0.02	-0.23	-0.24	0.46	-0.21	0.57
<i>C. polykonos</i>	F	0.97	0.60	0.93	0.46	-0.34	1.10	0.86
<i>C. polykonos</i>	M	0.58	1.05	1.41	0.99	-0.08	1.42	0.31
<i>C. vellerosus</i>	M	0.44	0.22	0.57	1.92	-0.65	-1.00	0.67
<i>C. angolensis</i>	F	0.30	0.53	0.29	-0.40	0.94	-0.24	0.17
<i>C. angolensis</i>	M	-0.99	-0.94	-1.05	-0.89	-0.39	-1.39	-0.91
<i>C. guereza</i>	F	-0.75	-0.34	0.09	-0.22	-1.23	0.22	-0.96
<i>C. guereza</i>	M	-1.09	-1.31	-1.04	-1.68	-1.53	-0.36	-1.18
<i>P. hosei</i>	F	0.36	0.02	0.16	-0.39	-0.29	0.18	0.29
<i>P. hosei</i>	M	1.92	1.01	0.87	1.11	1.07	1.26	2.11
<i>P. rubicunda</i>	F	0.53	-0.68	-0.37	-0.19	-1.17	0.02	0.72
<i>P. rubicunda</i>	M	1.01	-0.06	0.37	0.73	-1.02	0.21	1.18
<i>P. aygula</i>	F	0.54	0.13	0.31	-0.35	-0.32	1.13	0.45
<i>P. aygula</i>	M	-0.42	-1.12	-0.95	-0.56	-1.17	-0.53	-0.23
<i>P. nelalophos</i>	F	0.99	0.82	0.36	0.68	1.59	1.02	1.14
<i>P. nelalophos</i>	M	0.70	0.20	0.16	-0.08	0.24	0.63	0.75
<i>P. frontata</i>	F	0.53	0.82	0.53	0.61	1.25	0.40	0.54
<i>P. frontata</i>	M	0.62	0.65	0.39	0.64	1.07	0.39	0.69
<i>S. cristata</i>	F	-1.51	-1.41	-1.83	-1.50	-0.07	-1.64	-1.34
<i>S. cristata</i>	M	-1.32	-1.05	-1.22	-0.82	-0.36	-1.40	-1.21
<i>S. obscura</i>	F	-1.85	-1.17	-1.60	-1.60	0.12	-1.59	-1.84
<i>S. obscura</i>	M	-1.15	-0.72	-0.92	-0.79	-0.07	-0.53	-1.14
<i>S. entellus</i>	F	1.56	2.23	1.95	1.11	2.24	2.01	1.28
<i>S. entellus</i>	M	1.55	1.96	2.01	1.42	1.29	1.56	1.30
<i>P. roxellanae</i>	F	-0.69	0.88	0.85	1.39	0.71	0.87	-0.87
<i>P. roxellanae</i>	M	-1.08	-0.51	-0.67	-0.24	-0.01	-0.54	-1.05
<i>P. nanaeus</i>	F	-0.71	-1.49	-1.55	-1.25	-0.91	-1.33	-0.52
<i>P. nanaeus</i>	M	0.36	0.59	0.24	-0.37	1.20	0.12	0.26
<i>H. larvatus</i>	F	1.20	1.75	1.55	2.50	1.71	0.48	1.30
<i>H. larvatus</i>	M	-0.21	-0.99	-0.95	-0.59	-0.81	-0.82	0.02

Table 33. Residuals of species by sex values from subfamilial LS lines of foot segments on body mass. * Residuals from forced LS line.

Species	Sex	Ray3	Ht3	Ph3	Ph3*	AMt3	BPh3
<i>M. talapoin</i>	F	-2.12	-1.90	-1.58	-0.40	-1.49	-1.07
<i>M. talapoin</i>	H	-1.01	-0.86	-1.04	-0.02	-0.40	0.15
<i>C. pogonias</i>	F	.	0.08	.	.	-0.21	.
<i>C. pogonias</i>	H	0.45	0.72	0.30	0.52	0.00	0.61
<i>C. campbelli</i>	F	0.51	0.26	0.21	0.85	-0.44	-0.35
<i>C. campbelli</i>	H	0.81	0.84	0.41	0.64	0.21	0.71
<i>C. nona</i>	F	-0.13	-0.07	-0.30	0.23	-0.38	-0.38
<i>C. nona</i>	H	2.40	2.46	1.50	1.74	2.70	2.23
<i>C. ascanius</i>	F	-1.45	-1.30	-1.29	-0.76	-1.88	-1.37
<i>C. ascanius</i>	H	0.61	0.84	0.00	0.29	0.42	0.26
<i>C. cephus</i>	F	-0.52	0.25	-0.50	0.04	0.79	-0.13
<i>C. cephus</i>	H	0.13	1.13	-0.35	-0.01	0.47	0.03
<i>C. petaurista</i>	F	0.36	-0.20	0.17	0.63	-1.28	-0.41
<i>C. petaurista</i>	H	0.86	0.81	0.55	0.84	0.07	0.25
<i>C. pygerythrus</i>	F	-1.09	-1.01	-0.89	-0.38	-0.20	-1.03
<i>C. pygerythrus</i>	H	-0.76	-0.41	-0.78	-0.49	-0.31	-0.99
<i>C. mitis</i>	F	0.25	0.15	0.35	0.60	0.11	0.09
<i>C. mitis</i>	H	0.65	0.49	0.65	0.54	-0.85	-0.48
<i>C. nictitans</i>	F	.	1.05	.	.	-0.16	.
<i>C. nictitans</i>	H	0.91	1.53	0.55	0.61	0.82	1.21
<i>C. albogularis</i>	F	-0.98	-0.78	-0.66	-0.40	-1.66	-1.07
<i>C. albogularis</i>	H	0.19	-0.21	0.33	0.16	-0.78	-0.14
<i>B. patas</i>	F	-0.61	-0.60	-1.51	-1.29	0.65	-0.48
<i>B. patas</i>	H	1.27	1.48	-0.31	-0.41	2.34	1.91

Table 33. (cont.)

Species	Sex	Ray3	Ht3	Ph3	Ph3*	AMt3	BPh3
<i>M. fascicularis</i>	F	-1.06	-1.52	-0.44	0.00	-1.00	-0.77
<i>M. fascicularis</i>	M	-0.74	-1.15	-0.05	0.14	0.06	0.31
<i>M. fuscata</i>	M	-2.26	-2.51	-0.92	-1.27	1.24	0.69
<i>M. mulatta</i>	F	.	0.28	.	.	0.01	0.78
<i>M. mulatta</i>	M	1.28	0.87	1.15	1.00	0.44	1.21
<i>M. nigra</i>	F	0.02	-0.63	0.77	0.87	2.44	1.89
<i>M. nigra</i>	M	0.46	0.39	0.64	0.49	-1.82	-2.69
<i>M. tonkeana</i>	F	-0.78	-1.38	0.20	0.11	0.88	.
<i>M. tonkeana</i>	M	1.49	0.61	1.84	1.76	1.04	-0.09
<i>M. nemestrina</i>	F	-0.19	-0.61	0.58	0.60	-0.46	-0.95
<i>M. nemestrina</i>	M	0.81	0.33	1.54	1.19	-0.25	0.26
<i>M. sylvanus</i>	F	-0.26	-0.52	0.15	-0.05	-1.21	0.69
<i>M. sylvanus</i>	M	1.50	1.11	1.61	1.26	1.03	0.21
<i>M. arctoides</i>	M	.	-1.23	.	.	-0.49	.
<i>M. assanensis</i>	M	.	-0.07	.	.	0.57	.
<i>M. thibetana</i>	M	-1.61	-2.80	0.54	0.04	-1.14	0.36
<i>C. albigena</i>	F	0.25	0.16	0.41	0.52	0.23	0.87
<i>C. albigena</i>	M	1.54	1.47	1.20	1.10	1.45	1.58
<i>C. galeritus</i>	F	0.75	0.89	0.41	0.51	0.84	-0.02
<i>C. galeritus</i>	M	0.27	0.29	0.54	0.27	0.00	-1.18
<i>C. torquatus</i>	F	0.77	0.41	0.56	0.56	-0.02	-0.42
<i>C. torquatus</i>	M	1.36	0.98	1.21	0.76	0.37	0.50
<i>T. gelada</i>	F	-0.93	0.25	-2.58	-2.73	0.16	1.66
<i>T. gelada</i>	M	-1.26	-0.06	-2.66	-3.01	0.60	1.73
<i>P. cynocephalus</i>	F	-0.13	0.43	-0.64	-0.91	0.30	0.19
<i>P. cynocephalus</i>	M	-0.76	-0.24	-0.87	-1.49	-0.50	-1.25
<i>P. hanadryas</i>	F	-0.27	0.10	-0.76	-0.91	-1.19	-0.22
<i>P. hanadryas</i>	M	-0.76	-0.57	-1.11	-1.62	-1.72	-0.57
<i>P. anubis</i>	F	-0.23	-0.33	-0.32	-0.68	0.20	0.00
<i>P. anubis</i>	M	-0.31	-0.13	-0.20	-0.96	-0.03	0.31
<i>P. ursinus</i>	F	-0.48	-0.32	-0.87	-1.23	0.00	-0.57
<i>P. ursinus</i>	M	-0.77	-0.73	-0.92	-1.67	-1.24	-0.74
<i>P. leucophaeus</i>	F	0.24	-0.32	0.86	0.57	-0.47	-1.41
<i>P. leucophaeus</i>	M	1.84	0.98	1.91	1.17	0.35	-0.09
<i>P. sphinx</i>	F	-0.50	-0.79	0.39	0.06	-0.87	-1.81
<i>P. sphinx</i>	M	.	1.59	.	.	1.64	.

Table 33. (cont.)

Species	Sex	Ray3	Ht3	Ph3	AMt3	BPh3
<i>P. vernus</i>	F	-0.56	-0.85	0.07	0.18	0.13
<i>P. vernus</i>	M	-0.99	-1.38	-0.57	0.10	2.09
<i>P. badius</i>	F	1.09	0.58	1.47	0.88	0.91
<i>P. badius</i>	M	-0.52	-1.20	-0.39	-1.35	0.23
<i>C. satana</i>	F	0.37	-0.17	1.61	-0.89	0.75
<i>C. satana</i>	M	.	0.69	.	-0.51	.
<i>C. polykonos</i>	F	1.97	1.04	2.12	1.37	-0.08
<i>C. polykonos</i>	M	0.26	0.18	0.58	0.36	0.46
<i>C. vellerosus</i>	M	0.35	0.51	0.10	-0.58	-2.87
<i>C. angolensis</i>	F	0.46	0.12	1.06	0.04	0.93
<i>C. angolensis</i>	M	-1.29	-0.82	-1.16	-0.50	-0.51
<i>C. guereza</i>	F	-0.85	-0.86	-0.47	0.26	0.39
<i>C. guereza</i>	M	-1.01	-0.72	-1.11	0.00	-0.06
<i>P. hosei</i>	F	-0.70	0.51	-0.63	0.65	-0.07
<i>P. hosei</i>	M	1.92	2.12	1.08	0.71	0.37
<i>P. rubicunda</i>	F	0.92	1.16	0.15	0.27	0.05
<i>P. rubicunda</i>	M	1.37	1.47	0.75	0.57	0.28
<i>P. aygula</i>	F	0.57	0.71	0.21	-0.75	-1.53
<i>P. aygula</i>	M	-0.41	0.10	-1.39	-0.05	-1.01
<i>P. nelalophos</i>	F	0.55	0.93	0.18	1.03	0.58
<i>P. nelalophos</i>	M	0.65	0.90	0.01	0.78	0.17
<i>P. frontata</i>	F	.	0.27	.	1.63	.
<i>P. frontata</i>	M	0.65	0.49	-0.59	-1.28	-0.89
<i>S. cristata</i>	F	-1.81	-1.28	-1.73	-1.99	-1.54
<i>S. cristata</i>	M	-1.35	-1.22	-1.30	-1.79	-1.33
<i>S. obscura</i>	F	-0.86	-1.93	0.01	-1.01	0.71
<i>S. obscura</i>	M	-1.49	-1.20	-1.37	-0.55	-0.12
<i>S. entellus</i>	F	.	0.85	.	1.19	.
<i>S. entellus</i>	M	.	1.01	.	2.37	.
<i>P. roxellanae</i>	F	.	-1.63	.	0.31	.
<i>P. roxellanae</i>	M	.	-1.29	.	0.12	.
<i>P. nanaeus</i>	F	0.16	-0.23	1.22	-1.67	-0.34
<i>P. nanaeus</i>	M	-0.24	0.16	0.06	0.35	0.02
<i>H. larvatus</i>	F	0.86	0.64	0.86	0.66	1.58
<i>H. larvatus</i>	M	-0.06	0.36	-0.83	-0.90	0.69

Table 34. Means and ranges of variation (in parentheses) of values for indices describing the relative length of the hallux. Conventions as in Table 23.

Species	Sex	N	Ray1/Foot	N	Ray1/Sole	Ray1/Ht3	N	Ray1/Ray3
<i>M. talapoin</i>	F	5	38 (37-39)	6	49 (48-51)	91 (88-95)	5	59 (57-61)
<i>M. talapoin</i>	M	4	38 (37-39)	4	49 (48-51)	90 (88-93)	4	59 (58-60)
<i>C. pogonias</i>	M	1	39	1	49	93	1	62
<i>C. campbelli</i>	F	1	40	1	52	97	1	63
<i>C. campbelli</i>	M	2	41 (40-42)	2	52 (50-53)	98 (94-102)	2	65 (63-67)
<i>C. mona</i>	F	2	40 (40-40)	2	51 (51-52)	94 (94-95)	2	62 (62-62)
<i>C. mona</i>	M	5	39 (38-40)	5	50 (48-52)	93 (89-98)	5	61 (60-64)
<i>C. ascanius</i>	F	9	38 (36-40)	10	48 (46-51)	91 (85-94)	9	60 (56-63)
<i>C. ascanius</i>	M	10	38 (37-40)	10	49 (47-50)	90 (87-93)	10	60 (57-62)
<i>C. cephus</i>	F	1	42	1	54	100	1	66
<i>C. cephus</i>	M	2	37 (34-40)	2	47 (42-51)	87 (80-93)	2	58 (55-61)
<i>C. petaurista</i>	F	2	39 (39-40)	2	51 (50-52)	92 (91-93)	2	60 (60-61)
<i>C. petaurista</i>	M	1	38	1	48	88	1	58
<i>C. pygerythrus</i>	F	8	36 (34-38)	10	46 (42-49)	90 (82-93)	8	59 (55-61)
<i>C. pygerythrus</i>	M	8	36 (35-37)	8	45 (44-47)	86 (84-89)	8	58 (56-59)
<i>C. nitis</i>	F	11	37 (36-39)	11	48 (46-50)	90 (86-94)	11	58 (56-61)
<i>C. nitis</i>	M	7	39 (37-41)	8	49 (47-53)	92 (87-101)	7	60 (58-65)
<i>C. albogularis</i>	F	9	38 (36-40)	9	49 (46-51)	91 (88-95)	9	60 (57-63)
<i>C. albogularis</i>	M	4	38 (37-39)	6	48 (47-49)	92 (90-96)	4	60 (59-61)
<i>E. patas</i>	F	1	31	1	38	79	1	55
<i>E. patas</i>	M	1	33	1	40	80	1	56
Total		94		101			94	

Table 34. (cont.)

Species	Sex	N	Ray1/Foot	N	Ray1/Sole	Ray1/Mt3	N	Ray1/Ray3
<i>M. fascicularis</i>	F	6	40 (39-41)	10	52 (51-54)	99 (94-103)	6	63 (61-65)
<i>M. fascicularis</i>	M	9	39 (36-43)	9	51 (45-56)	98 (88-107)	9	63 (58-69)
<i>M. fuscata</i>	M	2	38 (37-39)	2	48 (47-49)	96 (94-99)	2	63 (61-64)
<i>M. mulatta</i>	F	0		10	51 (48-52)	98 (96-102)	0	
<i>M. mulatta</i>	M	2	38 (38-38)	9	49 (46-51)	94 (89-101)	2	61 (61-61)
<i>M. nigra</i>	F	1	42	1	55	107	1	67
<i>M. nigra</i>	M	2	40 (39-41)	3	51 (50-53)	100 (96-101)	2	64 (63-66)
<i>M. tonkeana</i>	F	1	42	1	54	108	1	69
<i>M. tonkeana</i>	M	1	40	2	51 (50-52)	102 (01-103)	1	65
<i>M. nemestrina</i>	F	4	42 (42-43)	6	55 (52-57)	106 (100-110)	4	67 (65-69)
<i>M. nemestrina</i>	M	4	41 (40-43)	4	53 (51-55)	104 (98-108)	4	66 (63-69)
<i>M. sylvanus</i>	F	1	39	1	49	95	1	62
<i>M. sylvanus</i>	M	2	37 (37-38)	3	48 (47-48)	93 (92-95)	2	61 (61-61)
<i>M. arctoides</i>	M	0		1	46	92	0	
<i>M. thibetana</i>	M	3	34 (34-35)	3	45 (44-46)	95 (92-96)	3	58 (56-59)
<i>C. albigena</i>	F	9	38 (37-39)	9	49 (47-51)	93 (90-96)	9	61 (59-62)
<i>C. albigena</i>	M	10	38 (37-40)	11	49 (47-51)	93 (89-97)	10	61 (59-63)
<i>C. galeritus</i>	M	5	41 (40-42)	5	53 (52-54)	103 (99-105)	5	67 (65-69)
<i>C. torquatus</i>	F	4	40 (39-40)	6	51 (50-54)	97 (93-101)	4	63 (63-64)
<i>C. torquatus</i>	M	7	41 (39-41)	11	52 (50-54)	98 (93-102)	7	64 (61-66)
<i>T. gelada</i>	F	1	33	1	40	77	1	56
<i>T. gelada</i>	M	3	34 (33-35)	3	41 (40-42)	80 (78-82)	3	58 (57-59)
<i>P. cynocephalus</i>	F	4	36 (35-37)	6	44 (43-46)	88 (85-91)	4	61 (58-62)
<i>P. cynocephalus</i>	M	10	36 (35-39)	10	45 (42-47)	90 (87-97)	10	62 (59-67)
<i>P. hamadryas</i>	F	2	36 (35-36)	2	44 (43-45)	87 (86-87)	2	59 (59-60)
<i>P. hamadryas</i>	M	4	36 (35-36)	5	43 (41-45)	86 (83-89)	4	60 (58-61)
<i>P. anubis</i>	F	2	35 (34-36)	2	43 (42-45)	88 (85-90)	2	59 (58-61)
<i>P. anubis</i>	M	5	36 (35-37)	7	44 (42-46)	89 (85-95)	5	61 (60-62)
<i>P. ursinus</i>	F	2	35 (35-35)	3	44 (43-45)	90 (88-93)	2	61 (61-61)
<i>P. ursinus</i>	M	1	36	2	43 (42-44)	88 (85-91)	1	64
<i>P. leucophaeus</i>	F	2	44 (44-44)	2	57 (57-57)	111 (109-112)	2	71 (70-72)
<i>P. leucophaeus</i>	M	1	41	1	53	101	1	66
<i>P. sphinx</i>	F	4	42 (41-44)	4	54 (52-57)	105 (101-111)	4	67 (65-70)
<i>P. sphinx</i>	M	0		1	57	109	0	
Total		114		156			114	

Table 34. (cont.)

Species	Sex	N	Ray1/Foot	N	Ray1/Sole	Ray1/Ht3	N	Ray1/Ray3
<i>P. verus</i>	F	2	36 (36-37)	2	48 (48-48)	86 (84-89)	2	55 (54-55)
<i>P. verus</i>	M	5	37 (36-37)	5	48 (47-49)	89 (86-93)	5	57 (55-58)
<i>P. badius</i>	F	5	36 (34-36)	5	47 (46-48)	86 (83-89)	5	54 (51-56)
<i>P. badius</i>	M	5	35 (34-37)	5	47 (45-50)	87 (84-89)	5	55 (53-56)
<i>C. satana</i>	F	1	37	1	49	92	1	56
<i>C. polykonos</i>	F	1	37	1	49	88	1	56
<i>C. polykonos</i>	M	3	36 (36-37)	3	47 (47-48)	90 (88-91)	3	57 (56-58)
<i>C. vellerosus</i>	M	1	35	1	45	83	1	53
<i>C. angolensis</i>	F	2	36 (35-37)	2	47 (46-48)	89 (88-89)	2	56 (55-56)
<i>C. angolensis</i>	M	1	38	2	49 (49-50)	93 (92-93)	1	59
<i>C. guereza</i>	F	7	35 (33-36)	8	46 (44-50)	87 (84-92)	7	54 (53-56)
<i>C. guereza</i>	M	9	35 (32-37)	10	46 (42-48)	86 (77-89)	9	54 (50-57)
<i>P. hosei</i>	F	1	36	2	49 (47-51)	87 (85-90)	1	54
<i>P. hosei</i>	M	2	38 (38-39)	2	50 (49-50)	87 (86-89)	2	57 (56-58)
<i>P. rubicunda</i>	F	6	37 (36-38)	10	48 (46-51)	84 (80-90)	6	55 (54-56)
<i>P. rubicunda</i>	M	9	37 (36-38)	11	48 (47-50)	84 (82-88)	9	55 (53-57)
<i>P. aygula</i>	F	3	39 (37-40)	3	51 (48-52)	91 (85-95)	3	59 (56-61)
<i>P. aygula</i>	M	3	37 (36-38)	3	47 (46-49)	85 (81-88)	3	55 (54-57)
<i>P. nelalophos</i>	F	3	38 (37-38)	4	50 (48-50)	90 (88-91)	3	58 (57-59)
<i>P. nelalophos</i>	M	4	38 (37-38)	4	49 (47-50)	87 (85-90)	4	57 (55-58)
<i>P. frontata</i>	M	1	37	1	47	84	1	56
<i>S. cristata</i>	F	7	39 (37-41)	13	51 (48-54)	93 (88-98)	7	59 (58-61)
<i>S. cristata</i>	M	6	39 (38-40)	12	51 (49-53)	94 (91-99)	6	60 (58-63)
<i>S. obscura</i>	F	2	41 (40-42)	6	53 (48-56)	99 (91-105)	2	63 (62-65)
<i>S. obscura</i>	M	3	40 (38-41)	7	52 (50-55)	97 (94-98)	3	62 (61-62)
<i>S. entellus</i>	F	0		5	43 (41-44)	82 (79-84)	0	
<i>S. entellus</i>	M	0		1	43	82	0	
<i>P. nanaeus</i>	F	1	41	1	55	100	1	62
<i>P. nanaeus</i>	M	1	37	1	49	93	1	59
<i>H. larvatus</i>	F	3	38 (37-39)	3	50 (49-50)	94 (92-96)	3	60 (58-61)
<i>H. larvatus</i>	M	6	40 (38-41)	6	52 (49-53)	96 (92-99)	6	62 (59-64)
Total		103		140			103	

Table 35. Means, ranges of variation (in parentheses) and standard deviations of values for indices describing the relative length of the hallux. Conventions as in Table 24.

Taxon	N	Mean (Range)	SD
Ray1/Foot			
Cercopithecins	21	37.8 (31.4-41.7)	2.3
Papionins	31	38.5 (33.4-44.1)	2.8
Colobines	29	37.3 (34.5-41.2)	2.6
Ray1/Sole			
Cercopithecins	21	48.2 (38.0-53.5)	3.6
Papionins	34	48.8 (39.8-56.7)	4.7
Colobines	31	48.5 (42.7-55.2)	2.6
Ray1/Ht3			
Cercopithecins	21	90.7 (79.0-100.2)	5.1
Papionins	34	95.8 (77.2-110.6)	8.1
Colobines	31	89.1 (81.5-105.0)	4.9
Ray1/Ray3			
Cercopithecins	21	59.9 (54.9-65.6)	2.6
Papionins	31	62.9 (56.3-71.0)	3.5
Colobines	29	57.1 (53.1-63.3)	2.8

Table 36. Means and ranges of variation (in parentheses) of values for indices describing the relative length of the hallux. Conventions as in Table 23.

Species	Sex	N	Mt1/Mt3	N	Ph1/Ph3	N	Ph1/Mt1
<i>M. talapoin</i>	F	7	60 (58-62)	5	57 (55-59)	6	52 (48-55)
<i>M. talapoin</i>	M	4	60 (59-61)	4	56 (56-57)	4	50 (48-52)
<i>C. pogonias</i>	F	4	60 (59-62)	0		0	
<i>C. pogonias</i>	M	13	62 (58-64)	1	59	1	47
<i>C. campbelli</i>	F	2	64 (62-66)	1	58	1	48
<i>C. campbelli</i>	M	2	65 (65-66)	2	63 (57-69)	2	50 (44-55)
<i>C. mona</i>	F	2	63 (62-64)	2	60 (58-61)	2	50 (48-52)
<i>C. mona</i>	M	11	62 (60-68)	5	58 (55-60)	5	48 (44-53)
<i>C. ascanius</i>	F	10	60 (57-64)	9	59 (55-65)	10	50 (48-53)
<i>C. ascanius</i>	M	10	61 (59-63)	10	59 (55-62)	10	48 (46-51)
<i>C. cephus</i>	F	4	63 (61-67)	1	63	1	49
<i>C. cephus</i>	M	17	62 (57-64)	2	53 (50-57)	2	44 (40-47)
<i>C. petaurista</i>	F	4	61 (59-63)	2	58 (57-58)	2	50 (49-51)
<i>C. petaurista</i>	M	1	61	1	52	1	45
<i>C. pygerythrus</i>	F	12	61 (56-63)	8	57 (53-60)	10	49 (48-52)
<i>C. pygerythrus</i>	M	14	60 (57-62)	8	55 (53-58)	9	47 (44-49)
<i>C. mitis</i>	F	12	62 (60-65)	11	52 (47-58)	11	46 (40-51)
<i>C. mitis</i>	M	8	62 (59-67)	7	56 (50-63)	8	48 (43-54)
<i>C. nictitans</i>	F	5	61 (59-62)	0		0	
<i>C. nictitans</i>	M	14	61 (59-65)	0		0	
<i>C. albogularis</i>	F	11	61 (59-63)	9	57 (54-66)	9	49 (46-52)
<i>C. albogularis</i>	M	9	62 (59-65)	4	55 (53-57)	6	47 (44-50)
<i>E. patas</i>	F	2	54 (54-54)	1	56	1	45
<i>E. patas</i>	M	3	54 (52-56)	1	57	1	43
Total		181		94		102	

Table 36. (cont.)

Species	Sex	N	Ht1/Ht3	H	Ph1/Ph3	H	Ph1/Ht1
<i>H. fascicularis</i>	F	10	67 (64-70)	6	57 (54-61)	10	48 (45-51)
<i>H. fascicularis</i>	M	10	67 (63-71)	9	55 (44-65)	9	47 (36-51)
<i>H. fuscata</i>	M	3	63 (60-65)	2	60 (57-62)	2	50 (47-53)
<i>H. mulatta</i>	F	10	66 (64-68)	0		10	50 (47-54)
<i>H. mulatta</i>	M	10	64 (60-68)	2	57 (55-58)	9	47 (44-50)
<i>H. nigra</i>	F	1	71	1	61	1	51
<i>H. nigra</i>	M	3	68 (66-69)	2	60 (58-62)	3	47 (46-49)
<i>H. tonkeana</i>	F	1	70	1	66	1	54
<i>H. tonkeana</i>	M	2	67 (67-68)	1	60	2	52 (51-52)
<i>H. nemestrina</i>	F	7	70 (67-75)	4	60 (56-65)	6	49 (46-53)
<i>H. nemestrina</i>	M	5	69 (65-73)	4	59 (54-65)	4	49 (46-52)
<i>H. sylvanus</i>	F	1	63	1	59	1	50
<i>H. sylvanus</i>	M	4	62 (61-63)	2	58 (57-60)	3	51 (50-52)
<i>H. arctoides</i>	M	2	63 (61-66)	0		1	52
<i>H. assanensis</i>	M	1	65	0		0	
<i>H. thibetana</i>	M	4	60 (54-63)	3	51 (49-52)	3	52 (51-53)
<i>C. albigena</i>	F	10	64 (61-67)	9	54 (52-56)	9	46 (43-48)
<i>C. albigena</i>	M	14	64 (61-67)	10	54 (52-56)	11	44 (43-46)
<i>C. galeritus</i>	F	4	66 (58-72)	0		0	
<i>C. galeritus</i>	M	8	70 (63-74)	5	59 (56-62)	5	43 (41-46)
<i>C. torquatus</i>	F	7	68 (66-70)	4	54 (51-57)	6	42 (39-46)
<i>C. torquatus</i>	M	11	68 (65-71)	7	57 (54-60)	11	44 (41-46)
<i>T. gelada</i>	F	1	57	1	54	1	35
<i>T. gelada</i>	M	4	58 (58-60)	3	57 (56-58)	3	37 (35-38)
<i>P. cynocephalus</i>	F	8	62 (60-64)	4	58 (56-60)	6	42 (40-44)
<i>P. cynocephalus</i>	M	11	63 (60-67)	10	60 (57-68)	10	43 (39-46)
<i>P. hanadryas</i>	F	2	60 (59-61)	2	58 (58-59)	2	45 (44-46)
<i>P. hanadryas</i>	M	5	59 (58-61)	4	61 (58-65)	5	45 (42-49)
<i>P. anubis</i>	F	5	60 (58-62)	2	58 (58-58)	2	46 (45-48)
<i>P. anubis</i>	M	15	62 (58-64)	5	58 (54-62)	7	45 (40-48)
<i>P. ursinus</i>	F	4	63 (62-64)	2	58 (58-59)	3	43 (42-44)
<i>P. ursinus</i>	M	4	64 (59-67)	1	60	2	41 (39-44)
<i>P. leucophaeus</i>	F	2	77 (77-78)	2	60 (58-62)	2	43 (42-44)
<i>P. leucophaeus</i>	M	2	71 (71-72)	1	57	1	42
<i>P. sphinx</i>	F	5	72 (68-77)	4	58 (56-60)	4	45 (44-48)
<i>P. sphinx</i>	M	3	73 (70-75)	0		1	47
Total		199		114		156	

Table 36. (cont.)

Species	Sex	N	Nt1/Nt3	N	Ph1/Ph3	N	Ph1/Nt1
<i>P. verus</i>	F	3	59 (58-59)	2	48 (48-48)	2	48 (46-49)
<i>P. verus</i>	M	6	60 (57-62)	5	50 (48-54)	5	48 (44-53)
<i>P. badius</i>	F	13	59 (57-64)	5	47 (41-49)	5	48 (45-49)
<i>P. badius</i>	M	14	59 (56-66)	5	49 (46-52)	5	50 (45-53)
<i>C. satana</i>	F	1	62	1	47	1	47
<i>C. satana</i>	M	2	60 (59-61)	0		0	
<i>C. polykonos</i>	F	2	61 (60-62)	1	50 (50-50)	1	47
<i>C. polykonos</i>	M	3	60 (60-61)	3	50 (48-52)	3	49 (46-51)
<i>C. vellerosus</i>	M	1	57	1	46	1	46
<i>C. angolensis</i>	F	4	61 (60-63)	2	48 (47-48)	2	47 (46-48)
<i>C. angolensis</i>	M	2	62 (62-63)	1	52	2	48 (47-49)
<i>C. guereza</i>	F	14	59 (56-62)	7	48 (44-50)	8	49 (46-51)
<i>C. guereza</i>	M	15	59 (56-63)	9	47 (40-53)	10	47 (39-51)
<i>P. hosei</i>	F	2	60 (58-62)	1	47	2	46 (46-47)
<i>P. hosei</i>	M	2	61 (59-61)	2	50 (47-54)	2	43 (40-46)
<i>P. rubicunda</i>	F	11	57 (52-61)	6	51 (49-54)	10	47 (43-53)
<i>P. rubicunda</i>	M	11	58 (56-60)	9	50 (48-53)	11	47 (45-50)
<i>P. aygula</i>	F	3	63 (59-66)	3	52 (49-53)	3	45 (43-47)
<i>P. aygula</i>	M	3	60 (58-63)	3	46 (46-47)	3	40 (40-41)
<i>P. nelalophos</i>	F	4	61 (60-62)	3	52 (49-57)	4	47 (43-52)
<i>P. nelalophos</i>	M	4	60 (58-62)	4	52 (50-55)	4	46 (45-49)
<i>P. frontata</i>	F	2	63 (63-63)	0		0	
<i>P. frontata</i>	M	2	62 (59-65)	1	50	1	43
<i>S. cristata</i>	F	13	65 (60-67)	7	51 (46-54)	13	44 (41-48)
<i>S. cristata</i>	M	12	65 (62-68)	6	52 (50-55)	12	45 (43-49)
<i>S. obscura</i>	F	7	67 (62-71)	2	54 (51-56)	6	47 (45-49)
<i>S. obscura</i>	M	8	66 (64-69)	3	54 (51-57)	7	47 (44-49)
<i>S. entellus</i>	F	7	56 (54-60)	0		5	48 (46-49)
<i>S. entellus</i>	M	2	56 (55-56)	0		1	47
<i>P. roxellanae</i>	F	6	67 (66-67)	0		0	
<i>P. roxellanae</i>	M	1	69	0		0	
<i>P. nanaeus</i>	F	2	64 (62-65)	1	57	1	55
<i>P. nanaeus</i>	M	5	61 (61-62)	1	53	1	51
<i>H. larvatus</i>	F	5	64 (60-66)	3	55 (54-56)	3	50 (46-54)
<i>H. larvatus</i>	M	8	64 (61-66)	6	59 (57-61)	6	51 (50-51)
Total		200		103		140	

Table 37. Means, ranges of variation (in parentheses) and standard deviations of values for indices describing the relative length of the hallux. Conventions as in Table 24.

Species	N	Mean (Range)	SD
Mt1/Mt3			
Cercopithecins	24	60.9 (53.9-65.4)	2.5
Papionins	34	65.5 (57.1-77.2)	4.6
Colobines	35	61.3 (55.8-68.6)	3.2
Ph1/Ph3			
Cercopithecins	21	57.1 (51.9-63.0)	2.9
Papionins	14	58.0 (51.0-65.8)	2.8
Colobines	29	50.5 (46.3-58.5)	3.1
Ph1/Mt1			
Cercopithecins	21	47.7 (43.4-52.3)	2.3
Papionins	34	46.0 (35.1-53.4)	4.2
Colobines	31	47.1 (40.4-54.7)	2.6

Table 38. Least Squares coefficients and statistics for regressions of hallucal segments on body mass. Conventions as in Table 25. * *Papio* species, *T. gelada*, *H. thibetana* and *E. patas* removed from sample.

Taxon	N	slope	SE	y-int	r ²	Taxon	N	slope	SE	y-int	r ²
lrxayl*lxmass						lrxlenphl*lxmass					
Cercopithecines	55	0.24	0.02	1.70	0.73	Cercopithecines	55	0.20	0.02	0.90	0.57
Cercopithecins	21	0.26	0.04	1.50	0.71	Cercopithecins	21	0.22	0.04	0.71	0.61
Papionins	34	0.17	0.04	2.36	0.41	Papionins	34	0.12	0.04	1.69	0.18
Cercopithecines	42	0.32	0.02	1.06	0.85 *	Cercopithecines	42	0.30	0.02	0.12	0.82 *
Cercopithecins	19	0.28	0.04	1.37	0.72 *	Cercopithecins	19	0.24	0.04	0.52	0.65 *
Papionins	23	0.31	0.04	1.12	0.73 *	Papionins	23	0.29	0.04	0.22	0.70 *
Colobines	31	0.27	0.03	1.48	0.69	Colobines	31	0.32	0.04	-1.11	0.67
Pr > F slope Pr > F mean						Pr > F slope Pr > F mean					
Subfamilies	0.2324		0.0015			Subfamilies	0.0149		0.0010		
Tribes	0.0662		0.0612			Tribes	0.0771		0.0939		
Subfamilies 0.6581 0.3714 *						Subfamilies 0.3001 0.5851 *					
Tribes 0.5042 0.1276 *						Tribes 0.4481 0.1778 *					
lrxlenatl*lxmass											
Cercopithecines	60	0.26	0.02	1.14	0.77						
Cercopithecins	24	0.29	0.04	0.91	0.72						
Papionins	36	0.20	0.03	1.71	0.50						
Cercopithecines	47	0.33	0.02	0.60	0.85 *						
Cercopithecins	22	0.32	0.04	0.65	0.80 *						
Papionins	25	0.31	0.04	0.76	0.69 *						
Colobines	35	0.25	0.03	1.32	0.69						
Pr > F slope Pr > F mean						Pr > F slope Pr > F mean					
Subfamilies	0.7586		0.0017								
Tribes	0.0611		0.0649								
Subfamilies 0.1367 0.3451 *											
Tribes 0.8345 0.1935 *											

Table 39. Residuals of species by sex values from subfamilial LS lines for hallucal dimensions on body mass. * Residuals from forced LS line.

Species	Sex	Rayl	Ht1	Ph1	Rayl*	Ht1*	Ph1*
M. talapoin	F	-1.56	-1.65	-1.27	-0.11	-0.33	0.19
M. talapoin	M	-0.90	-0.88	-0.87	0.33	0.23	0.39
C. pogonias	F	.	-0.21	.	.	0.34	.
C. pogonias	M	0.00	0.38	-0.09	0.31	0.60	0.24
C. campbelli	F	0.73	0.46	0.38	1.43	1.14	1.15
C. campbelli	M	1.07	0.96	1.11	1.27	1.16	1.31
C. mona	F	0.10	0.04	0.16	0.69	0.58	0.76
C. mona	M	1.60	1.69	1.34	1.87	1.93	1.64
C. ascanius	F	-1.13	-1.31	-0.79	-0.47	-0.71	-0.15
C. ascanius	M	0.26	0.24	0.24	0.58	0.52	0.57
C. cephus	F	0.39	0.21	0.36	0.95	0.74	0.95
C. cephus	M	-0.38	0.57	-0.85	0.06	0.86	-0.34
C. petaurista	F	0.13	-0.33	0.22	0.69	0.22	0.77
C. petaurista	M	0.07	0.26	-0.31	0.48	0.61	0.16
C. pygerythrus	F	-1.02	-1.07	-0.85	-0.36	-0.49	-0.19
C. pygerythrus	M	-1.05	-0.91	-1.00	-0.63	-0.56	-0.58
C. mitis	F	-0.29	-0.09	-0.51	0.09	0.23	-0.08
C. mitis	M	0.25	0.14	0.36	0.18	0.06	0.26
C. nictitans	F	.	0.41	.	.	0.71	.
C. nictitans	M	.	0.72	.	.	0.76	.
C. albogularis	F	-0.91	-0.89	-0.66	-0.54	-0.57	-0.31
C. albogularis	M	-0.61	-0.46	-0.42	-0.68	-0.57	-0.52
B. patas	F	-1.47	-1.99	-1.43	-1.16	-1.68	-1.11
B. patas	M	-0.07	-0.68	-0.39	-0.19	-0.74	-0.46

Table 39. (cont.)

Species	Sex	Ray1	Ht1	Ph1	Ray1*	Ht1*	Ph1*
<i>M. fascicularis</i>	F	-0.44	-0.47	-0.39	0.11	0.02	0.17
<i>M. fascicularis</i>	M	-0.37	-0.31	-0.35	-0.09	-0.08	-0.07
<i>M. fuscata</i>	M	-1.42	-2.00	-0.57	-1.72	-2.26	-0.99
<i>M. mulatta</i>	F	0.74	0.59	0.89	0.84	0.69	0.96
<i>M. mulatta</i>	M	0.78	0.70	0.79	0.65	0.58	0.64
<i>M. nigra</i>	F	0.91	0.68	1.15	1.01	0.80	1.21
<i>M. nigra</i>	M	0.95	0.88	0.94	0.74	0.69	0.72
<i>M. tonkeana</i>	F	0.51	0.01	1.22	0.38	-0.08	0.98
<i>M. tonkeana</i>	M	1.33	1.04	1.64	1.28	1.02	1.54
<i>M. nemestrina</i>	F	0.82	0.62	0.91	0.81	0.63	0.89
<i>M. nemestrina</i>	M	1.13	1.06	1.33	0.75	0.71	0.92
<i>M. sylvanus</i>	F	-0.14	-0.45	0.33	-0.32	-0.61	0.08
<i>M. sylvanus</i>	M	0.92	0.50	1.36	0.57	0.22	0.94
<i>M. arctoides</i>	M	-0.44	-0.96	0.36	-0.63	-1.11	0.06
<i>M. assanensis</i>	M	.	0.19	.	.	0.02	.
<i>M. thibetana</i>	M	-1.74	-2.65	-0.63	-2.03	-2.87	-1.07
<i>C. albigena</i>	F	0.05	0.22	-0.17	0.23	0.35	0.05
<i>C. albigena</i>	M	0.90	1.11	0.50	0.81	1.01	0.46
<i>C. galeritus</i>	F	.	1.01	.	.	1.04	.
<i>C. galeritus</i>	M	0.96	1.15	0.54	0.60	0.78	0.21
<i>C. torquatus</i>	F	0.74	1.03	0.01	0.72	0.98	0.09
<i>C. torquatus</i>	M	1.19	1.29	0.83	0.67	0.79	0.33
<i>T. gelada</i>	F	-1.55	-0.98	-2.73	-1.77	-1.29	-2.79
<i>T. gelada</i>	M	-1.52	-1.04	-2.38	-1.99	-1.57	-2.74
<i>P. cynocephalus</i>	F	-0.34	-0.08	-0.68	-0.65	-0.42	-0.96
<i>P. cynocephalus</i>	M	-0.57	-0.51	-0.51	-1.29	-1.22	-1.26
<i>P. hanadryas</i>	F	-0.56	-0.59	-0.56	-0.72	-0.76	-0.73
<i>P. hanadryas</i>	M	-1.06	-1.24	-0.79	-1.61	-1.77	-1.39
<i>P. anubis</i>	F	-0.61	-0.91	-0.35	-0.96	-1.23	-0.75
<i>P. anubis</i>	M	-0.46	-0.57	-0.20	-1.29	-1.36	-1.09
<i>P. ursinus</i>	F	-0.60	-0.46	-0.70	-1.01	-0.88	-1.11
<i>P. ursinus</i>	M	-1.58	-0.70	-1.60	-2.34	-1.54	-2.37
<i>P. leucophaeus</i>	F	1.47	1.66	0.95	1.06	1.25	0.58
<i>P. leucophaeus</i>	M	1.78	1.70	1.28	0.90	0.90	0.44
<i>P. sphinx</i>	F	0.43	0.59	0.33	0.05	0.21	-0.06
<i>P. sphinx</i>	M	2.58	2.27	2.54	1.51	1.33	1.43

Table 39. (cont.)

Species	Sex	Rayl	Htl	Phl
<i>P. verus</i>	F	-1.10	-1.51	-0.28
<i>P. verus</i>	M	-0.32	-1.61	-0.09
<i>P. badius</i>	F	-0.38	-0.03	-0.12
<i>P. badius</i>	M	-1.39	-2.08	-0.79
<i>C. satana</i>	F	-0.01	0.00	-0.06
<i>C. satana</i>	M	.	0.28	.
<i>C. polykonos</i>	F	1.53	1.04	1.27
<i>C. polykonos</i>	M	0.04	-0.12	0.24
<i>C. vellerosus</i>	M	-0.99	-0.83	-1.21
<i>C. angolensis</i>	F	-0.02	0.22	0.00
<i>C. angolensis</i>	M	-0.59	-0.69	-0.41
<i>C. guereza</i>	F	-1.66	-1.85	-1.09
<i>C. guereza</i>	M	-2.15	-1.67	-2.04
<i>P. hosei</i>	F	0.39	0.32	0.38
<i>P. hosei</i>	M	1.93	2.42	0.84
<i>P. rubicunda</i>	F	0.23	0.20	0.33
<i>P. rubicunda</i>	M	0.67	0.61	0.63
<i>P. aygula</i>	F	1.13	1.32	0.62
<i>P. aygula</i>	M	-0.82	-0.10	-2.10
<i>P. nelalophos</i>	F	1.19	1.13	1.09
<i>P. nelalophos</i>	M	0.62	0.65	0.45
<i>P. frontata</i>	F	.	0.96	.
<i>P. frontata</i>	M	0.32	0.92	-0.44
<i>S. cristata</i>	F	-0.54	-0.35	-0.90
<i>S. cristata</i>	M	-0.40	-0.29	-0.63
<i>S. obscura</i>	F	-0.10	-0.44	0.08
<i>S. obscura</i>	M	-0.04	0.11	-0.12
<i>S. entellus</i>	F	-0.65	-0.65	-0.59
<i>S. entellus</i>	M	-0.49	-0.77	-0.73
<i>P. roxellanae</i>	F	.	-0.29	.
<i>P. roxellanae</i>	M	.	0.29	.
<i>P. nanaeus</i>	F	1.54	0.39	2.62
<i>P. nanaeus</i>	M	0.07	0.10	0.47
<i>H. larvatus</i>	F	1.53	1.45	1.72
<i>H. larvatus</i>	M	0.98	0.89	0.83

Table 40. Frequencies of Permutations for Original and Collapsed Digit Ray Length Formulas.

Original Formula	Frequency	Collapsed Formula	Frequency
3=4>2=5	17	324>225	101
3=4>2>5	22		
3>4>2=5	17		
3>4>2>5	45		
3=4>5=2	17	324>522	47
3=4>5>2	17		
3>4>5=2	7		
3>4>5>2	6		
4=3>2=5	5	423>225	10
4=3>2>5	3		
4>3>2=5	1		
4=3>5=2	7	423>522	133
4=3>5>2	40		
4>3>5=2	6		
4>3>5>2	80		

Table 41. Digit Ray Length Formulas in Cercopithecoid Species.

Taxon	N	3>4>2>5	3>4>5>2	4>3>2>5	4>3>5>2	Taxon	N	3>4>2>5	3>4>5>2	4>3>2>5	4>3>5>2
<i>H. talapoin</i>	11	10	1			<i>P. verus</i>	6				6
<i>C. pogonias</i>	2	1			1	<i>P. badius</i>	17			1	16
<i>C. campbelli</i>	3	2		1		<i>C. satana</i>	1				1
<i>C. mona</i>	10	5	4		1	<i>C. polykomos</i>	3				3
<i>C. cephus</i>	3	2	1			<i>C. vellerosus</i>	1				1
<i>C. petaurista</i>	3	2	1			<i>C. angolensis</i>	3				3
<i>C. pygerythrus</i>	9	6	3			<i>C. guereza</i>	16		1		15
<i>C. mitis</i>	15	14	1			<i>P. hosei</i>	3				3
<i>C. albogularis</i>	15	9	5		1	<i>P. rubicunda</i>	15		1		14
<i>B. patas</i>	2	1		1		<i>P. aggula</i>	6				6
<i>H. fascicularis</i>	14	10	4			<i>P. melalophos</i>	6				6
<i>H. fuscata</i>	1	1				<i>P. frontata</i>	1				1
<i>H. aulatta</i>	2	1	1			<i>S. cristata</i>	11				11
<i>H. nigra</i>	3	3				<i>S. obscura</i>	4		1		3
<i>H. tonkeana</i>	2	1		1		<i>P. nanaeus</i>	2				2
<i>H. nenestrina</i>	9	5	3		1	<i>H. larvatus</i>	9				9
<i>H. sylvanus</i>	3	3									
<i>H. thibetana</i>	3	3									
<i>C. albigena</i>	20	1	8		11						
<i>C. galeritus</i>	5	5									
<i>C. torquatus</i>	11	9	1		1						
<i>T. gelada</i>	4	1	3								
<i>P. cynocephalus</i>	14	2	1	4	7						
<i>P. hanadryas</i>	6	1			5						
<i>P. anubis</i>	7	1	1	1	4						
<i>P. ursinus</i>	3	1		1	1						
<i>P. leucophaeus</i>	3	3									
<i>P. sphinx</i>	4	2	2								

Table 42. Summary Version of Digit Ray Length Formulas in Cercopithecids and results of G-Test. Formulas 423)225 and 423)522 treated together in G-Test.

Taxon	N	324)225	324)522	423)225	423)522
Cercopithecins	73	52	16	2	3
Papionins	114	49	28	7	30
Colobines	104		3	1	100
	291	101	47	10	133

Without Papio or C. albigena

	G	Prob.	df		G	Prob.	df
All groups	205.8	0.000	4	All groups	249.0	0.000	4
Subfamilies	183.9	0.000	2	Subfamilies	245.5	0.000	2
Tribes	21.9	0.000	2	Tribes	1.5	0.174	2

Table 43. Average proportionate difference in length between pairs of digit rays.

Taxon	N	3:4	2:5	3:2	4:5	Taxon	N	3:4	2:5	3:2	4:5
<i>H. talapoin</i>	11	1	1	6	6	<i>P. verus</i>	6	-1	-3	7	6
<i>C. pogonias</i>	2	0	-1	5	5	<i>P. badius</i>	17	-1	-4	7	5
<i>C. campbelli</i>	3	0	0	6	6	<i>C. satana</i>	1	-1	-2	7	6
<i>C. mona</i>	10	1	0	5	4	<i>C. polykonos</i>	3	-1	-3	7	5
<i>C. cephus</i>	3	1	1	5	6	<i>C. vellerosus</i>	1	-2	-3	8	7
<i>C. petaurista</i>	3	1	0	6	6	<i>C. angolensis</i>	3	-1	-3	7	6
<i>C. pygerythrus</i>	9	1	0	6	6	<i>C. guereza</i>	16	-1	-2	8	6
<i>C. mitis</i>	15	1	1	5	5	<i>P. hosei</i>	3	-1	-3	6	5
<i>C. albogularis</i>	15	0	0	5	5	<i>P. rubicunda</i>	15	-1	-3	7	5
<i>B. patas</i>	2	0	2	3	5	<i>P. aygula</i>	6	-1	-3	6	4
<i>H. fascicularis</i>	14	1	1	6	5	<i>P. nelalophos</i>	6	-1	-3	6	5
<i>H. fuscata</i>	1	1	0	6	5	<i>P. frontata</i>	1	-1	-2	7	6
<i>H. nulatta</i>	2	1	1	5	5	<i>S. cristata</i>	11	-1	-3	6	5
<i>H. nigra</i>	3	1	2	4	5	<i>S. obscura</i>	4	-1	-2	6	4
<i>H. tonkeana</i>	2	0	1	5	5	<i>P. nanaeus</i>	2	-1	-3	6	4
<i>H. nenestrina</i>	9	1	1	5	5	<i>H. larvatus</i>	9	-1	-1	6	5
<i>H. sylvanus</i>	3	1	-1	7	5						
<i>H. thibetana</i>	3	1	2	5	6						
<i>C. albigena</i>	20	0	-2	5	3						
<i>C. galeritus</i>	5	1	2	4	6						
<i>C. torquatus</i>	11	1	1	5	5						
<i>T. gelada</i>	4	1	0	5	4						
<i>P. cynocephalus</i>	14	0	0	4	4						
<i>P. hanadryas</i>	6	0	-1	4	4						
<i>P. anubis</i>	7	0	0	4	4						
<i>P. ursinus</i>	3	0	0	4	4						
<i>P. leucophaeus</i>	3	1	3	4	6						
<i>P. sphinx</i>	4	1	0	6	5						

Table 44. Average proportionate difference in length between pairs of digit rays. * significantly different from other groups at $p < 0.01$.

Taxon	N	Rays 3:4	Rays 2:5	Rays 3:2	Rays 4:5
Cercopithecins	73	0	1	5	5
Papionins	114	0	0	5	5
Colobines	104	-0 *	-3 *	7 *	5

Table 45. Average proportion digit ray lengths in Cercopithecoid species.

Taxon	N	Ray 2	Ray 3	Ray 4	Ray 5	Taxon	N	Ray 2	Ray 3	Ray 4	Ray 5
<i>M. talapoin</i>	11	23.8	26.7	26.3	23.2	<i>P. verus</i>	6	22.8	26.4	26.8	24.0
<i>C. pogonias</i>	2	23.6	26.3	26.2	23.9	<i>P. badius</i>	17	22.7	26.1	26.8	24.4
<i>C. campbelli</i>	3	23.7	26.5	26.4	23.5	<i>C. satana</i>	1	22.8	26.4	26.9	23.9
<i>C. mona</i>	10	23.9	26.3	26.0	23.8	<i>C. polykomos</i>	3	22.9	26.2	26.8	24.2
<i>C. cephus</i>	3	23.9	26.5	26.2	23.4	<i>C. vellerosus</i>	1	22.4	26.5	27.4	23.8
<i>C. petaurista</i>	3	23.6	26.7	26.3	23.5	<i>C. angolensis</i>	3	22.8	26.3	27.0	24.0
<i>C. pygerythrus</i>	9	23.7	26.6	26.2	23.5	<i>C. guereza</i>	16	22.7	26.6	26.9	23.8
<i>C. mitis</i>	15	24.0	26.4	26.0	23.6	<i>P. hosei</i>	3	23.0	26.0	26.6	24.3
<i>C. alboocularis</i>	15	23.8	26.4	26.1	23.7	<i>P. rubicunda</i>	15	22.9	26.3	26.6	24.2
<i>E. patas</i>	2	24.4	26.1	26.0	23.5	<i>P. aygula</i>	6	22.9	26.0	26.7	24.4
<i>M. fascicularis</i>	14	23.8	26.8	26.0	23.4	<i>P. melalophos</i>	6	22.9	26.1	26.7	24.3
<i>M. fuscata</i>	1	23.8	26.6	25.9	23.6	<i>P. frontata</i>	1	22.9	26.3	26.9	23.9
<i>M. mulatta</i>	2	23.8	26.5	26.2	23.5	<i>S. cristata</i>	11	23.0	26.1	26.6	24.3
<i>M. nigra</i>	3	24.2	26.3	25.9	23.5	<i>S. obscura</i>	4	23.1	26.1	26.5	24.2
<i>M. tonkeana</i>	2	23.9	26.3	26.3	23.6	<i>P. nanaeus</i>	2	23.0	26.0	26.6	24.4
<i>M. nemestrina</i>	9	23.9	26.5	26.2	23.5	<i>M. larvatus</i>	9	23.3	26.2	26.6	23.9
<i>M. sylvanus</i>	3	23.2	26.8	26.3	23.7						
<i>M. thibetana</i>	3	24.0	26.7	26.1	23.2						
<i>C. albigena</i>	20	23.5	26.0	26.0	24.5						
<i>C. galeritus</i>	5	24.2	26.5	26.2	23.2						
<i>C. torquatus</i>	11	23.9	26.5	26.1	23.5						
<i>T. gelada</i>	4	23.8	26.3	26.0	24.0						
<i>P. cynocephalus</i>	14	23.9	25.9	26.1	24.6						
<i>P. hanadryas</i>	6	23.8	25.9	26.1	24.3						
<i>P. anubis</i>	7	23.9	26.0	26.1	24.0						
<i>P. ursinus</i>	3	24.1	25.9	25.9	24.1						
<i>P. leucophaeus</i>	3	24.5	26.5	25.9	23.1						
<i>P. sphinx</i>	4	23.8	26.6	26.0	23.7						

Table 46. Frequencies of Permutations for Original and Collapsed Metatarsal Length Formulas.

Original Formula	Frequency	Collapsed Formula	Frequency
3=4>2>5	1	3>4>2>5	41
3=4>2=5	28		
3=4>2>5	6		
3>4=2>5	2		
3>4>2=5	3		
3>4>2>5	1		
3=4=5=2	1	3>5>5>2	65
3=4>5>2	2		
3=4>5=2	36		
3=4>5>2	25		
3>4>5>2	1		
4=3>2>5	2	4>3>2>5	35
4=3>2=5	24		
4=3>2>5	6		
4>3>2=5	3		
4=3=5=2	3	4>3>5>2	330
4=3>5>2	21		
4=3>5=2	59		
4=3>5>2	113		
4>3>5>2	58		
4>3>5=2	2		
4>3>5>2	74		
4=5>3>2	13	4>5>3>2	101
4=5>3=2	1		
4=5>3>2	11		
4>5>3=2	1		
4>5>3>2	57		
4>5>3>2	18		
5=4>3>2	2	others	5
5>4>3>2	1		
3=5=4>2	2		

Table 47. Metatarsal Length Formulas in Cercopithecoid Species.

Taxon	N	3≥4≥	3≥4≥	4≥3≥	4≥3≥	4≥5≥	others
		2≥5	5≥2	2≥5	5≥2	3≥2	
<i>M. talapoin</i>	14	1	8		5		
<i>C. pogonias</i>	17		2		15		
<i>C. campbelli</i>	4				4		
<i>C. nona</i>	13		3		10		
<i>C. ascanius</i>	20		8		12		
<i>C. cephus</i>	21		3	2	16		
<i>C. petaurista</i>	5		1		4		
<i>C. pygerythrus</i>	26	4	3	4	15		
<i>C. mitis</i>	20	6	4	2	8		
<i>C. nictitans</i>	19		4		13	2	
<i>C. albogularis</i>	20	1	2	1	16		
<i>B. patas</i>	6	2		4			
<i>H. fascicularis</i>	19	10	4		4		1
<i>H. fuscata</i>	2	1	1				
<i>H. nultatta</i>	20	5	3	4	8		
<i>H. nigra</i>	4	2	2				
<i>H. tonkeana</i>	3		1		2		
<i>H. nemestrina</i>	12	2	2	2	6		
<i>H. sylvanus</i>	5	1	3		1		
<i>H. arctoides</i>	2			1	1		
<i>H. assanensis</i>	1	1					
<i>H. tibetana</i>	4	2	1	1			
<i>C. albigena</i>	24		1		23		
<i>C. galeritus</i>	12	1	1	7	2	1	
<i>C. torquatus</i>	18		1	1	16		
<i>T. gelada</i>	5		3		2		
<i>P. cynocephalus</i>	19				17	2	
<i>P. hanadryas</i>	7				4	3	
<i>P. anubis</i>	20			1	13	6	
<i>P. ursinus</i>	8				6	2	
<i>P. leucophaeus</i>	4	2		2			
<i>P. sphinx</i>	8		4	1	3		

Table 47. (cont.)

Taxon	N	3242	3242	4232	4232	4252	others
		225	522	225	522	322	
<i>P. verus</i>	9				5	4	
<i>P. badius</i>	26				4	21	1
<i>C. satana</i>	3				3		
<i>C. polykomos</i>	3				3		
<i>C. vellerosus</i>	1				1		
<i>C. angolensis</i>	6				3	3	
<i>C. guereza</i>	28				27	1	
<i>P. hosei</i>	4					3	1
<i>P. rubicunda</i>	22				5	16	1
<i>P. aygula</i>	6				2	4	
<i>P. melalophos</i>	8				4	4	
<i>P. frontata</i>	4				3	1	
<i>S. cristata</i>	25				16	9	
<i>S. obscura</i>	15				6	8	1
<i>S. entellus</i>	9				6	3	
<i>P. roxellanae</i>	7			2	5		
<i>P. nanaeus</i>	6				1	5	
<i>H. larvatus</i>	13				10	3	

Table 48. Summary Version of Metatarsal Length Formulas in Cercopithecids and results of G Test.

Taxon	N	3≥4≥	3≥4≥	4≥3≥	4≥3≥	4≥5≥	others
		2≥5	5≥2	2≥5	5≥2	3≥2	
Cercopithecins	185	14	38	13	118	2	
Papionins	197	27	27	20	108	14	1
Colobines	195			2	104	85	4
	577	41	65	35	330	101	5

Without individuals with 4≥5≥3≥2

	G	Prob.	df		G	Prob.	df
All groups	237.4	0.000	10				
Subfamilies	218.3	0.000	5				
Tribes	19.1	0.002	5	Tribes	9.4	0.05	4

Table 49. Average proportionate difference in length between pairs of metatarsals.

Taxon	N	3:4	2:5	3:2	4:5	Taxon	N	3:4	2:5	3:2	4:5
<i>M. talapoin</i>	14	0	-1	4	3	<i>P. vernus</i>	9	-2	-5	5	2
<i>C. pogonias</i>	17	-0	-2	4	3	<i>P. badius</i>	26	-2	-5	5	1
<i>C. campbelli</i>	4	-0	-2	5	3	<i>C. satana</i>	3	-2	-4	5	3
<i>C. mona</i>	13	-0	-2	4	2	<i>C. polykomos</i>	3	-2	-4	4	2
<i>C. ascanius</i>	20	0	-2	4	2	<i>C. vellerosus</i>	1	-2	-3	5	4
<i>C. cephus</i>	21	0	-2	4	3	<i>C. angolensis</i>	6	-2	-4	5	3
<i>C. petaurista</i>	5	0	-2	4	3	<i>C. guereza</i>	28	-1	-3	5	3
<i>C. pygerythrus</i>	26	0	-1	3	3	<i>P. hosei</i>	4	-2	-5	4	1
<i>C. mitis</i>	20	0	-1	4	3	<i>P. rubicunda</i>	22	-1	-5	5	1
<i>C. nictitans</i>	19	-0	-3	5	3	<i>P. aygula</i>	6	-2	-5	5	2
<i>C. albogularis</i>	20	-0	-2	4	3	<i>P. nelalophos</i>	8	-2	-5	5	2
<i>E. patas</i>	6	0	2	2	4	<i>P. frontata</i>	4	-2	-4	5	3
<i>M. fascicularis</i>	19	0	0	4	4	<i>S. cristata</i>	25	-1	-4	5	2
<i>M. fuscata</i>	2	0	0	5	4	<i>S. obscura</i>	15	-2	-4	4	1
<i>M. nulatata</i>	20	0	0	4	4	<i>S. entellus</i>	9	-2	-3	3	2
<i>M. nigra</i>	4	0	0	3	2	<i>P. roxellanae</i>	7	-1	0	3	3
<i>M. tonkeana</i>	3	0	-1	3	3	<i>P. nanaeus</i>	6	-2	-5	4	1
<i>M. nenestrina</i>	12	0	-1	4	3	<i>H. larvatus</i>	13	-1	-4	5	2
<i>M. sylvanus</i>	5	0	-2	5	3						
<i>M. arctoides</i>	2	0	0	3	3						
<i>M. assanensis</i>	1	0	0	3	2						
<i>M. thibetana</i>	4	0	0	4	4						
<i>C. albigena</i>	24	-1	-4	6	3						
<i>C. galeritus</i>	12	-1	0	3	4						
<i>C. torquatus</i>	18	-1	-1	3	3						
<i>T. gelada</i>	5	0	-1	3	3						
<i>P. cynocephalus</i>	19	-1	-2	3	2						
<i>P. hanadryas</i>	7	-1	-2	2	2						
<i>P. anubis</i>	20	-1	-2	3	2						
<i>P. ursinus</i>	8	-1	-2	2	1						
<i>P. leucophaeus</i>	4	0	1	2	3						
<i>P. sphinx</i>	8	0	-2	4	3						

Table 50. Average difference in length between pairs of metatarsals.
 * Significantly different from other groups at $p < 0.01$.

Taxon	N	Mts 3:4	Mts 2:5	Mts 3:2	Mts 4:5
Cercopithecins	174	0	-2	4	3
Papionins	197	0	-1	4 *	3
Colobines	188	-2 *	-4 *	5 *	2

Table 51. Average proportion metatarsal lengths in Cercopithecoid Species.

Taxon	N	Mt 2	Mt 3	Mt 4	Mt 5	Taxon	N	Mt 2	Mt 3	Mt 4	Mt 5
<i>H. talapoin</i>	14	23.8	26.0	26.0	24.3	<i>P. verus</i>	9	23.0	25.5	26.3	25.3
<i>C. pogonias</i>	17	23.7	25.8	26.0	24.6	<i>P. badius</i>	26	23.0	25.2	26.3	25.6
<i>C. campbelli</i>	4	23.5	25.9	26.2	24.5	<i>C. satana</i>	3	23.1	25.4	26.4	25.1
<i>C. mona</i>	13	23.7	25.6	25.9	24.8	<i>C. polykomos</i>	3	23.3	25.4	26.3	25.1
<i>C. ascanius</i>	20	23.6	25.8	25.9	24.7	<i>C. vellerosus</i>	1	23.2	25.6	26.7	24.6
<i>C. cephus</i>	21	23.6	25.8	26.0	24.6	<i>C. angolensis</i>	6	23.1	25.4	26.4	25.1
<i>C. petaurista</i>	5	23.7	25.8	26.1	24.4	<i>C. guereza</i>	28	23.2	25.7	26.4	24.8
<i>C. pygerythrus</i>	26	24.1	25.7	25.9	24.4	<i>P. hosei</i>	4	23.1	25.1	26.1	25.7
<i>C. mitis</i>	20	23.9	25.9	25.9	24.3	<i>P. rubicunda</i>	22	23.0	25.4	26.1	25.5
<i>C. nictitans</i>	19	23.5	25.7	26.0	24.7	<i>P. aygula</i>	6	23.0	25.3	26.4	25.4
<i>C. albogularis</i>	20	23.8	25.7	25.9	24.6	<i>P. melalophos</i>	8	22.8	25.4	26.5	25.4
<i>E. patas</i>	6	24.8	25.6	25.7	23.9	<i>P. frontata</i>	4	23.0	25.6	26.4	25.0
<i>H. fascicularis</i>	19	24.0	26.2	25.8	24.0	<i>S. cristata</i>	25	23.2	25.4	26.2	25.2
<i>H. fuscata</i>	2	23.9	26.3	26.0	23.8	<i>S. obscura</i>	15	23.4	25.2	26.1	25.3
<i>H. mulatta</i>	20	24.0	25.9	25.9	24.2	<i>S. entellus</i>	9	23.7	25.3	26.1	24.9
<i>H. nigra</i>	4	24.4	25.8	25.5	24.3	<i>P. roxellanae</i>	7	24.2	25.5	26.0	24.4
<i>H. tonkeana</i>	3	24.1	25.7	25.8	24.5	<i>P. nanaeus</i>	6	23.1	25.2	26.2	25.6
<i>H. nenestrina</i>	12	23.9	25.7	25.9	24.4	<i>H. larvatus</i>	13	23.1	25.6	26.3	25.1
<i>H. sylvanus</i>	5	23.6	26.1	25.9	24.4						
<i>H. arctoides</i>	2	24.2	25.6	25.8	24.3						
<i>M. assanensis</i>	1	24.4	25.7	25.6	24.3						
<i>H. tibetana</i>	4	24.1	26.1	25.9	24.0						
<i>C. albigena</i>	24	22.8	26.0	26.4	24.8						
<i>C. galeritus</i>	12	24.1	25.7	26.1	24.2						
<i>C. torquatus</i>	18	23.9	25.6	26.0	24.5						
<i>T. gelada</i>	5	24.1	25.8	25.7	24.4						
<i>P. cynocephalus</i>	19	23.9	25.3	25.9	24.9						
<i>P. hanadryas</i>	7	24.0	25.2	25.9	25.0						
<i>P. anubis</i>	20	23.9	25.2	25.9	25.0						
<i>P. ursinus</i>	8	24.2	25.2	25.7	25.0						
<i>P. leucophaeus</i>	4	24.5	25.7	25.6	24.2						
<i>P. sphinx</i>	8	23.8	25.8	25.9	24.6						

Table 52. Frequencies of Permutations for Original and Collapsed Phalangeal Length Formulas.

Original Formula	Frequency	Collapsed Formula	Frequency
3=4=2=5	11	3>4>2>5	232
3=4>2>5	7		
3=4>2=5	33		
3=4>2>5	83		
3>4=2=5	2		
3>4>2>5	2		
3>4>2=5	16		
3>4>2>5	78		
3=4>5=2	15	3>4>5>2	23
3=4>5>2	5		
3>4=5=2	1		
3>4>5>2	1		
3>4>5=2	1		
4=3>2=5	16	4=3>2>5	21
4=3>2>5	5		
3=2=4=5	2	others	17
3>2=4>5	3		
4=3>5=2	6		
4=3>5>2	4		
4>3>5=2	1		
2=3=4>5	1		

Table 53. Phalangeal Length Formulas in Cercopithecoid Species.

Taxon	N	3>4>2>2>5	3>4>5>2>2	4=3>2>2>5	others	Taxon	N	3>4>2>2>5	3>4>5>2>2	4=3>2>2>5	others
<i>M. talapoin</i>	11	11				<i>P. verus</i>	6	4	2		
<i>C. pogonias</i>	2	2				<i>P. badius</i>	17	6	2	6	3
<i>C. campbelli</i>	3	3				<i>C. satana</i>	1	1			
<i>C. mona</i>	10	10				<i>C. polykomos</i>	4		2	1	1
<i>C. cephus</i>	3	3				<i>C. vellerosus</i>	1				1
<i>C. petaurista</i>	3	3				<i>C. angolensis</i>	3	2		1	
<i>C. pygerythrus</i>	9	9				<i>C. guereza</i>	16	5	7	2	2
<i>C. mitis</i>	15	12			3	<i>P. hosei</i>	3	2	1		
<i>C. albogularis</i>	15	14	1			<i>P. rubicunda</i>	15	13		2	
<i>B. patas</i>	2	2				<i>P. aggula</i>	6	3		1	2
<i>M. fascicularis</i>	15	14	1			<i>P. melalophos</i>	6	5			1
<i>M. fuscata</i>	1	1				<i>P. frontata</i>	1			1	
<i>M. mulatta</i>	2	2				<i>S. cristata</i>	11	5	2	3	1
<i>M. nigra</i>	3	3				<i>S. obscura</i>	4	2	1		1
<i>M. tonkeana</i>	2	1		1		<i>P. nanaeus</i>	2	1			1
<i>M. nemestrina</i>	9	9				<i>M. larvatus</i>	9	6		3	
<i>M. sylvanus</i>	3	3									
<i>M. thibetana</i>	3	3									
<i>C. albigena</i>	20	16	2		2						
<i>C. galeritus</i>	5	5									
<i>C. torquatus</i>	11	11									
<i>T. gelada</i>	4	3	1								
<i>P. cynocephalus</i>	14	14									
<i>P. hanadryas</i>	6	6									
<i>P. anubis</i>	7	7									
<i>P. ursinus</i>	3	3									
<i>P. leucophaeus</i>	3	3									
<i>P. sphinx</i>	4	4									

Table 54. Summary Version of Phalangeal Length
Formulas in Cercopithecids and Results of G Test.

Taxon	N	3242225	3242522	4=3)225	others
Cercopithecins	73	69	1		3
Papionins	115	108	4	1	2
Colobines	105	55	18	20	12
	293	232	23	21	17

	G	Prob.	df
All groups	78.2	0.000	6
Subfamilies	75.5	0.000	3
Tribes	-	1.000	1 *

* For comparisons of tribes all cells with n<5 were collapsed because their expected frequency was less than 20%. This resulted in a two by two contingency table and Fisher's Exact 2-tailed Test was used.

Table 55. Average proportionate difference in length between pairs of phalanges

Taxon	N	3:4	2:5	3:2	4:5	Taxon	N	3:4	2:5	3:2	4:5
<i>H. talapoin</i>	11	2	5	9	12	<i>P. verus</i>	6	1	2	12	13
<i>C. pogonias</i>	2	2	5	8	11	<i>P. badius</i>	17	0	1	10	11
<i>C. campbelli</i>	3	1	5	8	11	<i>C. satana</i>	1	1	1	12	12
<i>C. mona</i>	10	3	5	7	9	<i>C. polykomos</i>	3	0	-1	12	10
<i>C. cephus</i>	3	3	6	8	11	<i>C. vellerosus</i>	1	-1	-3	14	13
<i>C. petaurista</i>	3	3	5	9	10	<i>C. angolensis</i>	3	1	2	10	12
<i>C. pygerythrus</i>	9	3	5	9	10	<i>C. guereza</i>	16	0	0	12	11
<i>C. mitis</i>	15	2	4	7	8	<i>P. hosei</i>	3	0	2	10	11
<i>C. albogularis</i>	15	3	4	8	9	<i>P. rubicunda</i>	15	0	3	10	12
<i>E. patas</i>	2	2	4	8	9	<i>P. aggula</i>	6	0	0	10	10
<i>H. fascicularis</i>	14	2	3	9	9	<i>P. nelalophos</i>	6	0	2	9	10
<i>H. fuscata</i>	1	2	3	6	7	<i>P. frontata</i>	1	-0	1	10	12
<i>H. nulatta</i>	2	2	3	8	8	<i>S. cristata</i>	11	0	1	9	10
<i>H. nigra</i>	3	1	4	7	10	<i>S. obscura</i>	4	0	0	10	10
<i>H. tonkeana</i>	2	0	4	7	10	<i>P. nanaeus</i>	2	0	1	10	11
<i>H. nenestrina</i>	9	2	4	9	10	<i>H. larvatus</i>	9	0	4	7	11
<i>H. sylvanus</i>	3	2	2	10	10						
<i>H. thibetana</i>	3	2	4	8	10						
<i>C. albigena</i>	20	2	2	3	3						
<i>C. galeritus</i>	5	2	6	8	11						
<i>C. torquatus</i>	11	3	6	9	11						
<i>T. gelada</i>	4	2	0	8	7						
<i>P. cynocephalus</i>	14	2	3	7	8						
<i>P. hanadryas</i>	6	2	2	8	8						
<i>P. anubis</i>	7	2	4	8	9						
<i>P. ursinus</i>	3	2	3	8	9						
<i>P. leucophaeus</i>	3	2	7	7	11						
<i>P. sphinx</i>	4	4	4	9	9						

Table 56. Average proportionate difference in length between pairs of phalanges. * Significantly different from other groups at $p < 0.01$.

Taxon	N	Phs 3:4	Phs 2:5	Phs 3:2	Phs 4:5
Cercopithecins	73	2	5	8	10
Papionins	114	2	3	7	8 *
Colobines	106	0 *	1 *	10 *	11 *

Table 57. Average proportion phalangeal lengths in Cercopithecoid Species.

Taxon	N	Ph 2	Ph 3	Ph 4	Ph 5	Taxon	N	Ph 2	Ph 3	Ph 4	Ph 5
<i>H. talapoin</i>	11	23.5	28.2	27.1	21.1	<i>P. verus</i>	6	22.3	28.3	27.8	21.6
<i>C. pogonias</i>	2	23.7	28.0	26.9	21.4	<i>P. badius</i>	17	22.6	27.7	27.7	22.0
<i>C. campbelli</i>	3	23.7	27.8	27.0	21.5	<i>C. satana</i>	1	22.1	28.4	27.8	21.7
<i>C. mona</i>	10	24.0	27.7	26.3	21.9	<i>C. polykomos</i>	3	22.0	27.8	27.7	22.5
<i>C. cephus</i>	3	23.9	28.1	26.7	21.4	<i>C. vellerosus</i>	1	21.0	28.1	28.7	22.2
<i>C. petaurista</i>	3	23.6	28.2	26.6	21.6	<i>C. angolensis</i>	3	22.6	27.9	27.6	21.9
<i>C. pygerythrus</i>	9	23.7	28.2	26.6	21.6	<i>C. guereza</i>	16	22.0	28.1	27.8	22.1
<i>C. nitis</i>	15	24.1	27.5	26.2	22.2	<i>P. hosei</i>	3	22.7	27.8	27.6	21.9
<i>C. albogularis</i>	15	23.8	27.9	26.4	21.9	<i>P. rubicunda</i>	15	22.9	27.9	27.6	21.6
<i>E. patas</i>	2	23.8	27.8	26.4	22.1	<i>P. aggula</i>	6	22.6	27.5	27.4	22.5
<i>H. fascicularis</i>	14	23.5	27.9	26.6	22.0	<i>P. melalophos</i>	6	23.0	27.6	27.3	22.2
<i>H. fuscata</i>	1	24.0	27.3	26.1	22.7	<i>P. frontata</i>	1	22.5	27.5	28.0	22.1
<i>H. nולatta</i>	2	23.6	27.7	26.4	22.4	<i>S. cristata</i>	11	22.8	27.4	27.3	22.5
<i>H. nigra</i>	3	23.8	27.5	26.8	21.9	<i>S. obscura</i>	4	22.5	27.5	27.6	22.4
<i>H. tonkeana</i>	2	23.7	27.2	27.1	22.1	<i>P. nanaeus</i>	2	22.5	27.5	27.6	22.3
<i>H. nenestrina</i>	9	23.6	28.0	26.7	21.8	<i>H. larvatus</i>	9	23.6	27.5	27.2	21.8
<i>H. sylvanus</i>	3	22.9	28.2	26.9	22.0						
<i>H. thibetana</i>	3	23.9	27.8	26.5	21.8						
<i>C. albigena</i>	20	24.7	26.1	25.3	24.0						
<i>C. galeritus</i>	5	24.0	28.0	26.7	21.3						
<i>C. torquatus</i>	11	23.9	28.4	26.5	21.2						
<i>T. gelada</i>	4	23.1	27.3	26.5	23.1						
<i>P. cynocephalus</i>	14	23.8	27.3	26.5	22.4						
<i>P. hanadryas</i>	6	23.4	27.6	26.6	22.5						
<i>P. anobis</i>	7	23.7	27.7	26.5	22.1						
<i>P. ursinus</i>	3	23.6	27.7	26.6	22.0						
<i>P. leucophaeus</i>	3	24.3	27.9	26.6	21.2						
<i>P. sphinx</i>	4	23.5	28.3	26.3	21.9						

Table 50. Frequencies of Permutations for Original and Collapsed Metatarsal Cross-sectional Area Formulas.

Original Formula	Frequency	Collapsed Formula	Frequency	Original Formula	Frequency	Collapsed Formula	Frequency
3>4>2>5	121	3>2>4>2>5	302	2>3>4>5	7	others	41
3>4=2>5	105			2=3>4>5	6		
3>4>2=5	43			2=3>4=5	2		
3>4=2=5	10			2>3=4>5	1		
3=4>2>5	10			3>2>5=4	4		
3=4>2=5	8			3>2=5=4	2		
3=4>2=5	3			3>2=5>4	2		
3=4=2=5	2			3>2>5>4	2		
				3=2=5>4	1		
3>4>5=2	25	3>2>4>5>2	47	4>3>2=5	2		
3>4>5>2	14			4>3>2>5	2		
3=4>5=2	4			4=3=2>5	1		
3=4>5>2	2			4=3>2>5	1		
3>4=5=2	1			4=3>5=2	1		
3>4=5>2	1			4=3>5>2	1		
				3>5>2=4	1		
3>2=4>5	92	3>2>2>4>5	200	3>5=2>4	1		
3>2>4>5	71			3>5>4=2	1		
3>2>4=5	10			2>5>3=4	1		
3=2>4>5	10			2=4=3>5	1		
3>2=4=5	7			2=3>5=4	1		
3=2=4>5	6						
3=2=4=5	3						
3=2>4=5	1						

Table 59. Collapsed Metatarsal Cross-sectional Area
Formulas in Cercopithecoid Species.

Taxon	N	3242225	3242522	3222425	others
M. talapoin	14	6		8	
C. pogonias	17	7		10	
C. campbelli	4	3		1	
C. mona	13	5	1	7	
C. ascanius	20	10		9	1
C. cephus	21	16		5	
C. petaurista	5	2	1	2	
C. pygerythrus	23	16	1	6	
C. mitis	20	8		12	
C. nictitans	19	9		9	1
C. albogularis	16	1		15	
E. patas	4	2	2		
M. fascicularis	19	4		10	5
M. fuscata	3	2	1		
M. mulatta	20	11	1	6	2
M. nigra	4	2		2	
M. tonkeana	3	2		1	
M. nemestrina	12	4		7	1
M. sylvanus	5	2	1	1	1
M. arctoides	2			2	
M. assanensis	1			1	
M. thibetana	4	1		2	1
C. albigena	24	9		12	3
C. galeritus	12	3		6	3
C. torquatus	18	5		11	2
T. gelada	5	4		1	
P. cynocephalus	19	7		10	2
P. hanadryas	7	4		1	2
P. anubis	19	12		3	4
P. ursinus	8	2		2	4
P. leucophaeus	4	3		1	
P. sphinx	8			8	

Table 59. (cont.)

Taxon	N	3242225	3242522	3222425	others
<i>P. verus</i>	9	9			
<i>P. badius</i>	26	17	8	1	
<i>C. satana</i>	3	1	2		
<i>C. polykomos</i>	5	1	3		1
<i>C. vellerosus</i>	1	1			
<i>C. angolensis</i>	6	5	1		
<i>C. guereza</i>	20	16	4		
<i>P. hosei</i>	4	2	2		
<i>P. rubicunda</i>	22	15	7		
<i>P. aggula</i>	6	4	2		
<i>P. melalophos</i>	8	3	4		1
<i>P. frontata</i>	4	4			
<i>S. cristata</i>	25	22		3	
<i>S. obscura</i>	15	7	1	6	1
<i>S. entellus</i>	9	4	2	1	2
<i>P. roxellanae</i>	6	1		5	
<i>P. nanaeus</i>	6	6			
<i>H. larvatus</i>	13	10		2	1

Table 60. Summary of Metatarsal Cross-sectional Area Formulas in Cercopithecoid Species and results of G test.

Taxon	N	3242225	3242522	3222425	others
Cercopithecins	176	85	6	83	2
Papionins	197	77	3	87	30
Colobines	188	128	36	18	6
	561	290	45	188	38

	G	Prob.	df
All groups	150.4	0.000	6
Subfamilies	120.7	0.000	3
Tribes	29.7	0.000	3
Tribes	15.7	0.000	2 *

* Because 25% of the cells had expected counts of less than 5 in comparison of cercopithecine tribes, formula 3242522 was collapsed with "others".

Table 61. Average proportionate difference in cross-sectional area between pairs of metatarsals in cercopithecoid species.

Taxon	N	1:4	2:5	3:2	4:5	Taxon	N	1:4	2:5	3:2	4:5
<i>H. talapoin</i>	14	10	15	10	15	<i>P. verus</i>	9	9	7	18	16
<i>C. pogonias</i>	17	11	14	8	12	<i>P. badius</i>	26	6	3	18	15
<i>C. campbelli</i>	4	7	8	13	15	<i>C. satana</i>	3	3	0	18	16
<i>C. mona</i>	13	10	8	11	9	<i>C. polykomos</i>	5	7	10	14	18
<i>C. ascanius</i>	20	12	12	12	12	<i>C. vellerosus</i>	1	5	15	17	27
<i>C. cephus</i>	21	11	10	12	12	<i>C. angolensis</i>	6	8	4	18	14
<i>C. petaurista</i>	5	8	8	14	15	<i>C. guereza</i>	20	8	2	19	14
<i>C. pygerythrus</i>	23	9	11	12	13	<i>P. hosei</i>	4	8	1	15	9
<i>C. nitis</i>	20	12	16	11	15	<i>P. rubicunda</i>	22	9	2	17	10
<i>C. nictitans</i>	19	11	11	11	11	<i>P. aggula</i>	6	7	4	18	16
<i>C. albogularis</i>	16	12	12	10	9	<i>P. melalophos</i>	8	9	1	19	12
<i>E. patas</i>	4	6	3	13	10	<i>P. frontata</i>	4	9	5	17	13
<i>H. fascicularis</i>	19	12	17	7	11	<i>S. cristata</i>	25	6	10	10	14
<i>H. fuscata</i>	3	13	4	15	6	<i>S. obscura</i>	15	9	7	10	9
<i>H. nulatata</i>	20	7	10	8	11	<i>S. entellus</i>	9	2	5	8	11
<i>H. nigra</i>	4	9	9	9	9	<i>P. roxellanae</i>	6	10	22	6	18
<i>H. tonkeana</i>	3	6	9	8	10	<i>P. nanaeus</i>	6	6	5	15	15
<i>H. nenestrina</i>	12	10	14	8	12	<i>H. larvatus</i>	13	9	6	12	9
<i>H. sylvanus</i>	5	6	4	8	5						
<i>H. arctoides</i>	2	6	8	3	5						
<i>H. assanensis</i>	1	11	9	8	7						
<i>H. thibetana</i>	4	10	6	10	5						
<i>C. albigena</i>	24	11	15	9	13						
<i>C. galeritus</i>	12	10	15	9	14						
<i>C. torquatus</i>	18	9	13	7	10						
<i>T. gelada</i>	5	9	11	11	13						
<i>P. cynocephalus</i>	19	13	13	9	9						
<i>P. hanadryas</i>	7	4	7	8	10						
<i>P. anubis</i>	19	5	8	7	9						
<i>P. ursinus</i>	8	7	10	4	7						
<i>P. leucophaeus</i>	4	9	13	10	13						
<i>P. sphinx</i>	8	10	12	6	8						

Table 62. Average difference in cross-sectional area between pairs of metatarsals in cercopithecoid species. * Significantly different at $p < 0.01$

Taxon	N	3:4	2:5	3:2	4:5
Cercopithecins	174	0 *	12	11	12
Papionins	197	9	12	8 *	10 *
Colobines	188	7 *	5	15 *	13 *

Table 63. Average Proportions of Cross-sectional Area.

Taxon	N	Mt2	Mt3	Mt4	Mt5	Taxon	N	Mt2	Mt3	Mt4	Mt5
H. talapoin	14	25.3	30.7	25.3	18.7	P. verus	9	22.4	31.9	26.5	19.3
C. pogonias	17	25.7	30.3	24.5	19.5	P. badius	26	21.6	31.0	27.3	20.2
C. campbelli	4	23.4	30.4	26.5	19.8	C. satana	3	20.8	30.2	28.4	20.7
C. mona	13	24.3	30.2	24.8	20.8	C. polykomos	5	21.8	31.3	27.4	19.5
C. ascanius	20	24.6	31.3	24.7	19.4	C. vellerosus	1	22.7	31.9	28.8	16.6
C. cephus	21	24.2	31.0	25.1	19.8	C. angolensis	6	21.8	31.5	26.7	20.0
C. petaurista	5	23.2	30.8	26.4	19.6	C. guereza	20	21.2	31.8	26.9	20.2
C. pygerythrus	23	24.2	30.8	25.5	19.6	P. hosei	4	22.2	30.2	25.9	21.7
C. nitis	20	25.3	31.7	24.8	18.2	P. rubicunda	22	21.8	30.9	26.1	21.2
C. nictitans	19	24.6	30.7	24.8	19.9	P. aygula	6	21.5	31.2	27.3	20.0
C. albugularis	16	25.3	30.5	24.1	20.2	P. melalophos	8	21.2	31.4	26.4	20.9
E. patas	4	23.1	29.6	26.0	21.4	P. frontata	4	22.3	31.2	26.3	20.1
H. fascicularis	19	26.7	30.4	23.8	19.1	S. cristata	25	24.3	29.7	26.3	19.7
H. fuscata	3	22.2	30.9	25.2	21.7	S. obscura	15	24.4	29.7	25.0	21.0
H. nulatta	20	25.0	29.3	25.4	20.3	S. entellus	9	23.9	27.9	26.7	21.6
H. nigra	4	24.9	29.8	24.7	20.6	P. roxellanae	6	27.2	30.4	25.0	17.4
H. tonkeana	3	24.9	28.9	25.5	20.7	P. nanaeus	6	22.3	30.4	27.1	20.2
H. nenestrina	12	25.8	30.2	24.8	19.3	H. larvatus	13	23.8	30.1	25.0	21.1
H. sylvanus	5	24.1	28.4	25.0	22.5						
H. arctoides	2	25.8	27.6	24.5	22.1						
H. assanensis	1	25.2	29.8	24.0	21.1						
H. thibetana	4	24.5	29.6	24.1	21.8						
C. albigena	24	25.7	30.6	24.7	19.0						
C. galeritus	12	25.6	30.6	25.0	18.8						
C. torquatus	18	25.9	29.6	24.5	20.0						
T. gelada	5	24.4	30.4	25.5	19.7						
P. cynocephalus	19	25.8	30.8	23.8	19.7						
P. hanadryas	7	24.3	28.4	26.1	21.1						
P. anubis	19	25.2	28.2	25.4	21.3						
P. ursinus	8	26.2	28.1	24.4	21.3						
P. leucophaeus	4	25.0	30.4	25.2	19.5						
P. sphinx	8	26.2	29.4	23.9	20.5						

Table 64. Frequencies of Permutations for Original and Collapsed Phalangeal Breadth Formulas.

Original Formula	Frequency	Collapsed Formula	Frequency	Original Formula	Frequency	Collapsed Formula	Frequency
3=4>2=5	106	3≥4>2≥5	163	2=5=3=4	6	others	24
3=4=2=5	32			3=2=4=5	3		
3=4>2>5	10			3=2=4>5	1		
3=4>2>5	7			3=5=4=2	2		
3>4=2=5	5			4=2=3=5	2		
3>4>2>5	2			4=2=5=3	2		
3>4>2>5	1			5=2=3=4	2		
				4=3=2>5	1		
3=4>5=2	57	3≥4>5≥2	89	4=3>2>5	1		
3=4=5=2	23			4>5=3=2	1		
3=4>5>2	3			5=3=2=4	1		
3>4=5=2	3			2>3>4>5	1		
3>4>5=2	3			3=2=5=4	1		
4=3>5=2	17	4≥3>5≥2	25				
4=3=5=2	4						
4=3>5>2	2						
4=3>5>2	1						
4>3>5=2	1						
2=3=5=4	12	2≥3=5=4	13				
2>3=5=4	1						

Table 65. Collapsed Phalangeal Breadth Formulas in Cercopithecoid Species.

Taxon	N	3242225	3242522	4232522	223=5=4	others	Taxon	N	3242225	3242522	4232522	223=5=4	others
<i>M. talapoin</i>	11	8	2			1	<i>P. verus</i>	6	3	3			
<i>C. pogonias</i>	2		2				<i>P. badius</i>	17	7	6	4		
<i>C. campbelli</i>	3	1	2				<i>C. satana</i>	1	1				
<i>C. mona</i>	10	1	8	1			<i>C. polykomos</i>	4	1	2	1		
<i>C. cephus</i>	3	2	1				<i>C. vellerosus</i>	1	1				
<i>C. petaurista</i>	3	2	1				<i>C. angolensis</i>	3	1	1	1		
<i>C. pygerythrus</i>	9	4	5				<i>C. guereza</i>	16	10	5	1		
<i>C. mitis</i>	15	5	3	2	1	4	<i>P. hosei</i>	3	2	1			
<i>C. albogularis</i>	15	8	3		1	3	<i>P. rubicunda</i>	15	5	8	2		
<i>E. patas</i>	2	2					<i>P. t. gula</i>	6	3	3			
<i>M. fascicularis</i>	15	5	5	2		3	<i>P. nelalophos</i>	6	4	1	1		
<i>M. fuscata</i>	1	1					<i>P. frontata</i>	1		1			
<i>M. mulatta</i>	2	2					<i>S. cristata</i>	12	9	2			1
<i>M. nigra</i>	3		3				<i>S. obscura</i>	4	3	1			
<i>M. tonkeana</i>	2			1		1	<i>P. nanaeus</i>	2		2			
<i>M. nenestrina</i>	9	2	4	3			<i>M. larvatus</i>	9	8				1
<i>M. sylvanus</i>	3	2	1										
<i>M. thibetana</i>	3		3										
<i>C. albigena</i>	20			2	11	7							
<i>C. galeritus</i>	5	4	1										
<i>C. torquatus</i>	11	9	2										
<i>T. gelada</i>	4	3				1							
<i>P. cynocephalus</i>	13	12		1									
<i>P. hanadryas</i>	6	2	2	2									
<i>P. anubis</i>	7	6		1									
<i>P. ursinus</i>	3	3											
<i>P. leucophaeus</i>	3	2	1										
<i>P. sphinx</i>	4	2	2										

Table 66. Summary of Collapsed Phalangeal Breadth Formulas in Cercopithecids and Results of G Test.

Taxon	N	3≥4≥2≥5	3≥4≥5≥2	4≥3≥5≥2	2≥3=5=4	others
Cercopithecins	73	33	27	3	2	8
Papionins	114	55	23	12	11	13
Colobines	106	58	36	10		2
	293	146	86	25	13	23

	G	Prob.	df
All groups	33.8	0.000	8
Subfamilies	23.1	0.000	4
Tribes	10.7	0.031	4

Table 67. Average proportionate difference in breadth between pairs of proximal phalanges in cercopithecoid species.

Taxon	N	3:4	2:5	3:2	4:5	Taxon	N	3:4	2:5	3:2	4:5
<i>M. talapoin</i>	11	5	1	14	10	<i>P. verus</i>	6	4	1	19	16
<i>C. pogonias</i>	2	2	-4	17	11	<i>P. badius</i>	17	1	1	15	16
<i>C. campbelli</i>	3	8	2	16	10	<i>C. satana</i>	1	-1	4	13	18
<i>C. mona</i>	10	3	-2	16	10	<i>C. polykomos</i>	3	3	-4	16	9
<i>C. cephus</i>	3	4	2	15	12	<i>C. vellerosus</i>	1	2	5	12	15
<i>C. petaurista</i>	3	2	1	18	16	<i>C. angolensis</i>	3	1	-2	12	9
<i>C. pygerythrus</i>	9	3	-1	14	10	<i>C. guereza</i>	16	1	0	11	10
<i>C. mitis</i>	15	1	1	8	8	<i>P. hosei</i>	3	0	0	11	10
<i>C. albogularis</i>	15	4	2	10	8	<i>P. rubicunda</i>	15	2	-1	15	13
<i>E. patas</i>	2	5	6	9	10	<i>P. aygula</i>	6	1	-2	14	11
<i>H. fascicularis</i>	15	2	-1	10	8	<i>P. nelalophos</i>	6	1	1	15	15
<i>H. fuscata</i>	1	0	2	11	13	<i>P. frontata</i>	1	7	-9	21	6
<i>H. mulatta</i>	2	1	3	9	12	<i>S. cristata</i>	12	4	4	10	10
<i>H. nigra</i>	3	2	-3	12	6	<i>S. obscura</i>	4	3	2	11	10
<i>H. tonkeana</i>	2	1	3	4	7	<i>P. nanaeus</i>	2	1	-4	17	12
<i>H. nenestrina</i>	9	1	-1	10	8	<i>H. larvatus</i>	9	2	5	10	13
<i>H. sylvanus</i>	3	4	1	13	10						
<i>H. thibetana</i>	3	1	-4	14	8						
<i>C. albigena</i>	20	3	2	-1	-1						
<i>C. galeritus</i>	5	4	1	12	9						
<i>C. torquatus</i>	11	2	3	11	12						
<i>T. gelada</i>	4	4	7	7	9						
<i>P. cynocephalus</i>	13	2	4	9	11						
<i>P. hanadryas</i>	6	0	2	7	8						
<i>P. anubis</i>	7	3	3	11	11						
<i>P. ursinus</i>	3	1	3	10	12						
<i>P. leucophaeus</i>	3	1	2	11	12						
<i>P. sphinx</i>	4	2	-1	13	10						

Table 68. Summary of average proportionate difference in breadth between pairs of proximal phalanges in cercopithecids. * Significantly different at $p < 0.01$.

Taxon	N	3:4	2:5	3:2	4:5
Cercopithecins	73	3	1	12	10
Papionins	114	2	2	8 *	8
Colobines	106	2	1	13 *	12

Table 69. Average Proportions of Phalangeal Breadths

Taxon	N	Ph2	Ph3	Ph4	Ph5	Taxon	N	Ph2	Ph3	Ph4	Ph5
<i>H. talapoin</i>	11	22.2	29.3	26.6	22.0	<i>P. verus</i>	6	20.7	30.5	28.3	20.5
<i>C. pogonias</i>	2	20.5	29.1	28.0	22.4	<i>P. badius</i>	17	21.3	29.1	28.7	20.9
<i>C. campbelli</i>	3	22.2	30.7	26.0	21.1	<i>C. satana</i>	1	21.9	28.7	29.2	20.3
<i>C. nona</i>	10	21.2	29.1	27.4	22.3	<i>C. polykonos</i>	3	20.9	28.5	28.0	22.7
<i>C. cephus</i>	3	21.9	29.6	27.3	21.2	<i>C. vellerosus</i>	1	22.6	29.0	27.9	20.6
<i>C. petaurista</i>	3	20.9	29.8	28.7	20.6	<i>C. angolensis</i>	3	21.8	27.7	27.5	22.9
<i>C. pygerythrus</i>	9	21.9	28.9	27.0	22.2	<i>C. guereza</i>	16	22.4	27.8	27.3	22.5
<i>C. mitis</i>	15	23.2	27.4	26.8	22.6	<i>P. hosei</i>	3	22.3	27.7	27.5	22.5
<i>C. alboquularis</i>	15	23.3	28.4	26.0	22.3	<i>P. rubicunda</i>	15	21.3	29.0	28.0	21.7
<i>E. patas</i>	2	24.1	28.6	26.1	21.3	<i>P. aggula</i>	6	21.5	28.4	27.9	22.3
<i>H. fascicularis</i>	15	22.5	27.8	26.7	22.9	<i>P. nelalophos</i>	6	21.4	29.0	28.5	21.1
<i>H. fuscata</i>	1	22.4	27.9	28.1	21.6	<i>P. frontata</i>	1	19.7	30.4	26.4	23.4
<i>H. nulatta</i>	2	23.0	27.8	27.4	21.8	<i>S. cristata</i>	12	23.4	28.4	26.5	21.7
<i>H. nigra</i>	3	22.0	27.9	26.6	23.5	<i>S. obscura</i>	4	22.9	28.5	26.6	21.9
<i>H. tonkeana</i>	2	24.4	26.5	26.3	22.7	<i>P. nenaesus</i>	2	20.6	28.8	28.3	22.3
<i>H. nenestrina</i>	9	22.6	27.4	26.9	23.1	<i>H. larvatus</i>	9	23.2	28.6	27.1	21.2
<i>H. sylvanus</i>	3	22.4	29.0	26.7	22.0						
<i>H. thibetana</i>	3	21.3	28.2	27.4	23.2						
<i>C. albigena</i>	20	25.9	25.4	24.1	24.6						
<i>C. galeritus</i>	5	22.7	28.7	26.4	22.2						
<i>C. torquatus</i>	11	22.9	28.4	27.2	21.6						
<i>F. gelada</i>	4	24.5	28.3	25.9	21.4						
<i>P. cynocephalus</i>	13	23.5	27.9	26.9	21.8						
<i>P. hanadryas</i>	6	23.5	27.0	26.8	22.7						
<i>P. anubis</i>	7	22.9	28.5	27.0	21.6						
<i>P. ursinus</i>	3	23.0	28.0	27.3	21.6						
<i>P. leucophaeus</i>	3	22.5	28.3	27.5	21.7						
<i>P. sphinx</i>	4	22.0	28.5	27.3	22.3						

Table 70. Summary of Correlation of Indices to Mass.

Negative	None	Positive
Tibia/Hindlimb	Foot/Tibia	Femur/Hindlimb
Tibia/Femur	Ph3/Foot	Tarsus/Foot
Foot/Hind	Ph3/Sole	Tarsus/Sole
Foot/Pentib	Ray1/Foot	Power arm/Load arm
Ht3/Foot	Ray1/Sole	
Ht3/Sole	Ray1/Ht3	
Ht3/Tarsus	Ray1/Ray3	
Ph3/Tarsus	Ht1/Ht3	
	Ph1/Ph3	
	Ph3/Ht3	
	Ph1/Ht1	

Table 71. Summary of Correlation of Indices to Mass and the scaling exponents of dimensions with mass. E, cercopithecines; O, colobines.

Negative	E	O	None	E	O	None	E	O	Positive	E	O
Tibia	.27	.24	Foot	.26	.27	Ray1	.32	.27	Femur	.32	.28
Hind	.28	.27	Tibia	.27	.24	Foot	.26	.27	Hind	.28	.27
Tibia	.27	.24	Ht3	.23	.22	Ray1	.32	.27	Tarsus	.32	.34
Femur	.32	.28	Foot	.26	.27	Sole	.28	.28	Foot	.26	.27
Foot	.26	.27	Ph3	.25	.27	Ray1	.32	.27	Tarsus	.32	.34
Hind	.28	.27	Foot	.26	.27	Ht3	.24	.22	Sole	.28	.28
Foot	.26	.27	Ph3	.25	.27	Ray1	.32	.27	Power	.38	.37
Pentib	.29	.27	Sole	.28	.28	Ray3	.23	.25	Load	.25	.26
Ht3	.24	.22	Ph3	.25	.27	Ht1	.33	.25			
Sole	.28	.28	Ht3	.24	.22	Ht3	.24	.22			
Ht3	.24	.22				Ph1	.30	.32			
Tarsus	.32	.34				Ph3	.25	.27			
Ph3	.25	.27				Ph1	.30	.32			
Tarsus	.32	.34				Ht1	.33	.25			

Table 72. Summary of Differences between Subfamilies in Value of Indices Relative to Body Mass and of Dimensions with each other.

Colobines > Cercopithecines	Colobines = Cercopithecines	Colobines (< Cercopithecines
Ht3/Sole	Femur/Hind	Tarsus/Foot
Ht3/Tarsus	Tibia/Hind	Tarsus/Sole
Ph3/Foot	Tibia/Femur	Power arm/Load arm
Ph3/Sole	Foot/Hind	Ph1/Ph3
Ph3/Tarsus	Foot/Pentib	
	Foot/Tibia	
	Ht3/Foot	
	Ray1/Foot	
	Ray1/Sole	
	Ray1/Ht3	
	Ht1/Ht3	
	Ph3/Ht3	
	Ph1/Ht1	
Length Ph3 * Breadth Ph3		
Length Ht3 * Area Ht3		

Table 73. Summary of Differences between Subfamilies in correlation of indices with mass and the difference in adjusted group means between the subfamilies. O>E, colobines have higher adjusted group mean; O=E, no difference in adjusted group means; O<E, colobines have lower adjusted group mean but not at 0.0001 level.

Colobines > Cercopithecines		Colobines = Cercopithecines				Colobines (< Cercopithecines	
Ht3	O>E	Femur	O>E	Ht3	O>E	Tarsus	O=E
Sole	O>E	Hind	O>E	Foot	O>E	Foot	O>E
Ht3	O>E	Tibia	O>E	Ph3	O>E	Tarsus	O=E
Tarsus	O=E	Hind	O>E	Ht3	O>E	Sole	O>E
Ph3	O>E	Tibia	O>E	Ray1	O=E	Power	O<E
Foot	O>E	Femur	O>E	Foot	O>E	Load	O>E
Ph3	O>E	Foot	O>E	Ray1	O=E	Ph1	O=E
Sole	O>E	Hind	O>E	Sole	O>E	Ph3	O>E
Ph3	O>E	Foot	O>E	Ray1	O=E		
Tarsus	O=E	Pentib	O>E	Ht3	O>E		
		Foot	O>E	Ht1	O=E		
		Tibia	O>E	Ht3	O>E		
				Ph1	O=E		
				Ht1	O=E		
LenHt3	O>E						
AreaHt3	O>E						
LenPh3	O>E						
BrdPh3	O=E						

Table 74. Summary of Indices in which species deviate from their respective subfamilial patterns.

Species	Index	Species	Index
<u>Macaca</u>	High Foot/Hindlinb High Foot/Fentib High Foot/Tibia High Tarsus/Sole Low Mt3/Sole Low Mt3/Tarsus High Ray1/Mt3 High Ph1/Mt1	<u>E. patas</u>	High Tibia/Hindlinb High Tibia/Femur High Tarsus/Foot High Power arm/Load arm Low Ph3/Foot Low Ph3/Sole Low Ph3/Tarsus Low Ph3/Mt3 Low Length Ph3*Breadth Ph3 Low Ray1/Foot Low Ray1/Sole Low Ray1/Mt3 Low Ray1/Ray3 Low Mt1/Mt3
<u>M. thibetana</u>	Low Tibia/Hindlinb High Foot/Hindlinb High Foot/Fentib High Foot/Tibia Low Mt3/Foot High Ph3/Mt3 Low Length Ph3*Breadth Ph3 Low Ray1/Foot Low Ray1/Sole	<u>S. entellus</u>	Low Ray1/Sole Low Ray1/Mt3 Low Mt1/Mt3
<u>M. fuscata</u>	Low Length Ph3*Breadth Ph3	<u>Presbytis</u>	Low Tarsus/Foot Low Tarsus/Sole High Mt3/Foot High Mt3/Sole High Mt3/Tarsus High Length Mt3*Area Mt3 Low Ph3/Foot Low Ph3/Sole Low Ph3/Mt3
<u>P. (Papio)</u>	Low Ph3/Foot Low Ph3/Sole Low Ph3/Tarsus Low Ph3/Mt3 Low Length Ph3*Breadth Ph3 Low Ray1/Foot Low Ray1/Sole		

Table 74. (cont.)

Species	Index	Species	Index
<u>P. (Mandrillus)</u>	High Ray1/Foot High Mt1/Mt3	<u>S. (Trachypithecus)</u>	High Ray1/Foot High Ray1/Sole High Ray1/Mt3 High Ray1/Ray3 High Ph1/Ph3
<u>T. gelada</u>	Low Femur/Hindlimb High Tibia/Hindlimb High Tibia/Femur High Mt3/Foot Low Ph3/Foot Low Ph3/Sole Low Ph3/Tarsus Low Ph3/Mt3 Low Length Ph3*Breadth Ph3 Low Ray1/Foot Low Ray1/Sole Low Ray1/Mt3 Low Ph1/Mt1		

Table 75. Summary of Scaling of Dimensions to Body Mass. Dimensions are lengths unless otherwise stated.

Negative Allometry	Isonetry	Positive Allometry
Hindlimb	Femur	Power arm
Pentib	Tarsus	
Tibia	Calcaneus	
Foot	Cuboid	
Sole	Ray1	
Load arm	Ht1	
Load arm calcaneus	Ph1	
Ray3	Area Ht3	
Ht3	Breadth Ph3	
Ph3		

Table 76. Subfamilial Differences in Adjusted Group Means for Regressions of Dimensions on Body Mass.

Colobines > Cercopithecines	Colobines = Cercopithecines
Hind	Tarsus
Femtib	Calcaneus
Femur	Load arm calcaneus
Tibia	Cuboid
Foot	Power Arm
Sole	Ray1
Load arm	Mt1
Ray3	Ph1
Mt3	Breadth Ph3
Ph3	
Area Mt3	

Table 77. Summary of dimensions in which species deviate from their respective subfamilial regression lines.

Species	Dimensions	Species	Dimensions
<u>E. patas</u>	long hindlinb long tibia long foot long sole long tarsus long calcaneus long calcaneal load arm long cuboid long power arm long load arm	<u>M. fuscata</u> (male)	short hindlinb short fentib short femur short tibia short foot short sole short tarsus short calcaneus short calcaneal load arm short power arm short load arm
<u>M. thibetana</u> (male)	short hindlinb short fentib short femur short tibia short sole short load arm short nt3 short ray1 short nt1	<u>T. gelada</u>	short ph3 short ray1 short ph1
		<u>S. entellus</u>	long tarsus long calcaneus long cuboid long power arm

Table 77. (cont.)

Species	Dimensions	Species	Dimensions
<u>M. arctoides</u> (male)	short tibia	<u>M. talapoin</u> (female)	short foot short calcaneal load arm short ray3 short nt3
<u>M. tonkeana</u> (male)	long tarsus long cuboid	<u>C. quereza</u> (male)	short ray1 short ph1
<u>P. ursinus</u> (male)	short ray1 short ph1	<u>C. polykomos</u> (female)	long foot (female) long ray3 (female) long ph3
<u>P. leucophaeus</u> (male)	long fentib long fenur long tibia	<u>C. vellerosus</u> (male)	long calcaneal load arm
<u>P. sphinx</u> (male)	long fentib long fenur long tibia	<u>P. badius</u> (male)	short fenur short tibia short cuboid short nt1
<u>C. nona</u> (male)	long hindlimb long fentib long fenur long tibia long foot long sole long tarsus long calcaneus long calcaneal load arm long cuboid long power arm long load arm long ray3 long nt3 long nt1	<u>P. aygula</u> (male)	short ph1
		<u>P. hosei</u> (male)	long hindlimb long fentib long sole long ray3 long nt3 long load long ray1 long nt1
		<u>S. cristata</u> (female)	short foot
		<u>P. nanaeus</u> (female)	long ph1
		<u>M. larvatus</u> (female)	long calcaneal load arm

Table 78. Summary of Differences between Subfamilies for Digit Formulas.

Formula	Common Permutations	Comments
<u>Ray Length</u>		
Cercopithecine	324>225 or 324>522	gradient along series not great; <u>Papio</u> and <u>C. albigena</u> similar to colobines in formula
Colobine	423>522	central rays project substantially beyond flanking rays
<u>Metatarsal Length</u>		
Cercopithecine	423>522 + others	gradient along series not great; more variable than colobines; <u>Papio</u> similar to colobines in formula
Colobine	423>522 + 425>322	gradient along series is great
<u>Phalangeal Length</u>		
Cercopithecine	324>225	gradient along series not great
Colobine	324>225 + others	gradient along series is great; more variable than cercopithecines
<u>Metatarsal Cross-sectional Area</u>		
Cercopithecine	324>225 + 322>425	central metatarsals not much larger than flanking; medial metatarsals in papionins larger; papionins more variable than cercopithecines
Colobine	324>225	central metatarsals are much larger than flanking, especially on medial side
<u>Phalangeal Breadth</u>		
Cercopithecine	324>225 + 324>522	more variable than colobines
Colobine	324>225 + 324>522	

Figure 9. Box-and-whisker plots illustrating: A. Tibia length as a percent of femur length; B. Foot length as a percent of femur + tibia length; C. Foot length as a percent of tibia length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

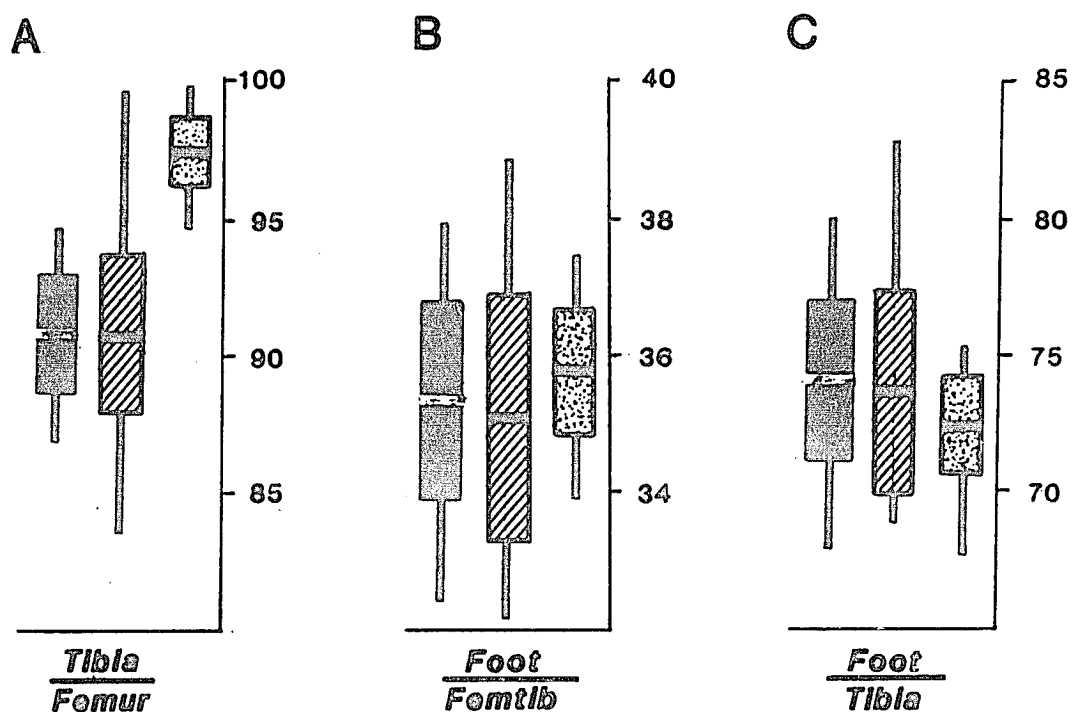


Figure 10. Bivariate plots illustrating: A. Tibia length as a percent of femur length vs ln body mass; B. Foot length as a percent of femur + tibia length vs ln body mass; C. Foot length as a percent of tibia length vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae. r , correlation coefficient.

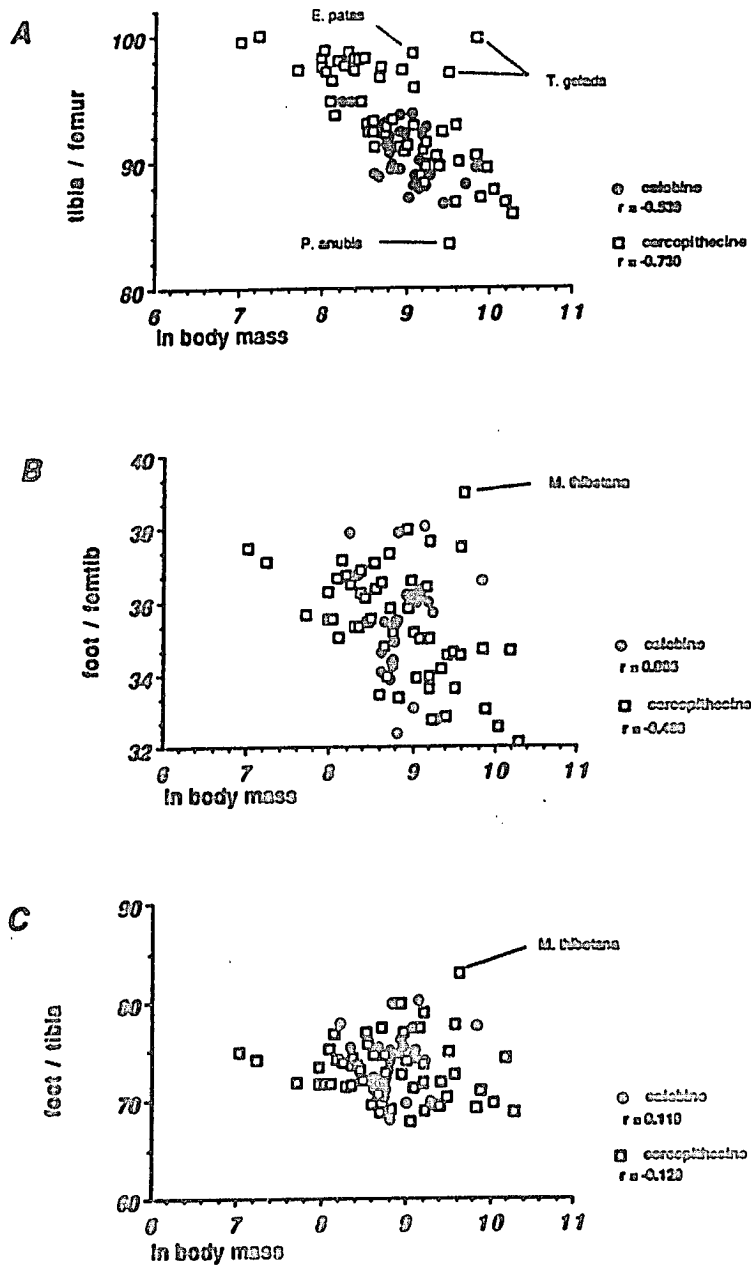


Figure 11. Box-and-whisker plots illustrating: A. Femur length as a percent of hindlimb length; B. Tibia length as a percent of hindlimb length; C. Foot length as a percent of hindlimb length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

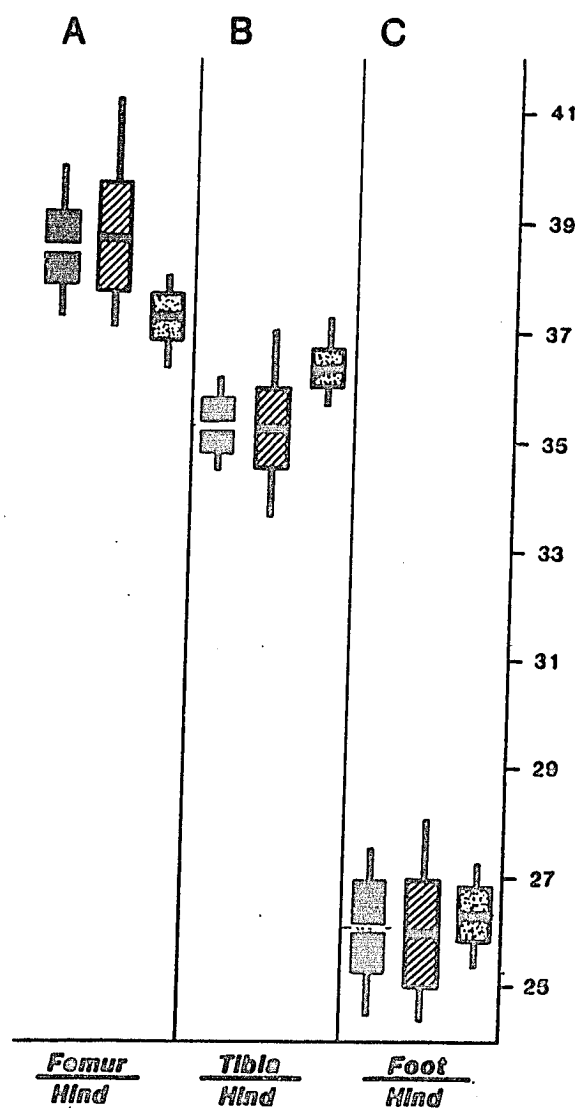


Figure 12. Bivariate plots illustrating: A. Femur length as a percent of hindlimb length vs ln body mass; B. Tibia length as a percent of hindlimb length vs ln body mass; C. Foot length as a percent of hindlimb length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

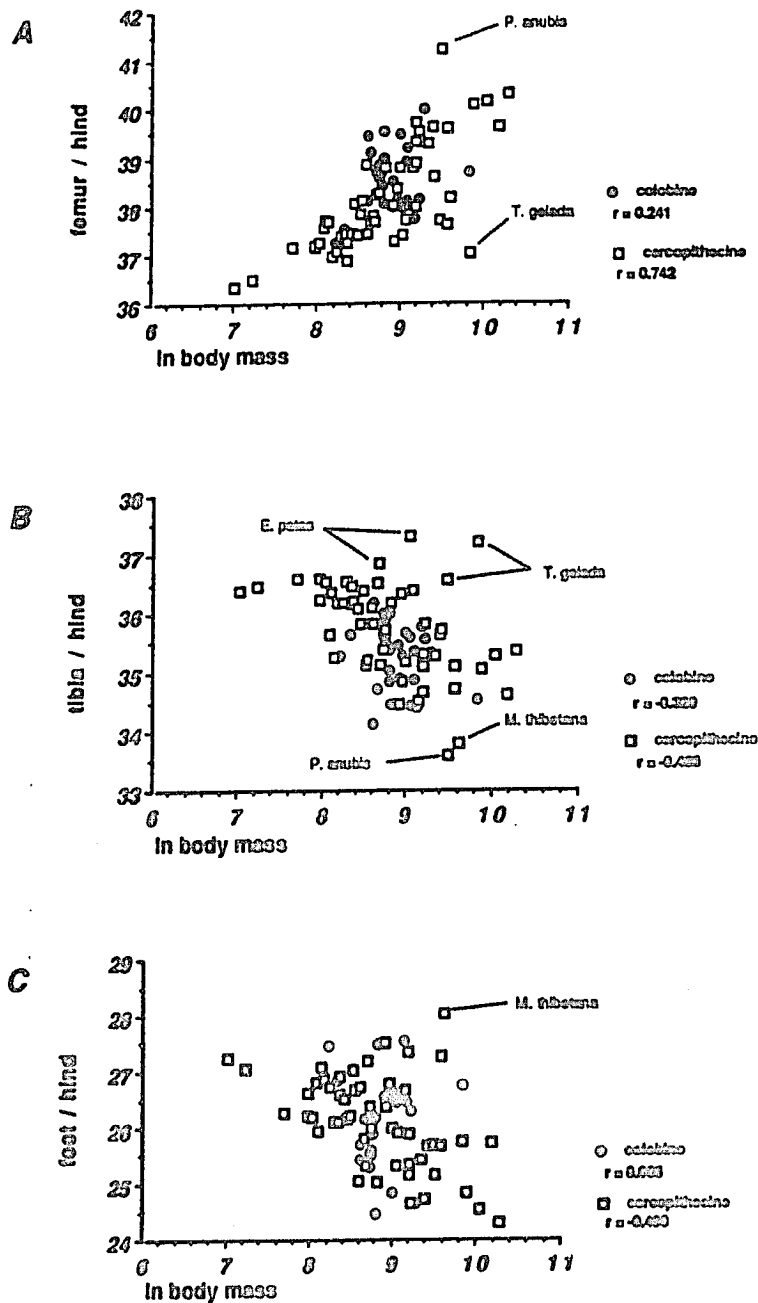


Figure 13. Bivariate plots illustrating regressions of: A. ln hindlimb length vs ln body mass; B. ln femtib length vs ln body mass; C. ln femur length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae.

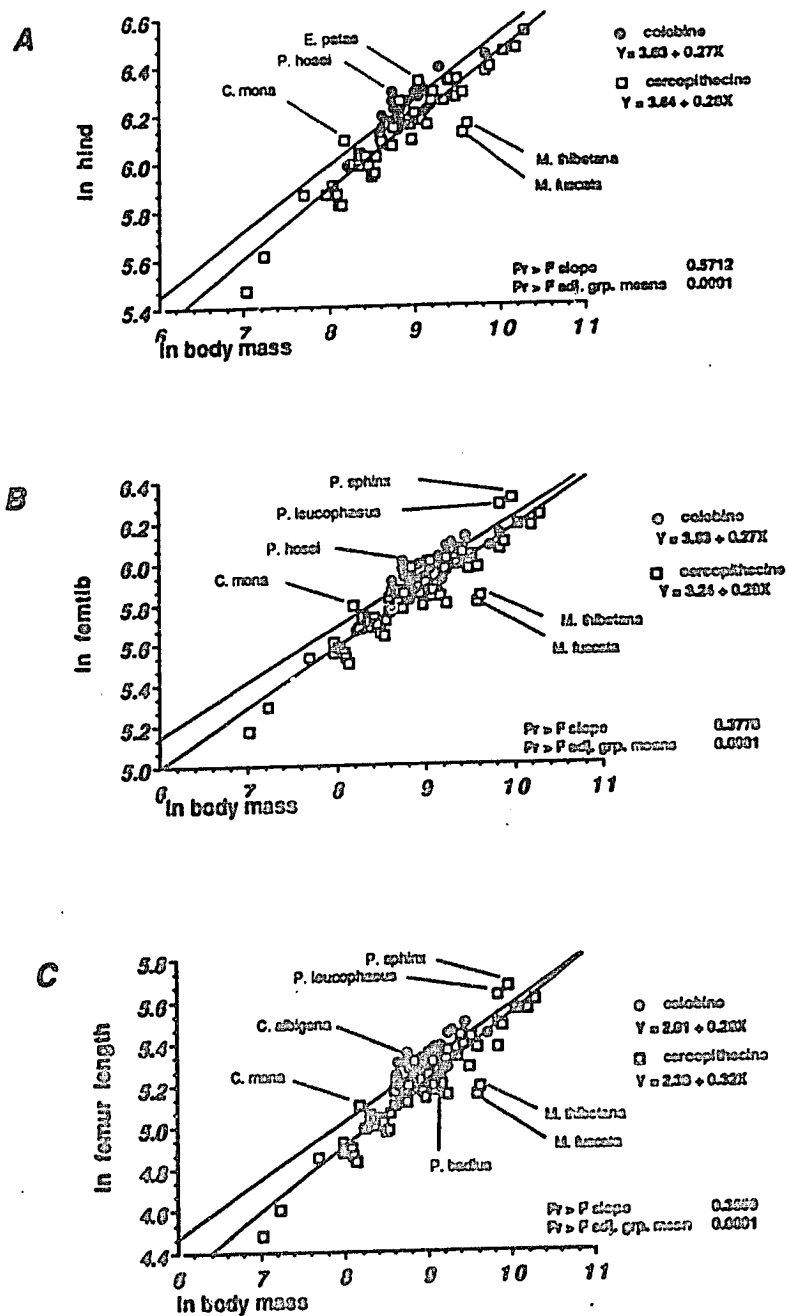


Figure 13. (cont.) D. ln tibia length vs ln body mass; E. ln foot length vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae.

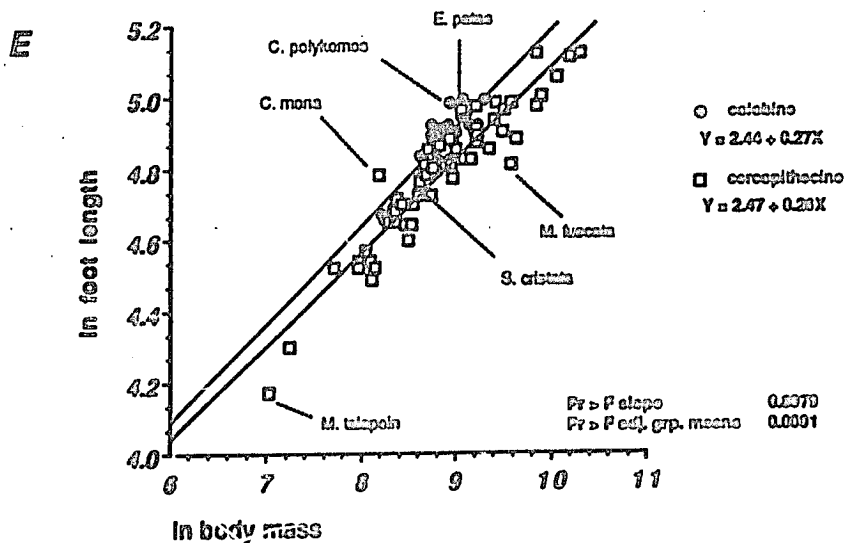
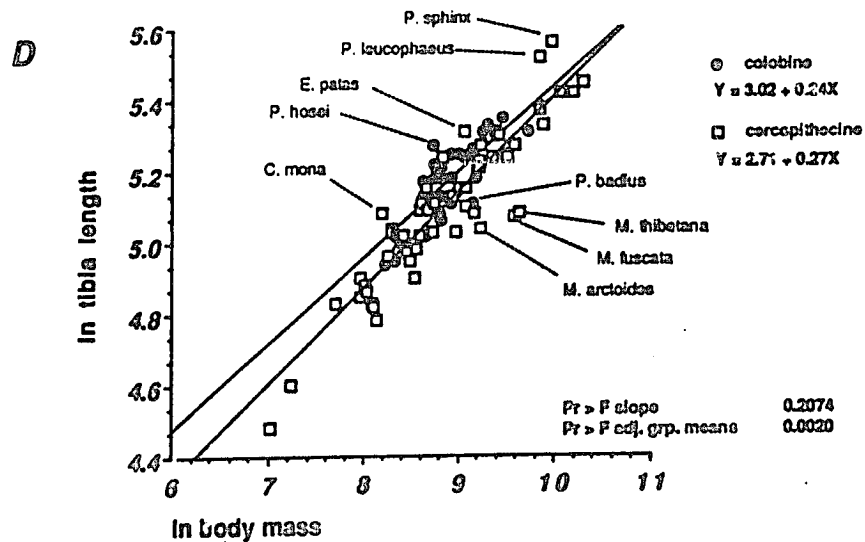


Figure 14. Box-and-whisker plots illustrating: A. Tarsus length as a percent of foot length; B. Third metatarsal length as a percent of foot length; C. Third proximal phalanx length as a percent of foot length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

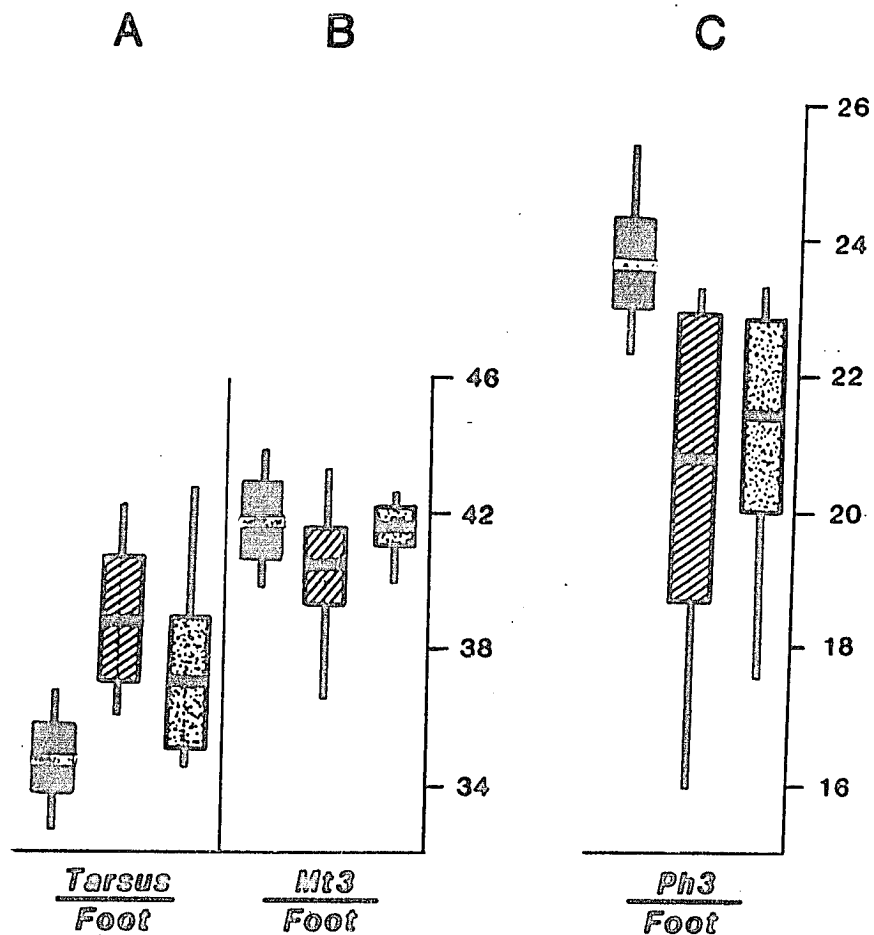


Figure 15. Bivariate plots illustrating: A. Tarsus length as a percent of foot length vs ln body mass; B. Third metatarsal length as a percent of foot length vs ln body mass; C. Third proximal phalanx length as a percent of foot length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

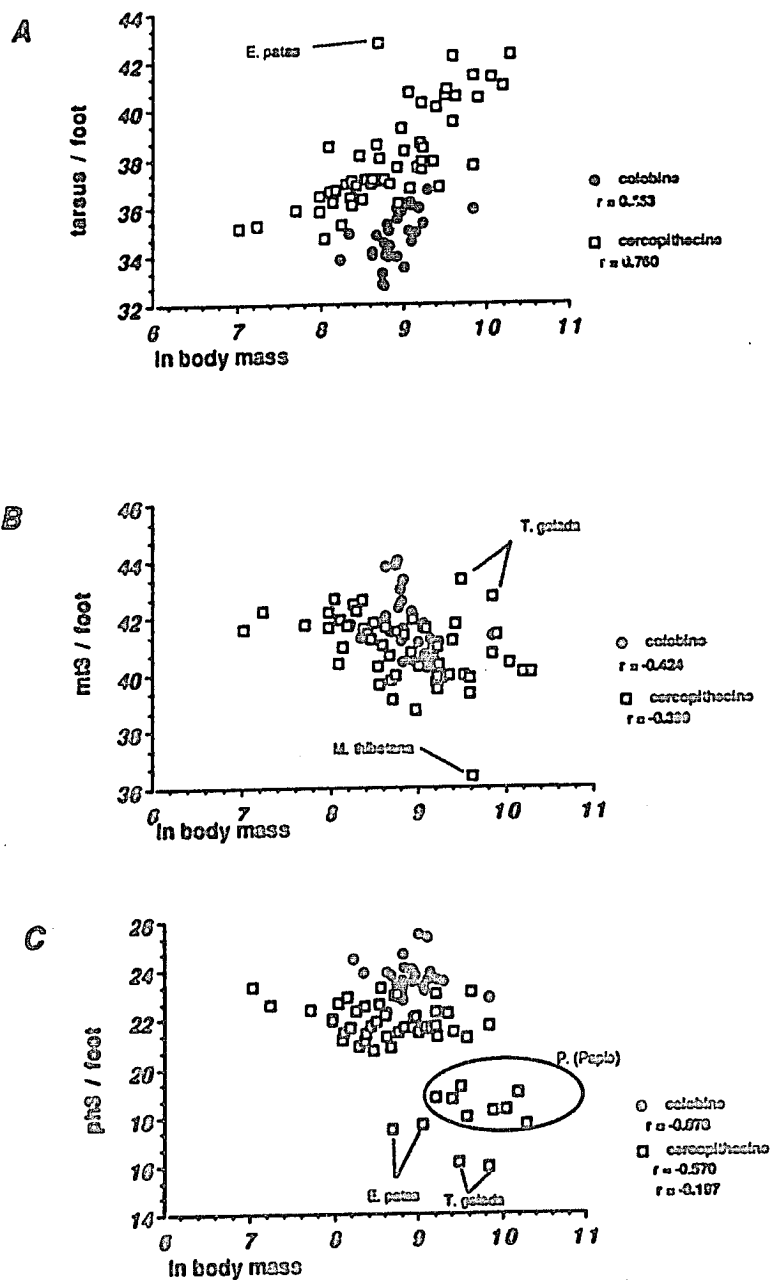


Figure 16. Box-and-whisker plots illustrating: A. Tarsus length as a percent of sole length; B. Third metatarsal length as a percent of sole length; C. Third proximal phalanx length as a percent of sole length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopitheciini.

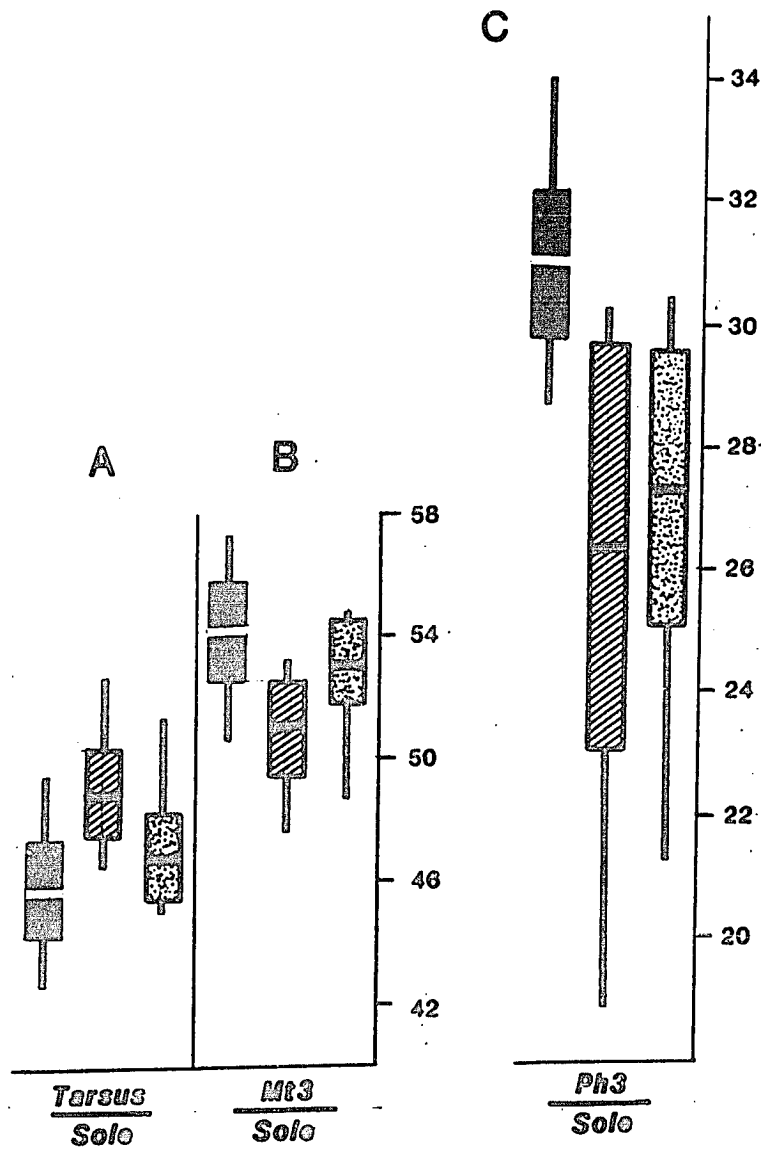


Figure 17. Bivariate plots illustrating: A. Tarsus length as a percent of sole length vs ln body mass; B. Third metatarsal length as a percent of sole length vs ln body mass; C. Third proximal phalanx length as a percent of sole length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

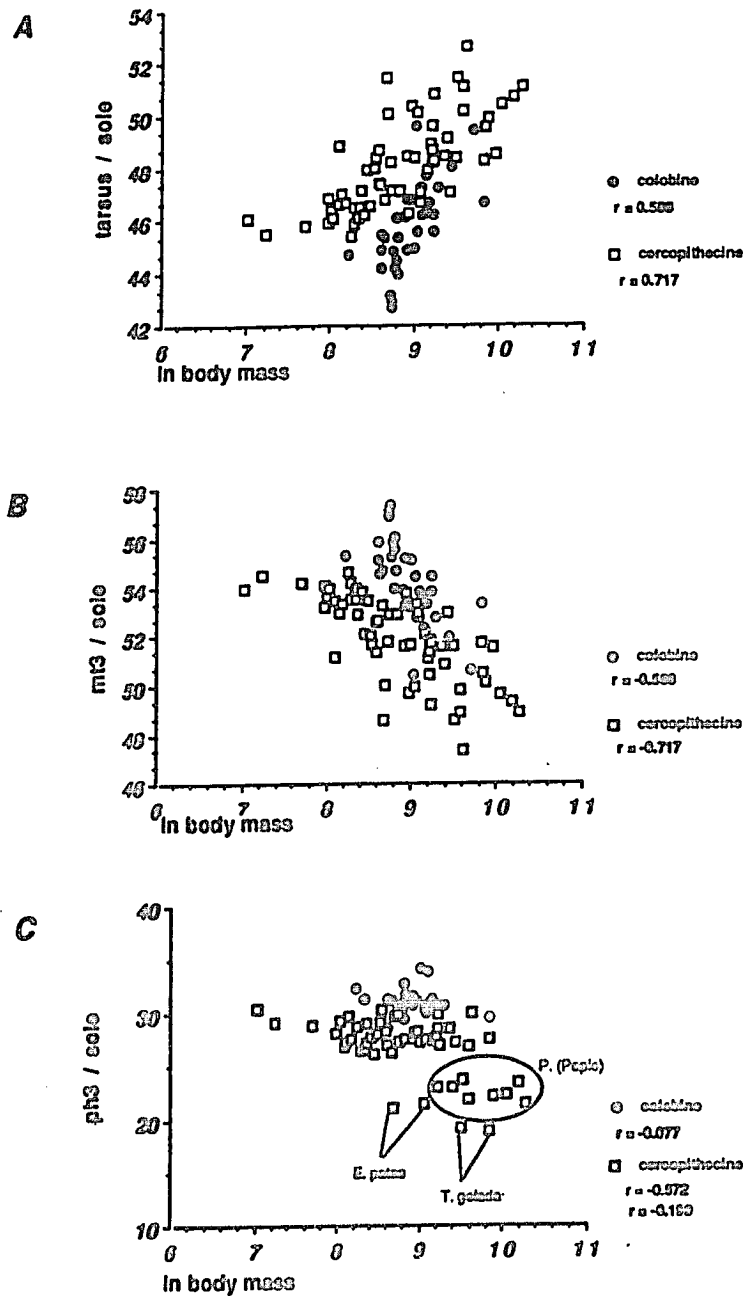


Figure 18. Box-and-whisker plots illustrating: A. Third metatarsal length as a percent of tarsus length; B. Power arm length as a percent of load arm length; C. Third proximal phalanx length as a percent of tarsus length; D. Third proximal phalanx length as a percent of third metatarsal length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

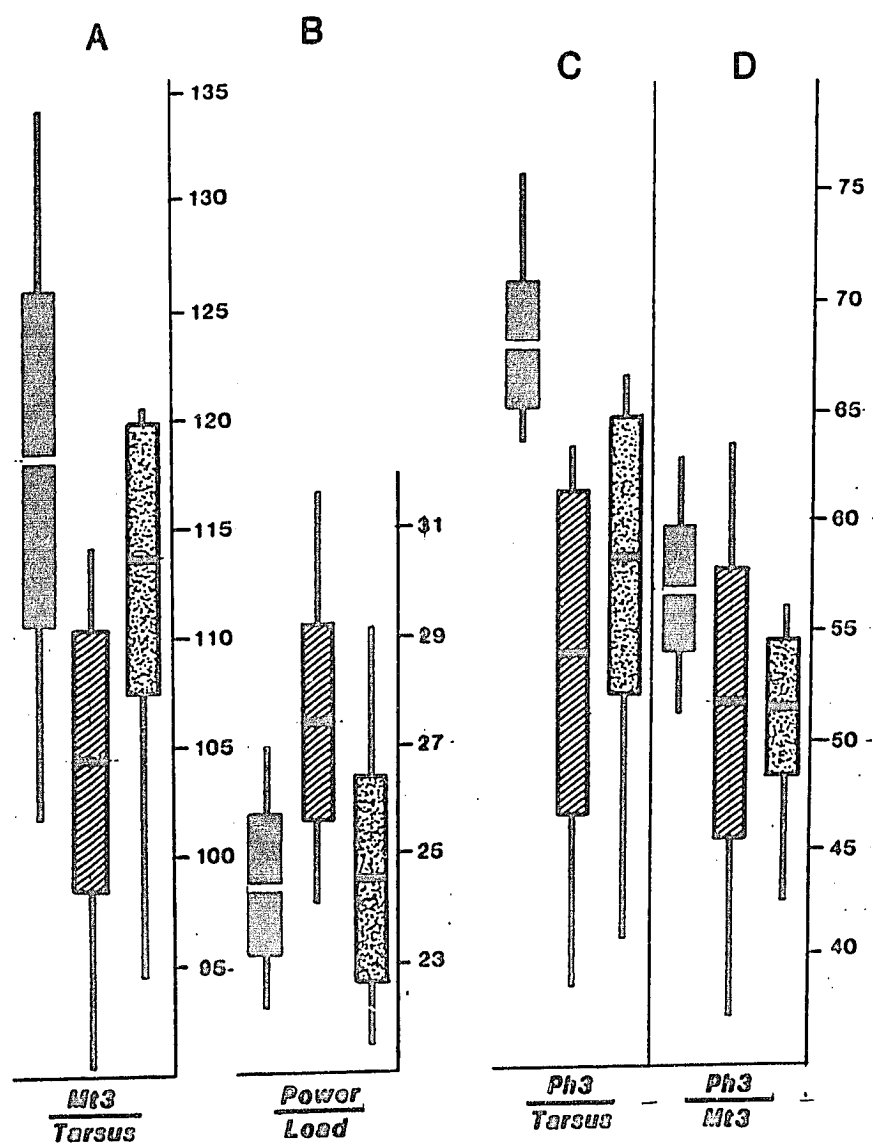


Figure 19. Bivariate plots illustrating: A. metatarsal three length as a percent of tarsus length vs ln body mass; B. Power arm length as a percent of load arm length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

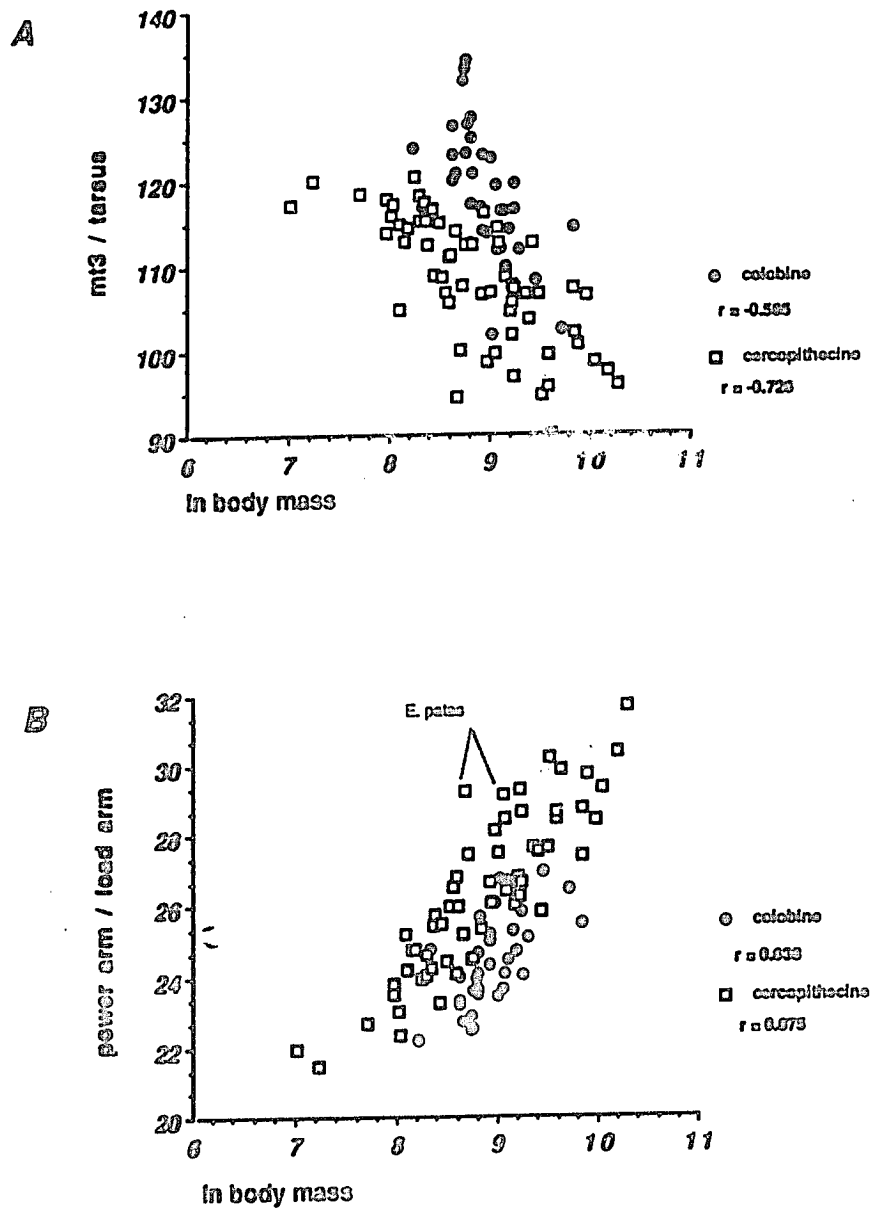


Figure 19. (cont.) C. Third proximal phalanx length as a percent of tarsus length vs ln body mass. D. Third proximal phalanx length as a percent of third metatarsal length vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae. r, correlation coefficient.

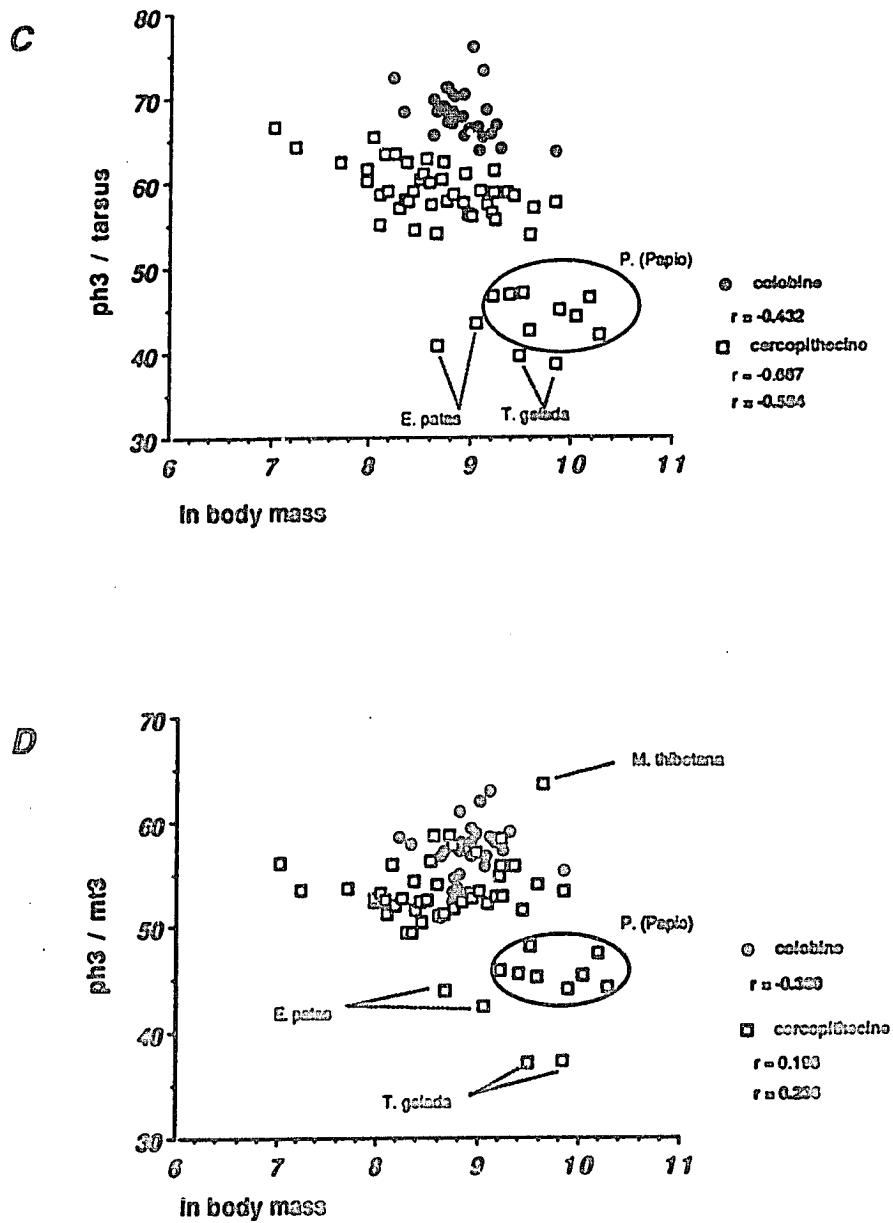


Figure 20. Bivariate plots illustrating: A. $\ln$ metatarsal three length vs $\ln$ metatarsal three cross-sectional area; B. $\ln$ proximal phalanx three length vs $\ln$ proximal phalanx breadth. Circles, Colobinae. Squares, Cercopitheciinae. r , correlation coefficient. Regression equation is of reduced major axis slope.

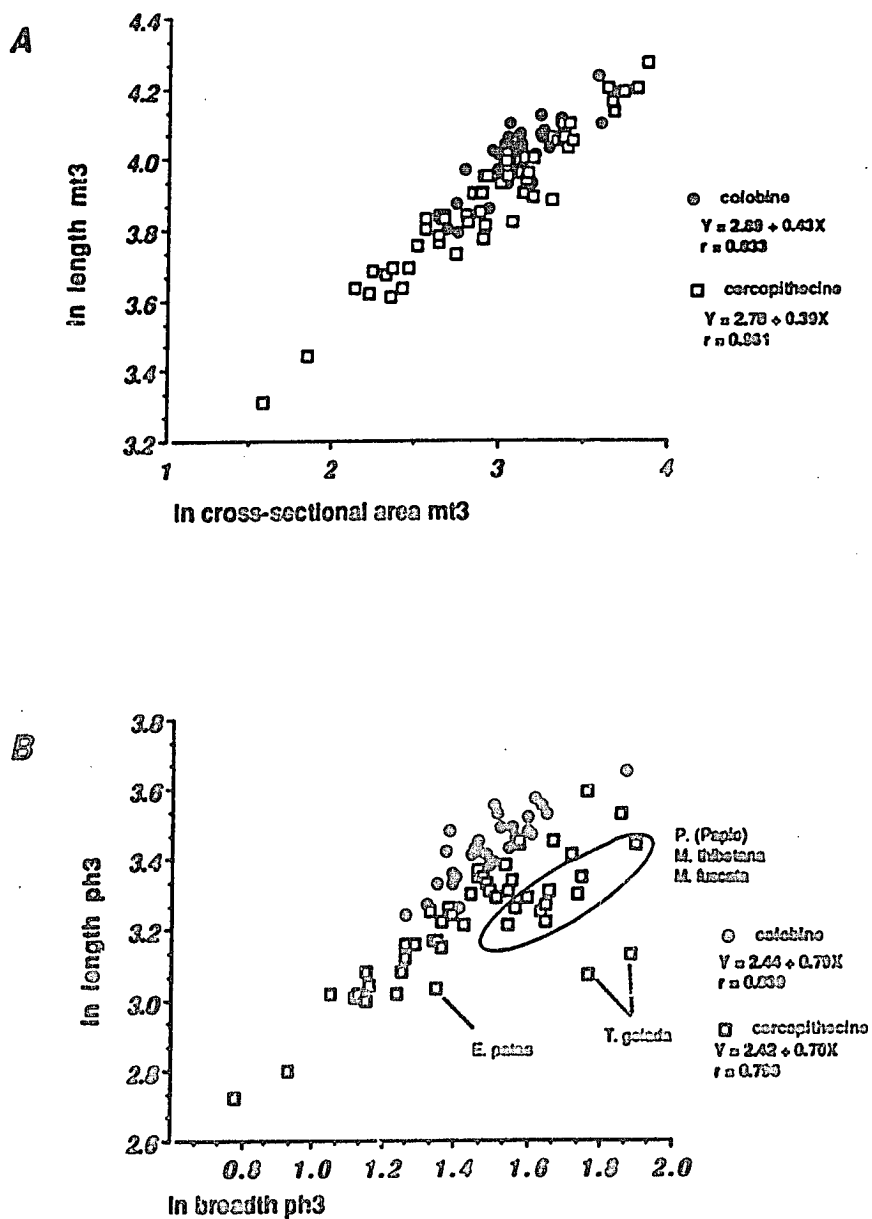


Figure 21. Bivariate plots illustrating regressions of: A. ln sole length vs ln body mass; B. ln tarsus length vs ln body mass; C. ln calcaneus length vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae.

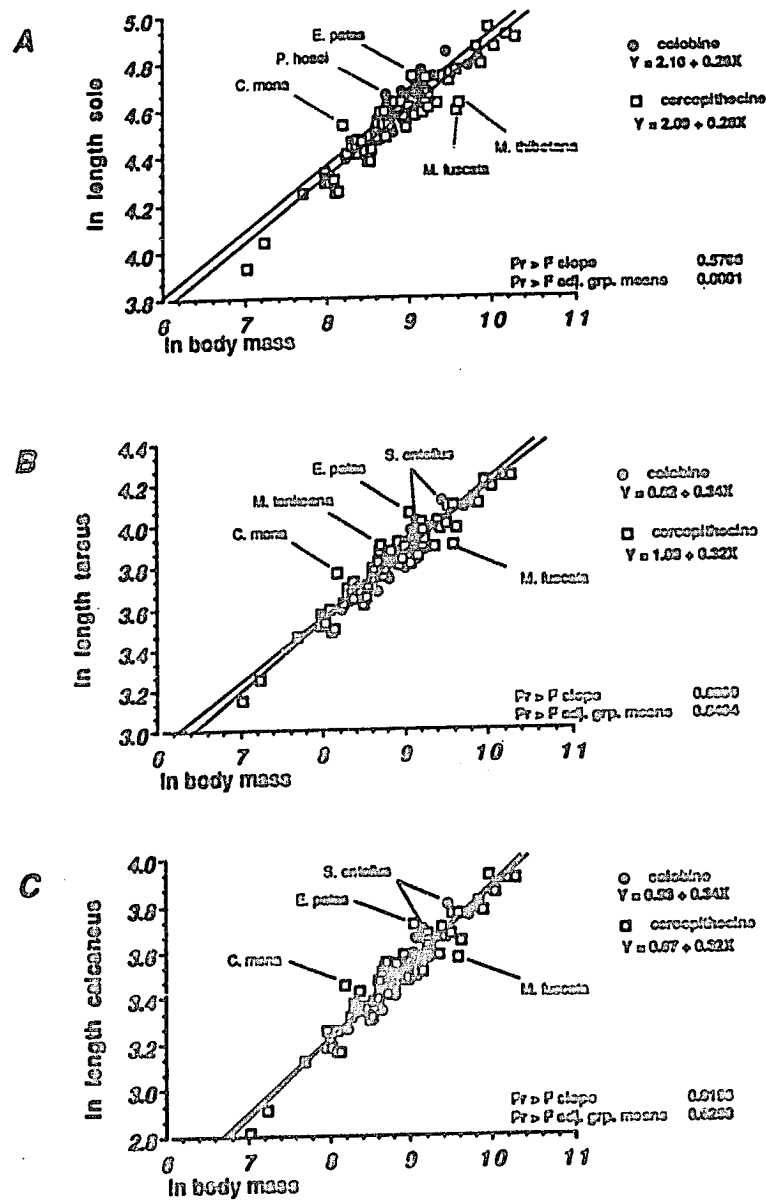


Figure 21. (cont.) D. ln calcaneal load arm length vs ln body mass; E. ln cuboid length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae.

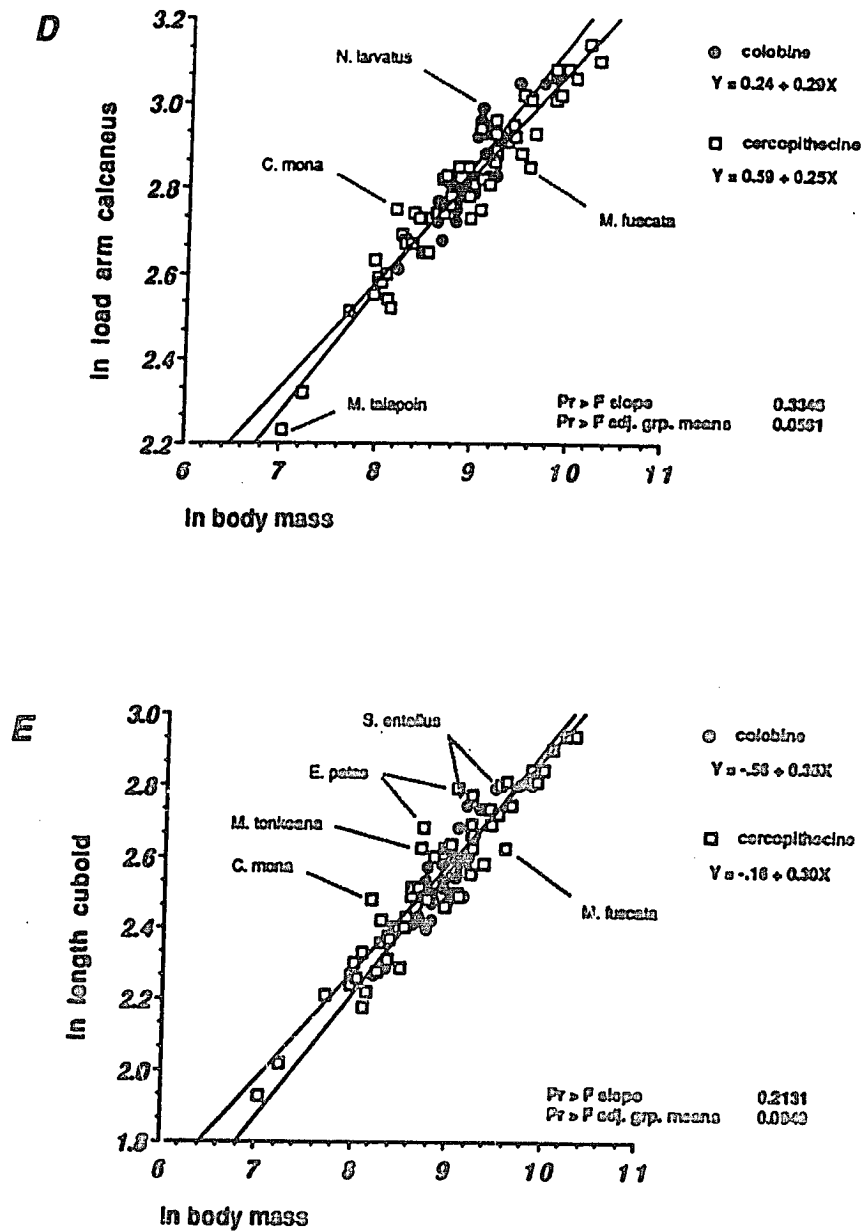


Figure 22. Bivariate plots illustrating regressions of: A. ln power arm length vs ln body mass; B. ln load arm length vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae.

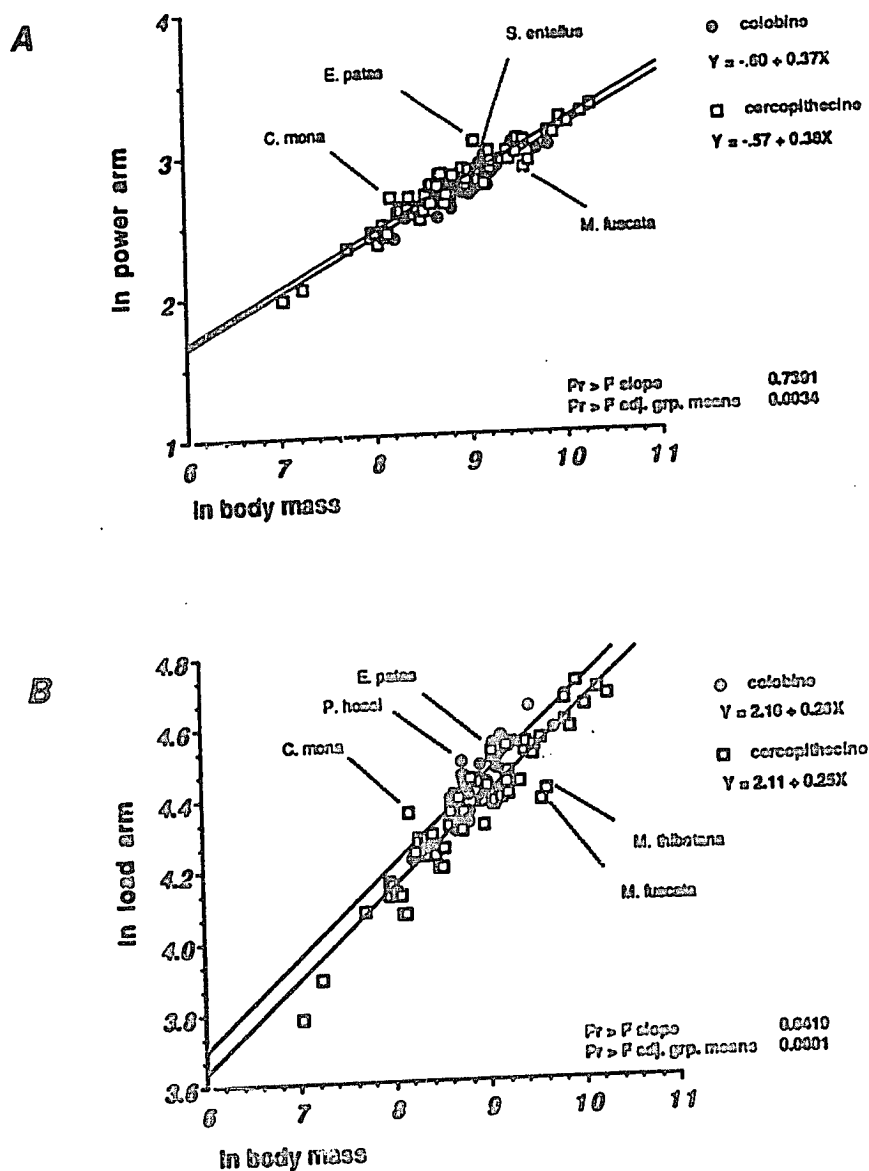


Figure 23. Bivariate plots illustrating regressions of: A. ln ray 3 length vs ln body mass; B. ln metatarsal 3 length vs ln body mass; C. ln proximal phalanx 3 length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae.

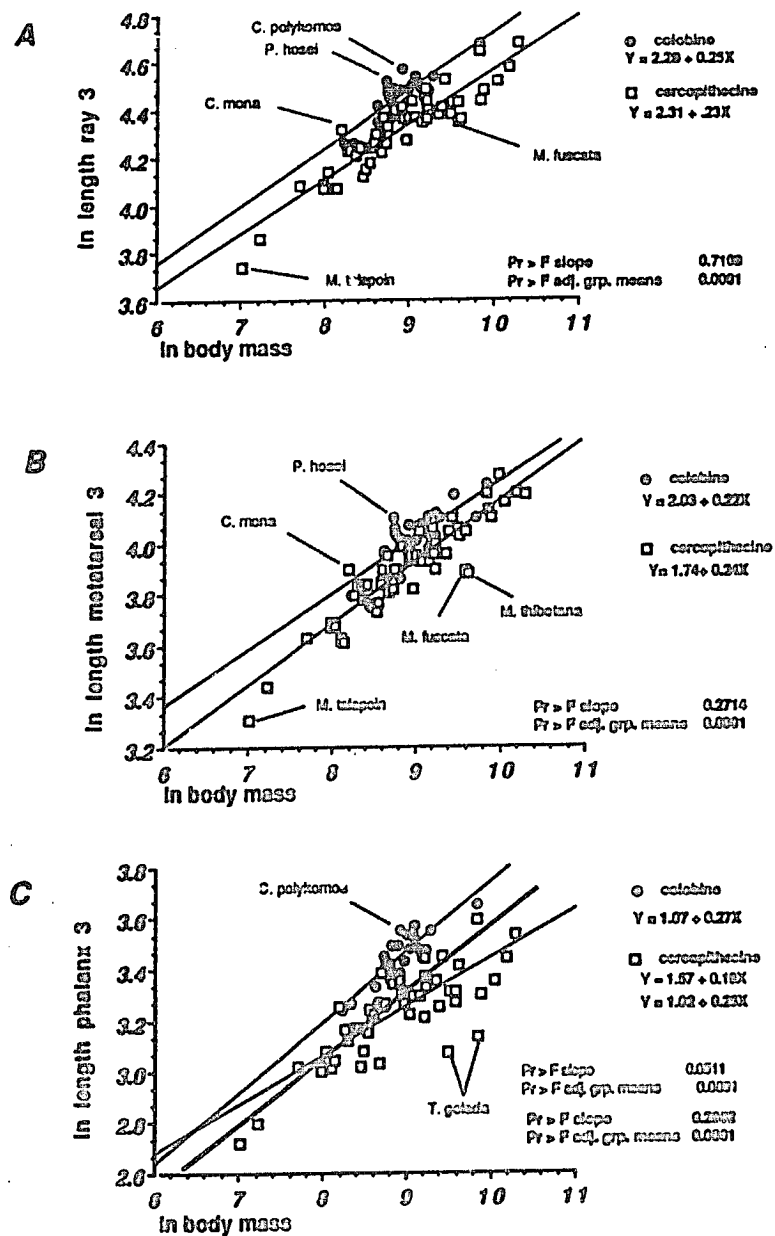


Figure 23. (cont.) D. ln metatarsal 3 cross-sectional area vs ln body mass; E. ln proximal phalanx 3 breadth vs ln body mass. Circles, Colobinae. Squares, Cercopitheciinae.

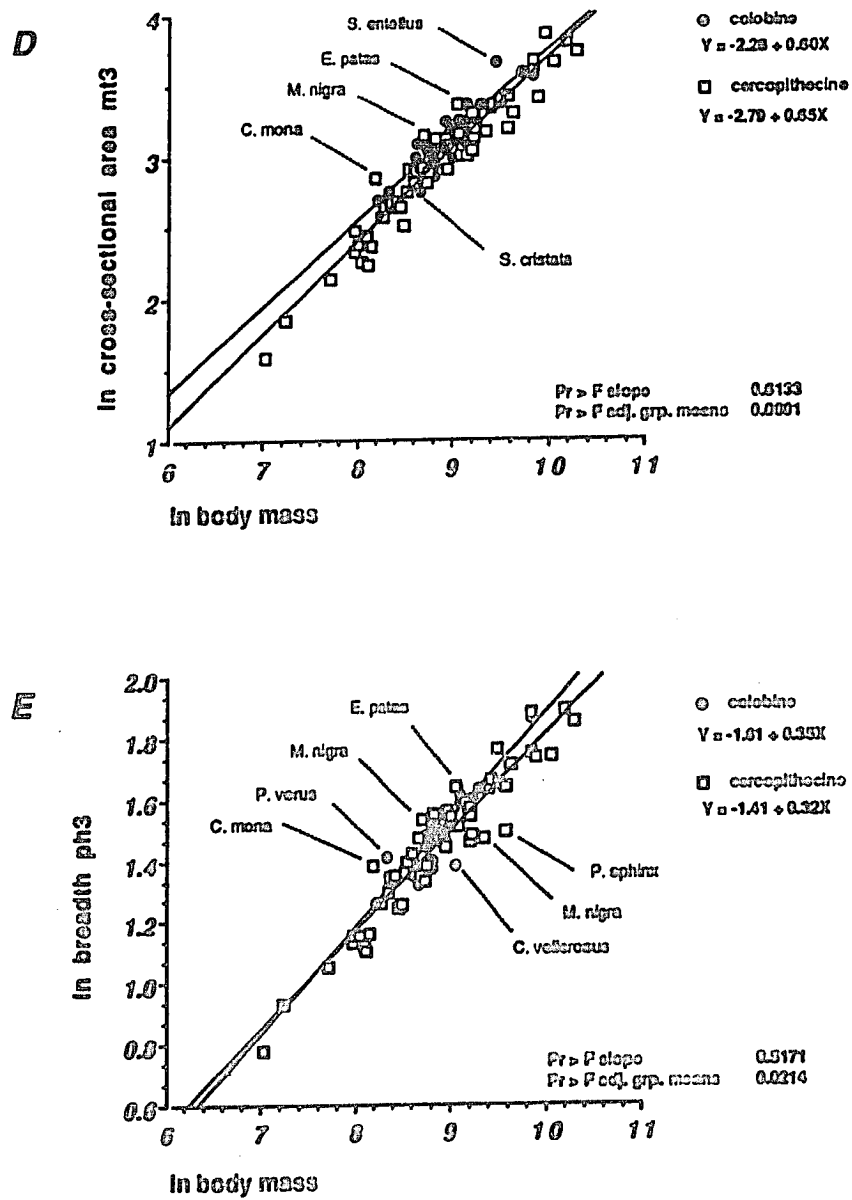


Figure 24. Box-and-whisker plots illustrating: A. Ray 1 length as a percent of foot length; B. Ray 1 length as a percent of sole length; C. Ray 1 length as a percent of third metatarsal length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

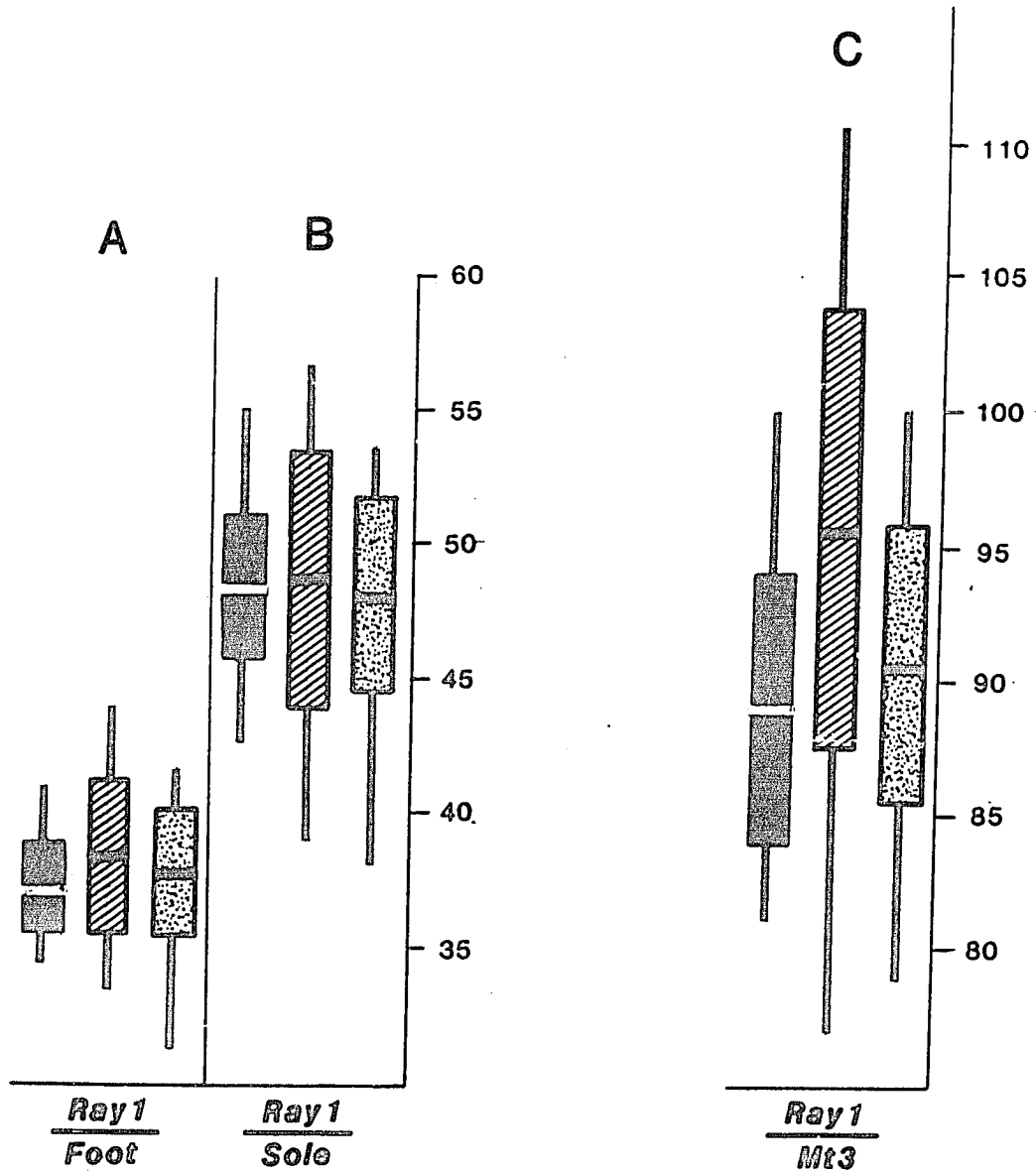


Figure 25. Bivariate plots illustrating: A. Ray 1 length as a percent of foot length vs ln body mass; B. Ray 1 length as a percent of sole length vs ln body mass; C. Ray 1 length as a percent of third metatarsal length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

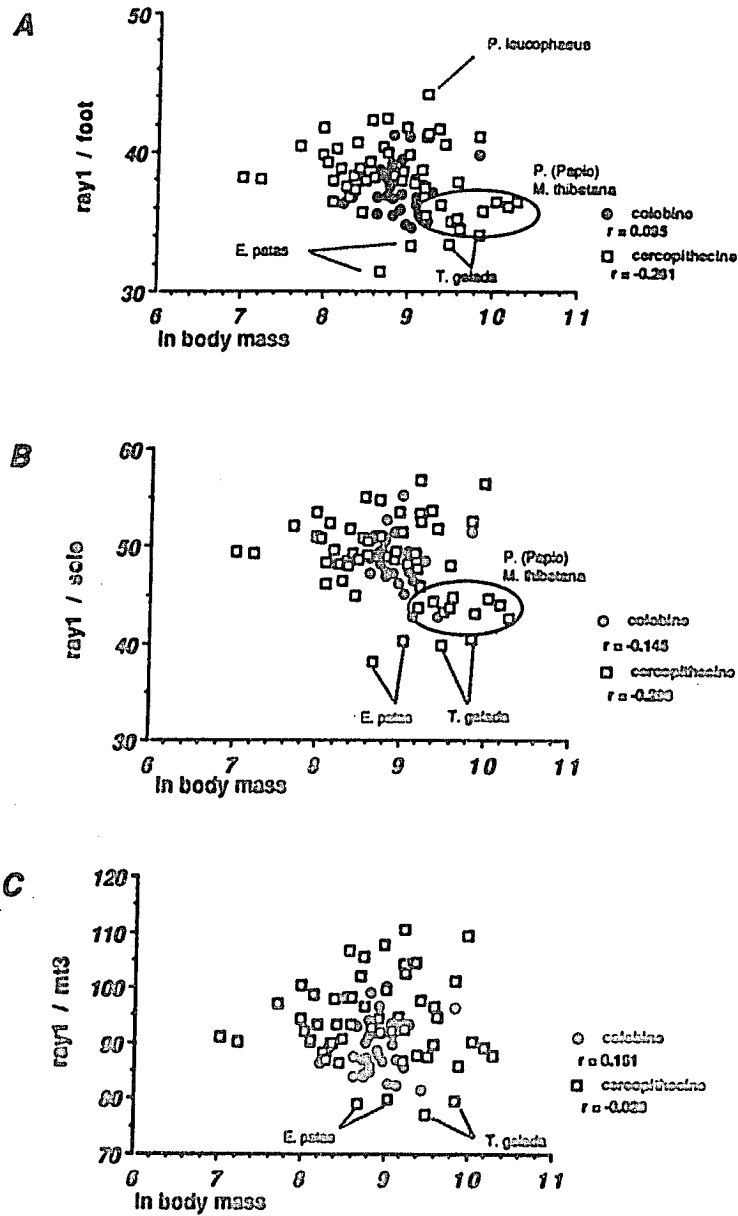


Figure 26. Box-and-whisker plots illustrating: A. Ray 1 length as a percent of ray 3 length; B. First metatarsal length as a percent of third metatarsal length; C. First proximal phalanx length as a percent of third proximal phalanx length; D. First proximal phalanx length as a percent of first metatarsal length. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

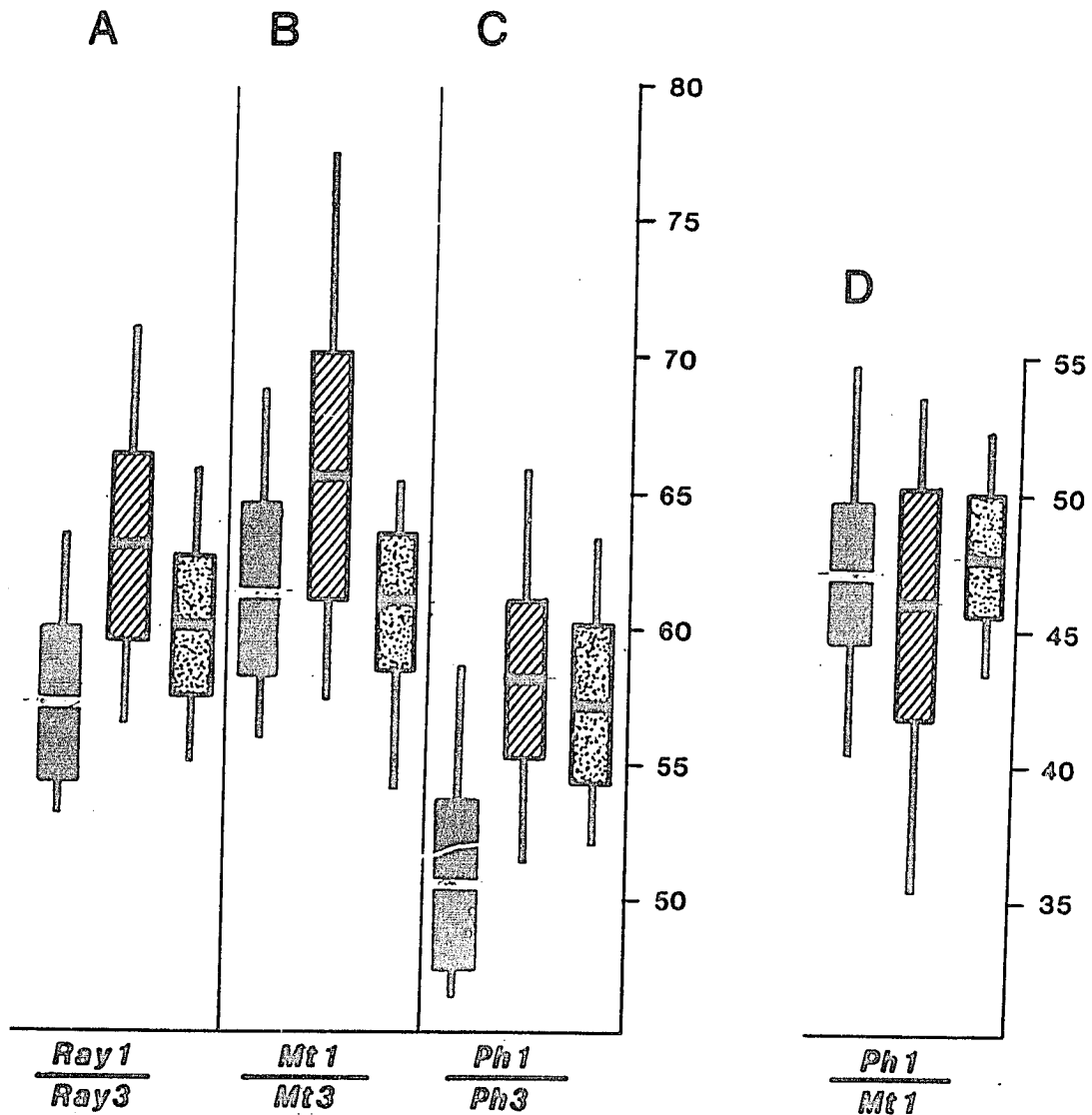


Figure 27. Bivariate plots illustrating: A. Ray 1 length as a percent of Ray 3 length vs ln body mass; B. First metatarsal length as a percent of third metatarsal length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae. r , correlation coefficient.

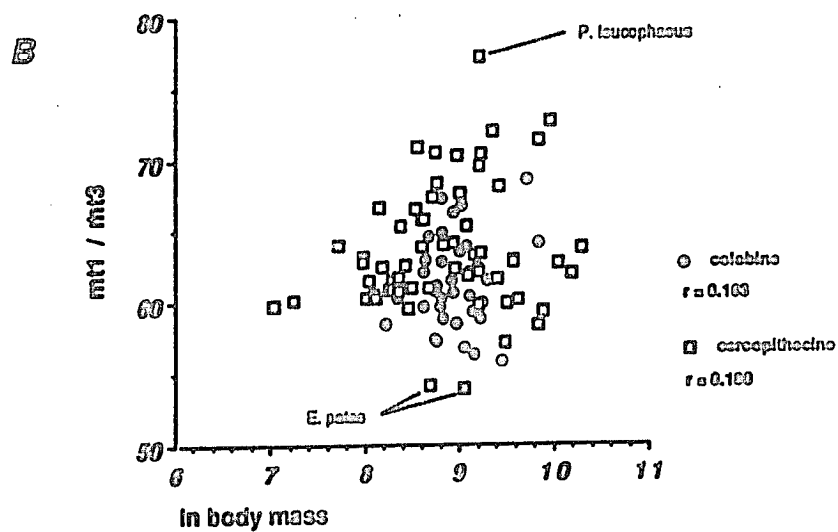
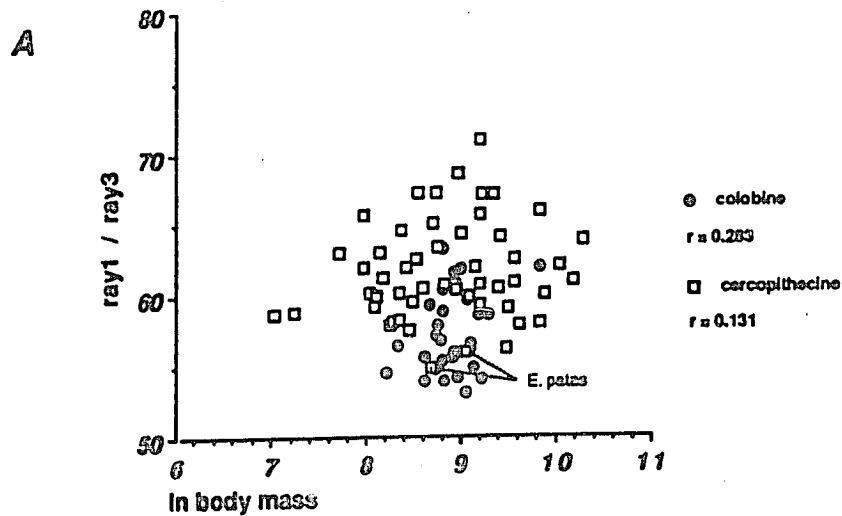


Figure 27. (cont.) C. First proximal phalanx length as a percent of third proximal phalanx length vs ln body mass; D. First proximal phalanx length as a percent of first metatarsal length. Circles, Colobinae. Squares, Cercopitheciinae. r , correlation coefficient.

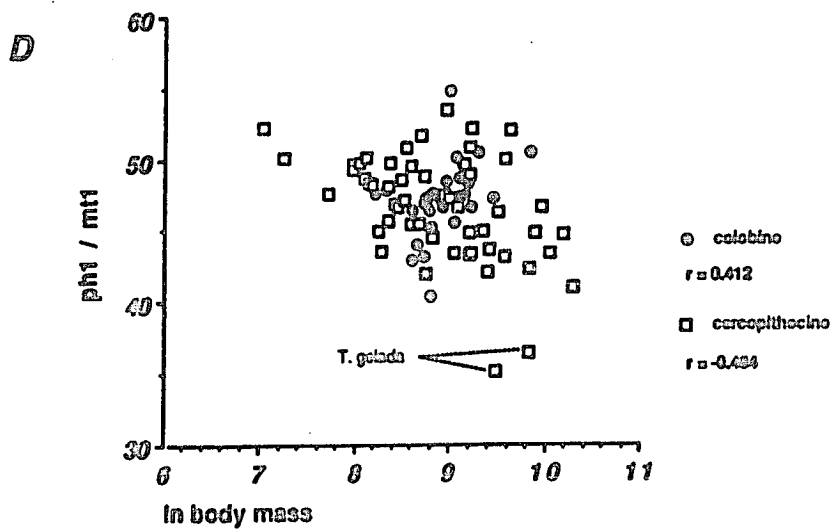
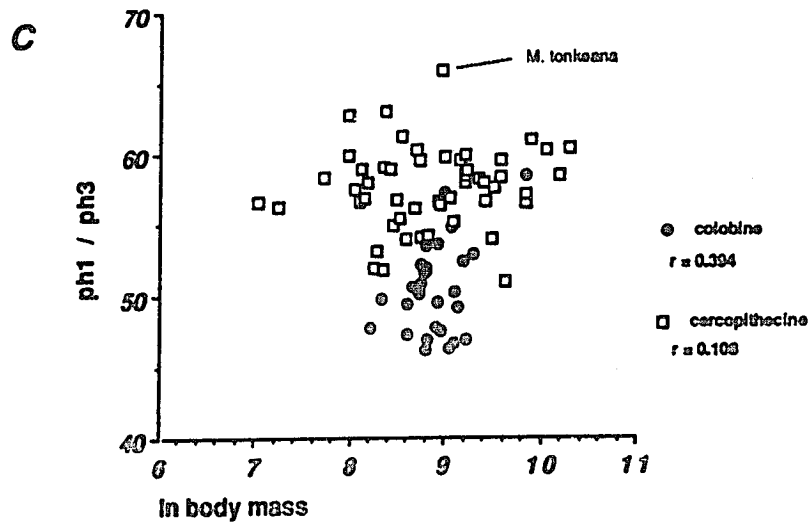


Figure 28. Bivariate plots illustrating regressions of: A. ln ray 1 length vs ln body mass; B. ln metatarsal 3 length vs ln body mass; C. ln proximal phalanx 1 length vs ln body mass. Circles, Colobinae. Squares, Cercopithecinae.

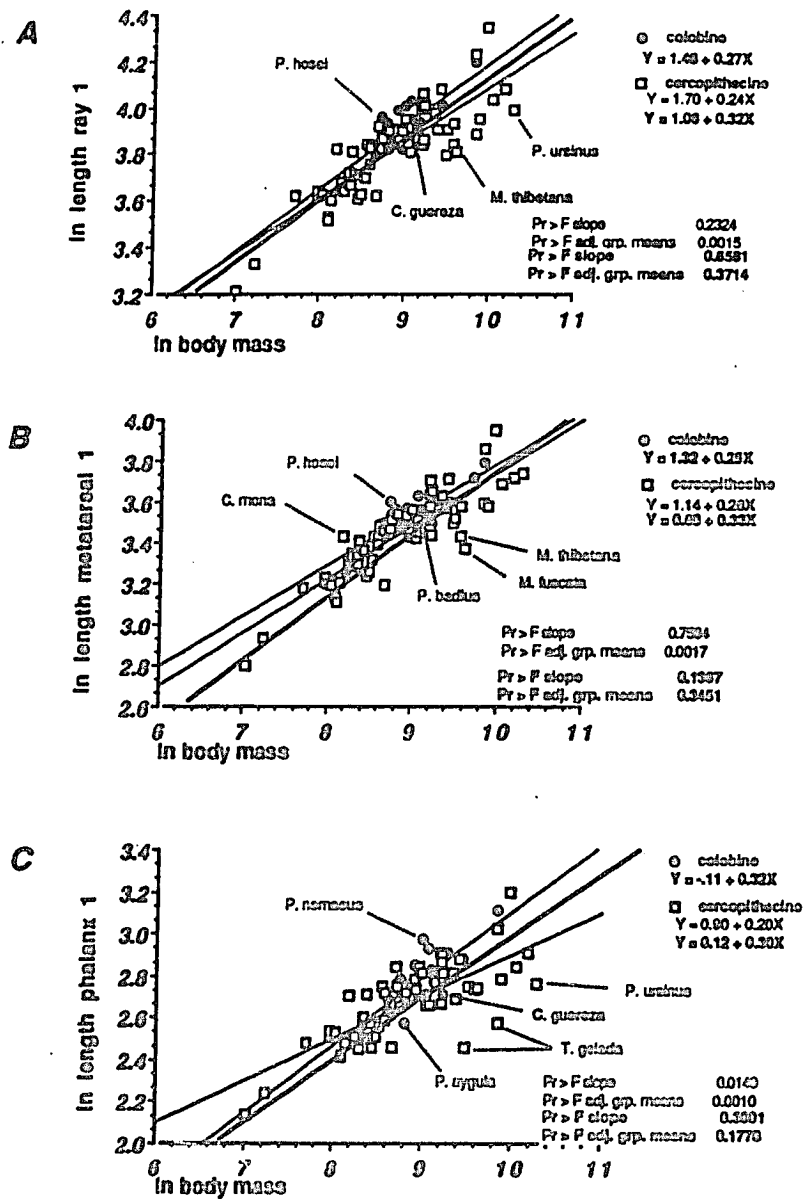


Figure 29. Box-and-whisker plots illustrating the lengths of digit rays 2-5 as a percent of the total sum of the lengths of rays 2-5. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

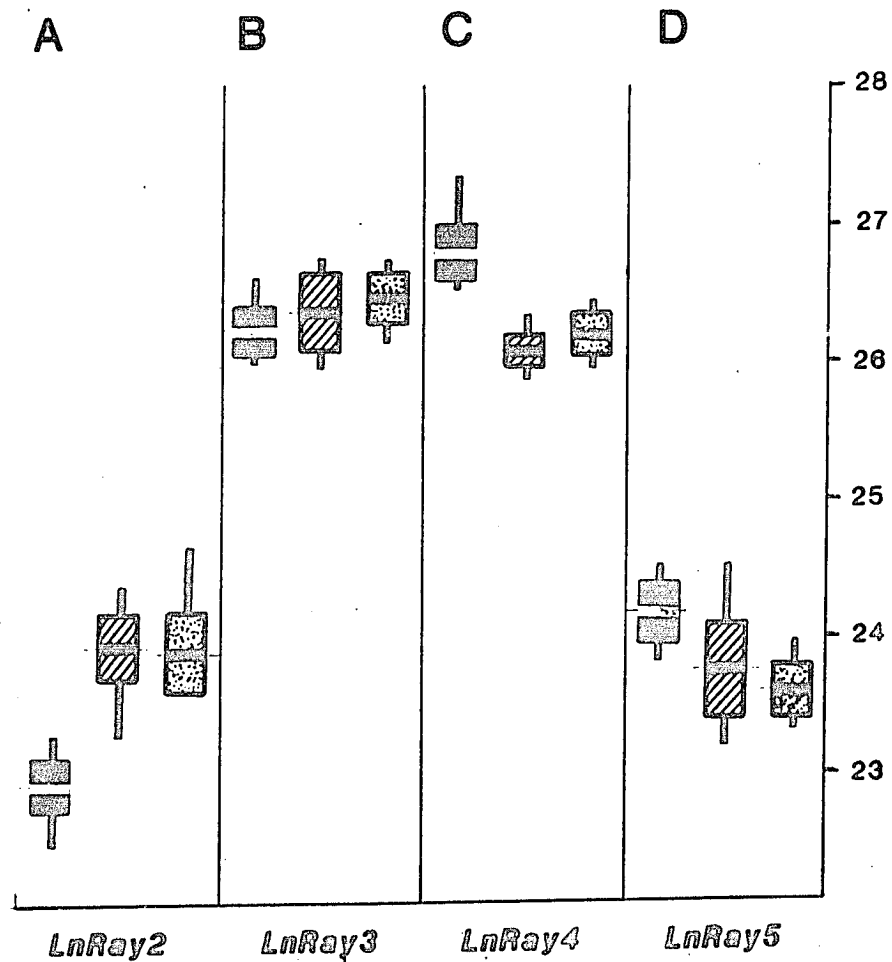


Figure 30. Box-and-whisker plots illustrating the lengths of metatarsals 2-5 as a percent of the total sum of the lengths of metatarsals 2-5. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

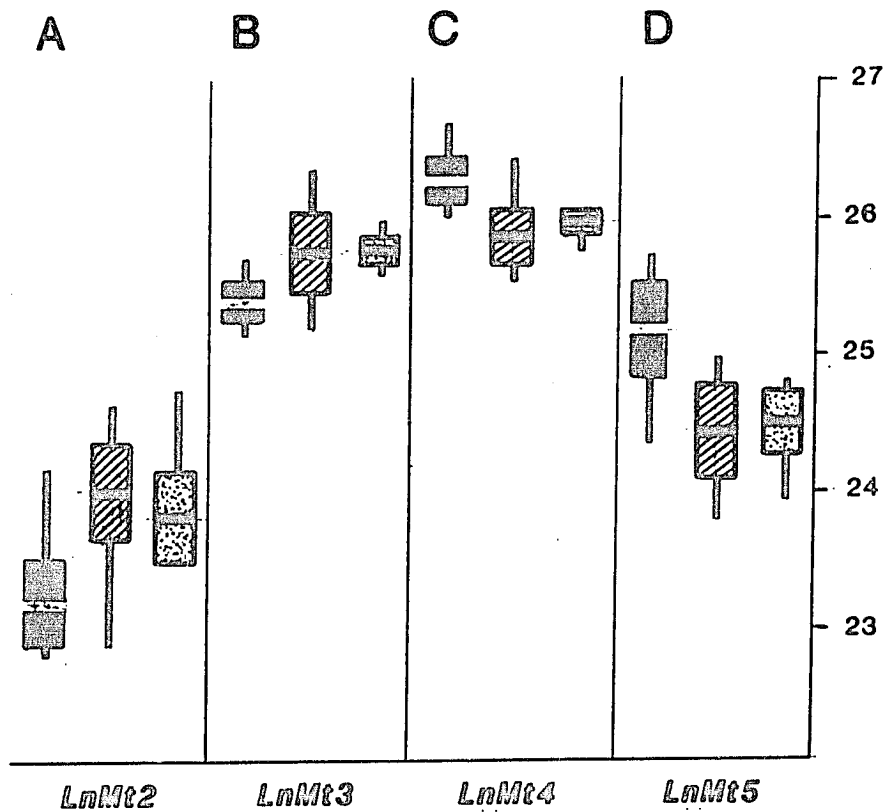


Figure 31. Box-and-whisker plots illustrating the lengths of proximal phalanges 2-5 as a percent of the total sum of the lengths of proximal phalanges 2-5. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

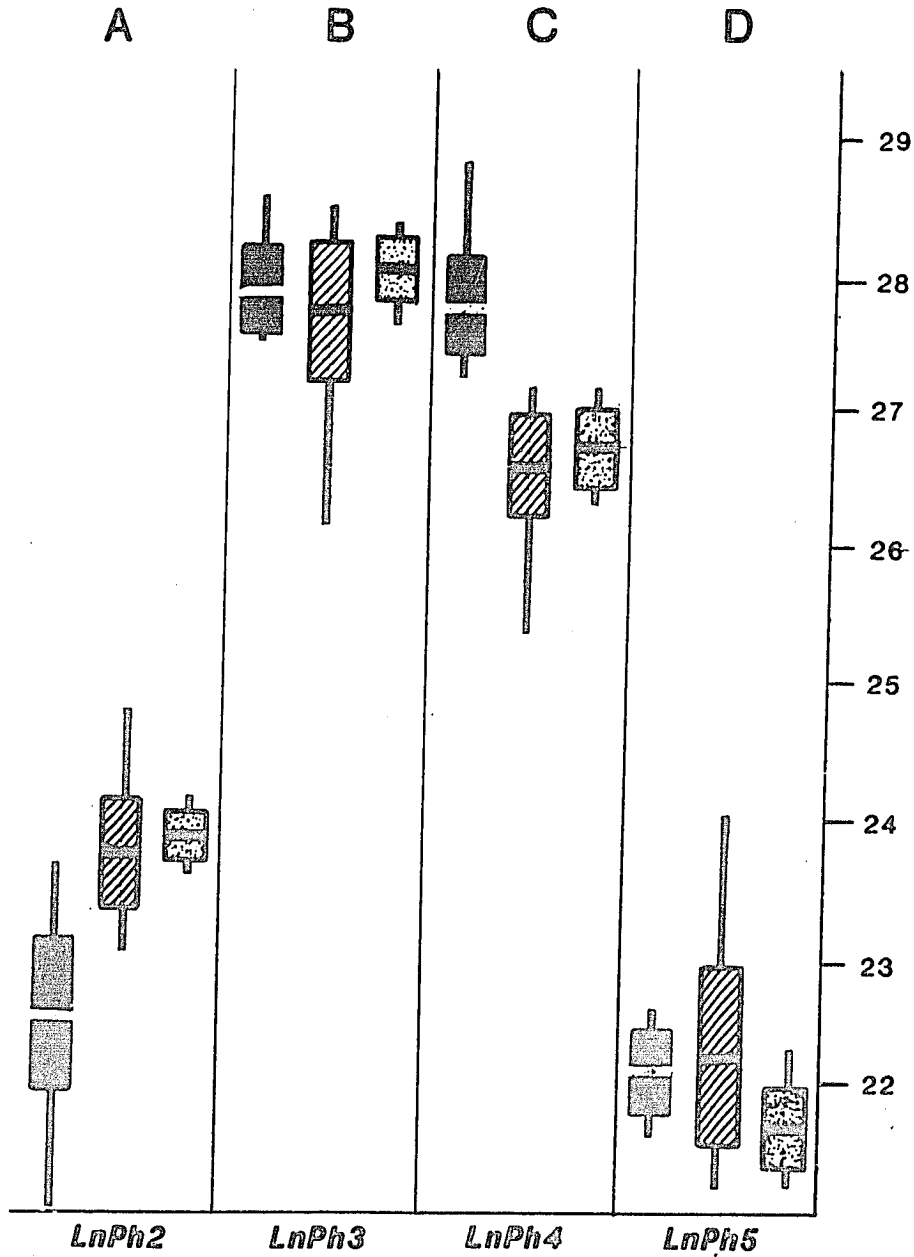


Figure 32. Box-and-whisker plots illustrating the cross-sectional areas of metatarsals 2-5 as a percent of the total sum of the cross-sectional areas of metatarsals 2-5. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.

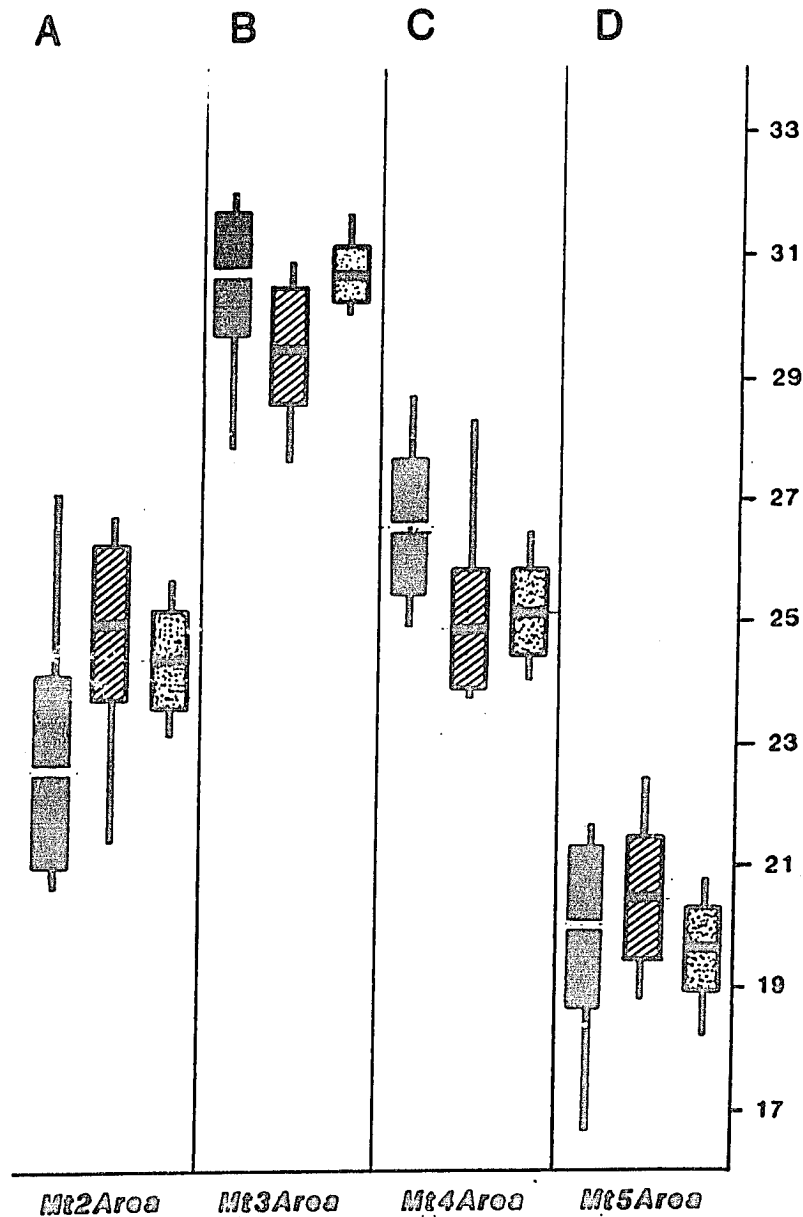
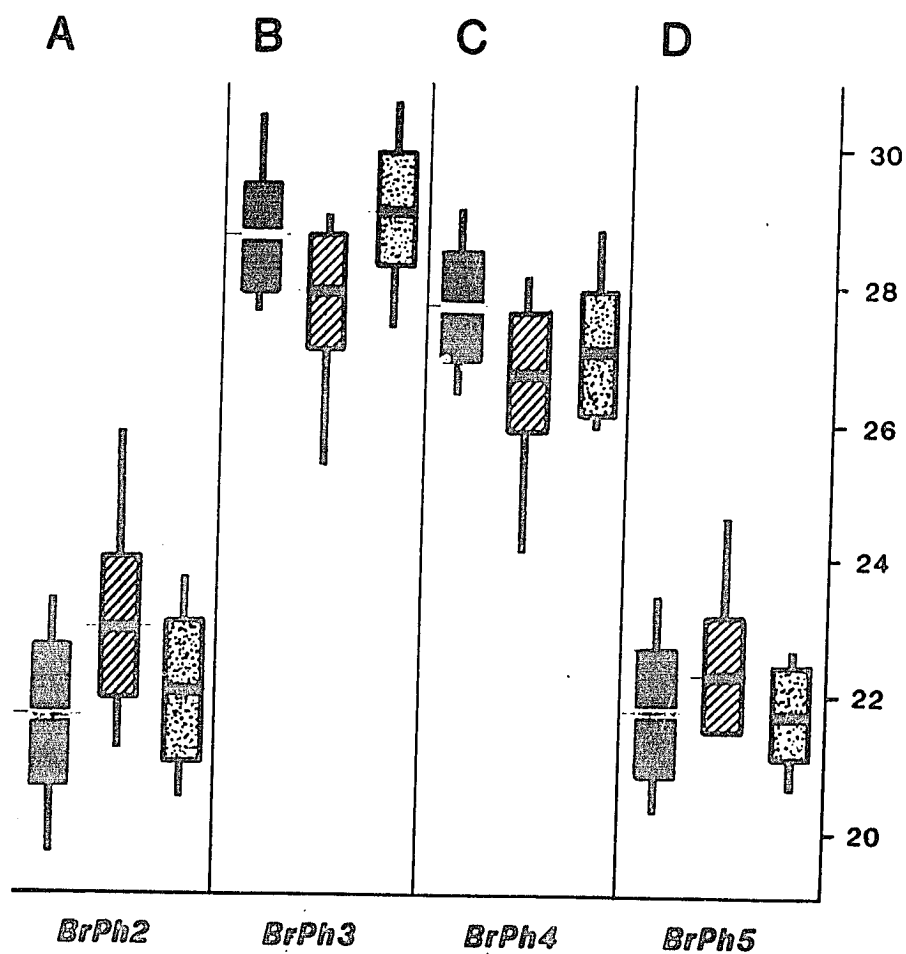


Figure 33. Box-and-whisker plots illustrating the breadths of proximal phalanges 2-5 as a percent of the total sum of the breadths of proximal phalanges 2-5. Horizontal bar, mean. Box, 1 standard deviation to either side of the mean. Vertical line, range. Black, Colobinae. Parallel lines, Papionini. Stippled, Cercopithecini.



Chapter 8. Discussion

Introduction

The major aim of this dissertation was to examine the biomechanical basis for the proportions of the feet in cercopithecids, identified by earlier workers (e.g., Gabis, 1960; Jolly, 1965; Midlo, 1934; Schultz, 1963a,; Washurn, 1942) as distinctive. Some major conclusions of these earlier workers were that (1) the tarsus was relatively long in terrestrial cercopithecids and relatively short in colobines; (2) the metatarsus was invariant in its relative length in cercopithecids; (3) the phalanges were relatively short in terrestrial cercopithecids and relatively long in colobines; and (4) the hallux was relatively short in terrestrial cercopithecines as well as in colobines. The values for the indices presented in the last chapter confirmed the conclusions reached by earlier workers. However, it was also evident that many of the values for indices were a function of body mass. Therefore, when the dimensions which comprised the indices were analysed for their bivariate relationship with body mass, somewhat different conclusions were reached concerning the relative lengths of the pedal segments. Indeed, the main conclusion of the analysis presented in the last chapter is that the most distinctive differences in the proportions of the foot among cercopithecids are the by-product of 3 phenomena: the modifications of the colobine hindlimb for leaping and of their foot for grasping, the assumption of digitigrady in terrestrial cercopithecines and the scaling of lever arms around the knee, ankle and metatarsophalangeal joints. Furthermore, most of the differences among cercopithecids in the propor-

tions of their hindlimb can be summarized by considering four sets of lever arms: (1) the hindlimb as a lever for the body during leaping; (2) the femur and tibia as lever arms around the knee joint; (3) the lever arms of the foot for the plantar flexors of the ankle joint; and (4) the lever arms for the tendon of the long digital flexors. The remaining differences among cercopithecids are a function of: (1) the robusticity of the digits, which is related to the mechanical ability of the digits to withstand compressive and bending stresses; (2) the size of the hallux; and (3) the digit formulas.

Hindlimb as a Lever Arm for the Body during Leaping

It was demonstrated in the last chapter that the hindlimb and all of its major segments were significantly longer in colobines than in cercopithecines of comparable body mass. In Chapter 3 a large body of evidence was summarized which suggested that all colobines leap more than cercopithecines. Chapter 4 presented a summary of the mechanical requirements for leaping as well as of the expected changes in the hindlimb to facilitate leaping. Given the behavioral data and the mechanical model, it is likely that the relatively long hindlimb of colobines is best interpreted as an adaptation to leaping. It would be more convincing that the long hindlimb of colobines, compared to cercopithecines, should be interpreted as an adaptation to leaping if the same distinction in relative hindlimb length were demonstrated for species which were well documented to differ in the amount which they leap.

Such pairs of species exist in colobines, in the form of the well-documented locomotor differences between the Trachypithecus and Presbytis species (Fleagle, 1977a,b, 1978; Davies, 1984) and the likely differences between the Procolobus species (verus, badius) and the Colobus species, which would be due to the different levels of the canopy occupied by these forms. Indeed, for all of these contrasts, an examination of the residual values for the regressions of the dimensions of relevance against body mass revealed that the Trachypithecus and Procolobus species consistently have negative residual values while the Presbytis species and Colobus species tend to have only positive residual values relative to their subfamilial regression lines. In other words, Trachypithecus and Procolobus have shorter hindlimbs than expected for colobines of their body mass, while Presbytis and Colobus have longer hindlimbs than expected for colobines of their body mass. Thus, it seems reasonable to interpret the long hindlimbs of colobines as an adaptation to leaping. Specifically, elongated hindlimbs would increase the distance, and therefore time, over which acceleration is generated, thus leading to a greater take-off velocity for the leap.

Steudel (1981) presented data from the pelvis which are relevant to the discussion here. She found that in a canonical analysis of 17 variables from the pelvis, colobines were consistently and quite distinctively separated from cercopithecines. The separation between species of these two subfamilies was attributed to their differences in two key dimensions: the length of the ischium and the length of the ilium from the acetabulum to the most posterior extension of the auricular surface.

For both of these dimensions, colobines consistently had smaller values than did cercopithecines. Both dimensions represent the lever arms for extensor muscles of the hindlimb. Ischium length is representative of the lever arm for the hamstring muscles, which are powerful extensors of the hindlimb while lower iliac length can be taken as representative of the lever arm for m. gluteus medius, one of the high-gear extensors of the hindlimb. Steudel (1981) discussed the fact that her results were contrary to what one would expect for leapers in the proportions of these lever arms. She also noted that Fleagle (1977a; and Washburn, 1942) found completely opposite results to hers for the length of the ischium: that Presbytis had a relatively longer ischium than did Trachypithecus.

Steudel (1981) presented an interesting argument to interpret her results. She suggested that the reason there might be discrepancy between her results and Fleagle's (1977a) was that the Presbytis species which Fleagle studied engaged in extensive bipedal hopping, a locomotor mode which requires great hamstring power. She suggested that, given published descriptions of leaping in Colobus (Mittermeier and Fleagle's, 1976; Morbeck, 1977; Ripley, 1967; Rose, 1978) it seemed that most leaps followed running take-offs and therefore did not require as much power by the hamstrings to reach take-off velocity. It certainly seems likely that colobines would take advantage of the momentum of flexible substrates or that gained from a running start to achieve their take-off velocity. However, Steudel's distinction between Presbytis and Colobus in their differential emphasis on hopping is strained, given the pub-

lished reports by Morbeck (1976, 1977). Furthermore, hopping, bounding and leaping appear to be parts of a spectrum or continuum of locomotor behavior that are more similar in their reliance on hindlimb propulsion than they are different.

While it would be desirable that both the in-lever and out-lever arms be considered together to make a convincing case for the relative reduction or elongation of any one lever arm, it seems reasonable here to interpret the elongated hindlimb in colobines as an adaptation to leaping.

Lever Arms of the Knee Joint

It was seen in the last chapter that the crural index had a negative correlation with body mass. The reason that this index was negatively correlated with body mass was that tibia length had a negative allometric relationship with body mass while femur length had an isometric relationship with body mass. Aiello (1981) and Jungers (1985) also reported that the crural index decreased with an increase in body mass in cercopithecids and for the same allometric reasons.

A decrease in the crural index would be expected with increased body mass no matter what the predominant locomotor mode of an animal. This expectation is a simple consequence of the scaling relationships of muscle cross-sectional area and bone lengths. As body size increases, the relative strength of the muscles which stabilize the knee during terrestrial or arboreal pronograde quadrupedalism, and which produce force at the foothold during climbing, decrease. The tibia is the out-

lever arm for the thigh muscles which stabilize the knee and for the adductor muscles of importance in climbing. Thus, in order to maintain mechanical similarity with smaller-bodied forms, larger animals must decrease the relative length of the tibia. Because of the mechanical constraints of size on the proportions of the hindlimb long bones, the values for other indices (besides the crural index) which include the lengths of these bones, will be influenced by the absolute body size of the species.

It was seen in Chapter 3 that T. gelada and E. patas are among the most terrestrially adapted cercopithecine species. Furthermore, E. patas is certainly the most cursorially adapted cercopithecine, if not cercopithecine. In Chapter 4 one of the factors which was described as possibly being emphasized to enhance cursorial locomotion was elongation of the distal limb elements relative to the proximal elements. For the crural index, this would be expressed as a high value for a particular body size.

Both sexes of Theropithecus gelada and the males of Erythrocebus patas had high values for the crural index describing the relative length of the tibia. Examination of their residual values from the cercopithecine regression lines which described the scaling of tibia and femur length against body mass, shows that the underlying basis for the high crural indices in these variates is not the same. Male E. patas had a rather long tibia for its body mass, giving rise to a high crural index, whereas T. gelada has a rather short femur for its body size, and therefore a high crural index. An especially high crural index would be

expected in animals adapted to terrestrial cursoriality, since a relatively elongated tibia serves to increase stride length and therefore contributes directly to an increase in speed.

Lever Arms for Triceps Surae

The two lever arms of the triceps surae muscle correspond directly to the the lengths of the foot, excluding the phalanges, proximal and distal to the proximal astragalocalcaneal joint. Schultz (1963a,b) pointed out that all cercopithecids had a high value for this index compared to other primates, except gorillas and humans, but saw no differences among his small sample of cercopithecids. It was seen in the last chapter, however, that there was variation in this index in cercopithecids and that the power arm/load arm ratio had a positive relationship with body size, as would be theoretically expected if mechanical similarity were being maintained across body sizes. The regression analysis of the lever arms against body mass indicated that the power arm had a positive allometric relationship with body mass while the load arm, and in particular the calcaneal and metatarsal portions of the load arm, had a negative allometric relationship with body mass. Given these scaling relationships, large animals would have a longer tarsus and shorter metatarsus than would small animals. This suggests then, that the reason terrestrial cercopithecines have a long tarsus, as observed by Gabis (1960) and Schultz (1963a,b), is that these species are also large. Thus, their unique pedal segment proportions are, in part, simply a consequence of the scaling of the lever arms for triceps surae in

order to maintain mechanical similarity.

It was also seen in the last chapter that, on average, colobines had a lower power arm/load arm ratio than did cercopithecines at comparable body masses. The reason that colobines had a lower average index than did cercopithecines at comparable body masses was that the two subfamilies did not differ in their adjusted group means for the regressions of the power arm, or calcaneal load arm, on mass, but colobines had a significantly longer third metatarsal, and therefore load arm, than did cercopithecines.

It was discussed in Chapter 4 that a leaper would be expected to have a longer power arms than cursors or arboreal quadrupeds around joints at which there is a great deal of rotation and which are important in propulsion. This is patently not the case for the comparison of the foot's power arm among cercopithecids. The likely explanation for this is twofold. First, the range of movement is not that great at the ankle joint compared to, for example, the hip joint. Secondly, most of the body is in motion during the take-off of a leap by the time the plantarflexors of the ankle provide the final propulsive push against the ground. As a consequence, their role in providing force for leaping is minimal. Therefore, it is not theoretically necessary that colobines would have a longer power arm for the triceps surae than would cercopithecines.

However, it was also pointed out in Chapter 4 that Demes and Günther (1989) predicted that large bodied leapers would have short distal extremities. The evidence of the power arm/load arm ratio in

colobines suggests that elongation of the forefoot is taking place rather than shortening, contra the expectations of Demes and Günther (1989). It is likely that elongation of the forefoot in colobines is part of the general elongation of the whole hindlimb, to optimize the distance over which acceleration is generated. On the other hand, the elongated forefoot of colobines could well be related to dissipating the forces at the end of a leap, as opposed to generating forces at the take-off of a leap. Whichever part of the leap forefoot elongation is related to, it is most likely that it is associated with leaping rather than some other aspect of colobine locomotor behavior as suggested by the contrast between the Trachypithecus and Presbytis species. In the scaling of all the relevant dimensions, the more quadrupedal Trachypithecus species consistently had much lower residual values than did the frequently leaping Presbytis species. The same contrast, albeit not so strongly, can be seen between the Procolobus species (verus, badius) compared to the Colobus species.

Erythrocebus patas had a higher power arm/load arm ratio than was expected for its body size. This clearly is not expected in a cursor, which is expected to have shorter power arms and longer load arms around joints at which there is a great deal of motion. Using a similar argument as that presented above for colobines, it is likely that the range of motion around the patas' ankle joint is limited. Furthermore, details not given in this dissertation, of the shape of the calcaneal tuber and carrying angle of the distal calcaneus, suggest that the ankle is not dorsiflexed to the extent seen in arboreal forms. In other words, a

digitigrade posture is likely to be assumed more often than a plantigrade posture in E. patas. The elongation of the power arm may simply be related to the tendency in E. patas to elongate the complete distal part of the hindlimb. This is also suggested by the fact that along with elongation of the tibia, as was seen above, both the calcaneal and cuboid elements of the tarsus are much longer than expected given the body size of E. patas.

Lever Arms for the Tendon of the Long Digital Flexors

In Chapter 4 the length of the phalanges was interpreted as the lever arm for the reaction force met with by the plantar pads and which is resisted by the moment arm of the long digital flexors. It was also shown in that chapter that an assumption of digitigrady contributed to elongation of the hindlimb in cursors, but also led to shortening the length of the phalanges in response to the greater reaction force at the digital pads. Thus, cursorial animals are expected to have relatively shorter phalanges for their body mass than do arboreal forms. Furthermore, no matter what the locomotor mode of cercopithecids, as long as they are holding the foot in compression rather than tension (as in suspensory forms), it is expected that as animals increase in body size there will be a concomitant decrease in the length of the phalanges, to maintain mechanical similarity across the range of body sizes.

The bivariate plot and regression of the third proximal phalanx length to body mass indicated that, as expected, the third proximal phalanx had a negative allometric relationship with body mass. Thus,

larger species had relatively shorter phalanges than did shorter species. Furthermore, the Papio species, E. patas and especially T. gelada had a shorter phalanx than expected for their body sizes. However, with the exception of T. gelada, none of the terrestrial species fell below the lower 95% confidence limit of either the original or modified LS lines, the latter estimated with the arboreal species only. Nevertheless, the terrestrial cercopithecines are consistent in having shorter phalanges than expected for their body sizes, given the negative allometry seen in arboreal forms. This suggests then, that based on the biomechanical relationships summarized above for enhancing speed in cursorial locomotion, terrestrial cercopithecines are assuming a more digitigrade posture of the foot when walking. As a consequence, due to the increased load on the digital pads of their phalanges, the phalanges are even shorter than expected for their body size in order to resist the large reaction force.

Theropithecus gelada has extremely short phalanges given its body weight and given the amount of shortening seen in other terrestrial cercopithecines. The likely explanation for this is that T. gelada is significantly more terrestrially adapted than are the Papio species or E. patas. The literature summarized in Chapter 3 on positional behavior indicated that all of the Papio species (with the exception of some populations of P. ursinus) and E. patas utilize trees to sleep, escape predators and feed. Only T. gelada exclusively occupied the ground, seeking cliff-faces for sleep. Furthermore, the Simopithecus proximal phalanges from Olduvai Bed II and Olororgesailie have equivalently propor-

tioned phalanges, judging from Figure 15 in Jolly (1972). Since the Olororgesailie Simopithecus was probably the size of a female gorilla, it is very unlikely that it could have maneuvered branch-walking with such short digits (Jolly, 1972). This suggests that Theropithecus has a long history of terrestrial life.

Two points are clear from the foregoing. The first is that along with the scaling effects of the power arm/load arm ratio contributing to terrestrial cercopithecines having a relatively longer tarsus than arboreal cercopithecines, the very short phalanges of terrestrial cercopithecines, which are indeed related to their terrestriality, also contributed to the tarsus appearing to be longer. The second point is that both Gabis (1960) and Schultz (1963a,b) reported that the third metatarsal was invariant in length among cercopithecoids, but this has been demonstrated to be untrue. The third metatarsal only appears invariant because of the allometric scaling of the power arm/load arm and the allometric scaling of the phalanges.

Colobines were identified by Gabis (1960) and Schultz (1963a,b) as having long proximal third phalanges relative to the length of the foot and relative to the length of the third metatarsal. In the last chapter, the most clear and dramatic separation of the subfamilies was seen in the bivariate plot and regression of the third proximal phalanx length against body mass. There was hardly any overlap among the variates of the two subfamilies and the adjusted group means were, of course, significantly different. Thus, at comparable body masses colobines had much longer proximal phalanges than did cercopithecines. Because the separa-

tion between the subfamilies was much stronger for phalangeal length than metatarsal length, the indices describing the length of the phalanx relative to the metatarsus clearly separated the two subfamilies.

The elongated colobine phalanges are probably related to their importance in grasping. There has been no study focusing on pedal grasping in cercopithecids. However, the relatively small size of the hallux in all cercopithecids compared to other primates (Midlo, 1934) suggests that the hallux grip is not so important in cercopithecids. That colobines have emphasized the phalanges as much as they have suggests that some form of grasping is important to them.

Digital Robusticity

Another set of comparisons, explicable in mechanical terms, serve to distinguish colobines from cercopithecines. These involve the robusticity of the metatarsals and phalanges. The bivariate plots of phalangeal length against cross-sectional breadth indicated that colobines had relatively more slender phalanges than did cercopithecines. It was also seen that the Papio species, M. thibetana, M. fuscata, E. patas and especially T. gelada had more robust phalanges than did the other cercopithecines. It was already discussed above that colobines have longer phalanges at comparable body sizes to cercopithecines. In addition, there was no difference in adjusted group means between colobines and cercopithecines for phalangeal breadth. As a consequence, the slender phalanges of colobines are due to their great length and not as a result of a difference in breadth relative to cercopithecines. Mechanically,

slender phalanges are less able to resist bending stresses than are the more robust phalanges of arboreal cercopithecines. This suggests, then, that the phalanges of colobines are subject primarily to tensile stress, which is additional evidence for the importance of grasping in colobines. At the other extreme, the terrestrial baboons and patas monkey have hyper-robust phalanges, primarily as a consequence of their short phalanges. However, in the case of T. gelada, the robust phalanges are also due to their being relatively broad for T. gelada's body mass.

Colobines not only have longer metatarsals than cercopithecines but also have larger cross-sectional areas at comparable body masses. Thus, while the colobine metatarsals appear slender, this is primarily a consequence of their great length. What is obscured by their appearance is the fact that the metatarsals, at least the third (and certainly the fourth as well) is relatively larger in its cross-sectional dimension, suggesting that at comparable body sizes, colobines are experiencing more stress, bending and compressive, through their metatarsals than do cercopithecines. This is probably related to the posture of the foot during leaping.

Hallux

All the indices which described the relative length of the hallux (ray1/foot, ray1/sole, ray1/ray3, ray1/mt3) indicated that T. gelada and E. patas had a reduced hallux. In E. patas the apparently relatively small hallux is due to both an elongated sole (including the tarsus and metatarsus) relative to body mass in combination with a short hallux

(including both the metatarsal and proximal phalanx) relative to body mass, as also noted by Jolly (1965). In T. gelada the hallux is indeed very reduced relative to body mass so that no matter what its residual values for the denominators of the indices, its hallux appears reduced. The short hallux is especially due to a reduced hallucal phalanx, although the metatarsal is also shorter than expected for T. gelada's body mass. However, because the phalanx is so short in T. gelada, T. gelada is the only variate to be highlighted in the bivariate plot of $ph1/mt1$ length on body mass. The Papio species and M. thibetana also had short halluces relative to sole length, but in none of these cases was the difference so great as in T. gelada or E. patas. Finally, the colobines had a short proximal hallucal phalanx relative to the third phalanx, but this was due to the great length of their third phalanx relative to body size rather than to a short hallucal phalanx relative to body size.

Formulas

Another line of evidence which suggests that colobines may be experiencing more stress along their central metatarsals is provided by the digit formulas. It was demonstrated in the last chapter that colobines are easily distinguished from cercopithecines (as noted by Washburn, 1942) by their digit formulas. The central digits project far distad to the flanking digits and are considerably more robust than their neighbors. The fifth digit is relatively longer and better developed than the second, which is quite diminutive in size relative to the fifth. It seems clear that the reduction in the length of the second digit is not

consequence of reduction in the size of the medial digits, since colobines and cercopithecines do not differ in this regard. It may well be related to a lateral shift in the weight-bearing axis of the foot in colobines, as evidenced by the "artiodactyle" condition of their central rays and relatively well developed fifth ray.

Without field observations to direct a line of biomechanical reasoning it is difficult to imagine how colobines are using their digits and why their use should lead to such striking differences from cercopithecines in their formulas. Furthermore, without field observations it is impossible to explain the documented similarities between Papio and C. albigena to colobines in their length formulas.

Exceptional Species

Three species were not discussed above, since their differences were not relevant to the contrasts historically made among cercopithecids. These species are M. thibetana, M. fuscata and S. entellus. The two macaques are noteworthy for having very short hindlimbs relative to their body masses. The extreme shortening is reflected in a large number of elements of the hindlimb but for the phalanges. In M. fuscata every single bone but for the phalanges is affected, whereas in M. thibetana the tarsals are also excluded. Little is known about M. thibetana's locomotor behavior but M. fuscata appears to be a typical macaque, as adept in the trees as on the ground. The one feature these two species have in common is their northerly distribution, suggesting then, that the phenomenon expressed in the scaling of their limbs accords with

Allen's Rule.

Semnopithecus entellus has been documented as the the most terrestrial of the colobines included in this study. It is intriguing that this species is similar to E. patas in having rather long tarsal elements for its body size, including the length of its pedal power arm. Semnopithecus entellus is also similar to E. patas in having large residual value for the cross-sectional area of the third metatarsal. This suggests that considerable stresses are being passed through the forefoot, as when the foot is held in a digitigrade fashion. Semnopithecus entellus is probably the best colobine with which to test the ubiquity of traits associated with terrestriality. Unfortunately, no phalangeal elements were available for the S. entellus sample included in this study.

The smallest species of each taxon, P. verus, M. talapoin and M. fascicularis quite often had very low residual values for the regressions of dimensions on body size. In all of these cases no clear pattern consistent with what is known about their locomotion emerged. Instead, it seems not uncommon that the smallest members of most lineages tend to assume the position that they did relative to the regression lines. This may reflect some non-apparent biological reality explicable in biomechanical terms, or may simply be due to their outlying positions relative to the empirically determined LS regression lines. The latter explanation seems more reasonable at this time and they will not be discussed any further.

Summary

It is clear that in a sample of cercopithecids, which range in body mass from 1.3 kg to 29 kg, the dimensions of the major segments of the hindlimb and foot scale with body mass to maintain mechanical similarity. Thus, the first major conclusion of this study is that indices which describe the relative lengths of lever arms around the knee joint, talocrural joint and metatarsophalangeal joint all decrease with an increase in body mass. The effect of this scaling has been to cause the majority of indices which traditionally have been used to describe the relative lengths of morphological segments to reveal differences that were primarily a function of the size of the animals. Indeed, the traditional focus on morphological and not functional units has obscured the true implications of some significant mechanical differences in the hindlimbs of cercopithecids. The second conclusion of this study is that the terrestrial cercopithecines indeed have a significant adaptation to their locomotor lifestyle, and that is the assumption of digitigrady to increase the length of the hindlimb. The obvious consequence of digitigrady is the reduction in the length of the phalanges. In the Papio species no other dimension of the foot and hindlimb, studied in this dissertation, revealed a special adaptation to terrestrial cursoriality. Theropithecus and E. patas, however, do present one other adaptation to cursoriality - a high crural index which, in addition to digitigrady, contributes to greater stride length and therefore speed of motion. Thus, all terrestrial cercopithecines share digitigrady and only Theropithecus and Erythrocebus add a high crural

index to their list of adaptations. This suggests, then, that Theropithecus and Erythrocebus are more committed to cursoriality than are the Papio species.

The third major conclusion revealed by the analysis of mechanically meaningful, as opposed to morphological, segments of the hindlimb and foot was that colobines have elongated the hindlimb, including the foot, to enhance leaping. In addition to elongating the hindlimb, colobines are characterized by a distinctive pseudo-artiodactyle condition of the digits as well as extremely elongated phalanges. These latter features suggest that colobines are grasping the substrate in a manner quite different from arboreal cercopithecines. Without field observations it is impossible to suggest how the colobine grasp would differ from the cercopithecine, but the specialized nature of the digits does suggest the sort of observations which should be made in the field.

The fourth conclusion reached in this study is that thermal conditions can have as profound an effect on the lengths of the segments of the hindlimb, relative to body mass, as do adaptations to particular locomotor modes. This conclusion was suggested by the dramatically shortened long bones and foot bones of M. fuscata and M. thibetana, two of the most northerly distributed species in the family. It is of interest that the only bones not affected by cold were the phalanges, suggesting the importance of grasping in the poorly documented positional repertoire of these animals.

In summary, significant differences exist among cercopithecids which are due to fundamental differences in locomotion. Research

strategies must be directed at analyzing mechanically meaningful aspects of the postcranium. Strategies which provide only descriptive characterizations of the morphology, such as those traditionally used to describe differences in the feet among cercopithecids, will not enhance our ability to unravel and explain the evolutionary biology and history of organisms, but will delay it.

APPENDIX 1.

Cercopithecoid specimens used in this study. Under each species name is the museum number, sex, age and locality. [sex] indicates that the sexual designation was inferred as discussed in text.

Cercopithecus pygerythrus cynosurus

TER 22087 M A ?Zaire: Kakanda

TER 11482 M A ?Zaire: Kanzenze

Cercopithecus pygerythrus johnstoni

TER 4023 F A BEA: Kerio River

TER 2152 M A BEA: Lume River

TER 2149 F A BEA: Lume River

KNN OM 3040 F A Kenya: Thomson's Falls

Cercopithecus pygerythrus pygerythrus

NMNH 351934 M A S. Africa: Natal

NMNH 469905 M A S. Africa: Cape Province

NMNH 351933 F A S. Africa: Natal

NMS 59 202 M YA N. Tanzania: Nahe Arusha

NMS 59 210 M OA N. Tanzania: Nahe Arusha

NMS 59 206 F A N. Tanzania: Nahe Arusha

NMS 59 203 M A N. Tanzania: Nahe Arusha

NMS 59 218 M A N. Tanzania: Nahe Arusha

NMS 59 207 F A N. Tanzania: Nahe Arusha

UWNT 000280 M OA Uganda

UWNT 000270 M A Uganda: Bukerere

UWNT 00134b M A Uganda: Bukerere

UWNT 000137 M A Uganda: Bukerere

UWNT 000138 F A Uganda: Bukerere

UWNT 000223 M VO Uganda: Kome Island

UWNT 000246 F YA Uganda: Gonba

UWNT 000265 F A Uganda: Gonba

UWNT 000233 F YA Uganda: Kiunu

KNN OM 3038 F OA Kenya: Makuna

KNN OM 3034 M A Kenya: Elementaita

KNN OM 3020 F A Kenya: Sukari Ranch Ruiru

Cercopithecus ascanius schmidtii

UWNT 000144 F - Uganda

UWNT 000052 F OA Uganda: Buto Forest

UWNT 000013 M A Uganda: Buto Forest

UWNT 000059 M YA Uganda: Buto Forest

UWNT 000021 F OA Uganda: Buto Forest

UWNT 000210 F OA Uganda: Masaka Road, 10 mi from Kampala

UWNT 000203 F A Uganda: Nabira Forest

UWNT 000174 M OA Uganda: Nabira Forest

UWNT 000093 M YA Uganda: Namagunga

UVHT 000102	H	A	Uganda: Kila
UVHT 000196	H	A	Uganda: Nanasuba
UVHT 000127	H	A	Uganda: Bukerere
UVHT 000141	F	YA	Uganda: Bukerere
UVHT 000128	F	YA	Uganda: Bukerere
UVHT 000122	H	YA	Uganda: Gonba
UVHT 000242	H	A	Uganda: Gonba
UVHT 000120	F	YA	Uganda: Gonba
UVHT 000220	F	YA	Uganda: Gonba
UVHT 000130	F	A	Uganda: Gonba
UVHT 000263	H	A	Uganda: Gonba
Cercopithecus cephus			
RHHH Cce a	H	A	Congo
AIUZ 1846	H	A	Caneroon
Cercopithecus cephus cephodes			
RHHH 1520	F	A	Gabon
RHHH 218470	H	A	Gabon: Fernan Vaz Ashanja
Cercopithecus cephus cephus			
PCN Herfield 753	F	A	Caneroon: Batouri Dist.
PCN Herfield 754	F	A	Caneroon: Batouri Dist.
PCN Herfield 94	H	A	Caneroon: Batouri Dist.. Lunbindu
PCN Herfield 381	H	A	Caneroon: Batouri Dist.. Meyoss
PCN Herfield 383	H	A	Caneroon: Batouri Dist.. Meyoss
PCN Herfield 411	H	A	Caneroon: Batouri Dist.. Meyoss
PCN Herfield 426	F	A	Caneroon: Batouri Dist.. Meyoss
PCN Herfield 213	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 618	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 659	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 688	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 794	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 872	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 878	H	A	Caneroon: Batouri Dist.. Obala
PCN CAN II 360	H	A	Caneroon: Batouri Dist.. Lelo
PCN Herfield 561	H	A	Caneroon: Batouri Dist.. Lelo
PCN CAN II 371	H	A	Caneroon: Batouri Dist.. Beri
Cercopithecus petaurista			
RHHH 429480	F	-	Togo: Ezine
RHHH 477318	F	OA	Ivory Coast: Kéhin
Cercopithecus petaurista buettikoferi			
RHHH Cpb a	H	YA	Liberia: Fisherman Lake, Bendo
GOT A 574	F	YA	Liberia: Central Province, Bia (Kran)
GOT F 2572	F	-	Liberia: NLC Camp, Ribe Gbe
Cercopithecus campbelli			
RHHH Cc a	H	OA	Liberia: Sofore Place, A Paul's River
RHHH Cc a	F	A	Liberia: Sofore Place, A Paul's River

<i>Cercopithecus campbelli campbelli</i>			
Got no nua	M	YA	Liberia
NNNN 481767	F	A	Liberia: Grand Gedeh Co.
<i>Cercopithecus nona</i>			
NNNN 481007	F	A	Caneroon: Kunha Division
PCN Herfield 25	H	A	Caneroon: Yabassi Dist.
PCN Herfield 67	H	OA	Caneroon: Yabassi Dist.
PCN Herfield 94	H	A	Caneroon: Yabassi Dist.
PCN Herfield 109	H	A	Caneroon: Yabassi Dist.
BN 1938.7.7.8	H	A	Caneroon: Yabassi Dist.. Nkan River
BN 1938.7.7.9	H	A	Caneroon: Yabassi Dist.. Nkan River
BN 1948.463	F	A	Caneroon: Namfe Division
BN 1948.475	H	A	Caneroon: Namfe Division. Tinta. Assunbo
BN 1948.479	H	YA	Caneroon: Namfe Division. Mainyu Bridge
BN 1948.481	M	A	Caneroon: Namfe Division. Mainyu Bridge
BN 1948.480	M	YA	Caneroon: Namfe Division. Mainyu Bridge
BN 1948.469	H	YA	Caneroon: Namfe Division. Bashauo
<i>Cercopithecus pogonias grayi</i>			
PCN Herfield 82	H	YA	Caneroon: Ybassi Dist.
PCN Herfield 88	F	OA	Caneroon: Ybassi Dist.
PCN Herfield 159	H	A	Caneroon: Ybassi Dist.
PCN Herfield 769	H	A	Caneroon: Batouri Dist.
PCN CAN II 317	H	A	Caneroon: Batouri Dist.. Beri
PCN Herfield 90	H	A	Caneroon: Batouri Dist.. Lunbinan
PCN Herfield 152	F	A	Caneroon: Batouri Dist.. Kanyol
PCN Herfield 277	F	A	Caneroon: Batouri Dist.. Kanyol
PCN Herfield 297	H	A	Caneroon: Batouri Dist.. Heyoss
PCN Herfield 303	H	YA	Caneroon: Batouri Dist.. Heyoss
PCN Herfield 344	H	A	Caneroon: Batouri Dist.. Heyoss
PCN Herfield 347	F	YA	Caneroon: Batouri Dist.. Heyoss
PCN Herfield 383	H	A	Caneroon: Batouri Dist.. Heyoss
PCN Herfield 306	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 654	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 660	F	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 908	H	A	Caneroon: Batouri Dist.. Obala
PCN Herfield 931	H	YA	Caneroon: Batouri Dist.. Obala
<i>Cercopithecus albogularis albogularis</i>			
NNNN 1342	F	OA	Dutch East Africa
ZHUC 654	H	A	Kenya. 40 mi S of Mombasa
KUH OH 4231	F	VO	Tigoni Primate Research Center
KUH OH 6619	F	A	Tigoni Primate Research Center
<i>Cercopithecus albogularis erythrarchus</i>			
NNNN 425430	H	OA	Rhodesia: Manicaland, Chirindi Forest
NNNN 425432	F	OA	Rhodesia: Manicaland, Chirindi Forest
NNNN 470262	H	OA	Rhodesia: Manicaland, Ngorina Reserve

<i>Cercopithecus albogularis kibonotensis</i>			
NNNN 018928	(H)	A	Kenya: Tabeta
TER 2140	F	A	BEA: Lune River
TER 2141	H	A	BEA: Lune River
<i>Cercopithecus albogularis kolbi</i>			
NNNN 452586	H	VO	Kenya: N Kinangap
NNNN 452587	H	A	Kenya: N Kinangap
PHNN 035129	(F)	(A)	Kenya: Tana River
BH 1972.59	H	OA	Kenya: Aberdare Mts., N. Kinangop
BH 1972.65	H	A	Kenya: Aberdare Mts., N. Kinangop
BH 1972.62	F	YA	Kenya: Aberdare Mts., N. Kinangop
BH 1972.66	F	OA	Kenya: Aberdare Mts., N. Kinangop
BH 1972.58	F	YA	Kenya: Uplands Forest Station
KNN OM 2869	F	A	Kenya: Thomson's Falls
KNN OM 6620	F	A	Kenya: Tigoni Primate Research Center
<i>Cercopithecus mitis stuhlmanni</i>			
NNNN 452550	F	A	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452556	F	VO	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452553	H	OA	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452554	F	YA	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452552	F	YA	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452557	F	VO	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452559	F	VO	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452551	H	YA	Kenya: Kaptagat, Vasin Gishu Dist.
BH 1972.81	F	A	Kenya: Kaptagat, Vasin Gishu Dist.
BH 1972.82	H	VO	Kenya: Kaptagat, Vasin Gishu Dist.
BH 1972.83	F	A	Kenya: Kaptagat, Vasin Gishu Dist.
BH 1972.86	F	YA	Kenya: Kaptagat, Vasin Gishu Dist.
NNNN 452549	F	VO	Kenya: Kaptagat, Tigoni Primate Res. Center
NNNN 052368	H	A	Zaire: Akenge
NNNN 052402	H	A	Zaire: Niapu
NNNN 052410	F	A	Zaire: Niapu
NNNN 052413	H	A	Zaire: Niapu
NNNN 052401	H	A	Zaire: Hedje
NNNN 052398	H	A	Zaire: Hedje
TER 5994	F	A	Zaire: NE Uele
<i>Cercopithecus nictitans</i>			
PCH Fr. Congo 144	H	OA	French Congo: Keba
PCH Herfield 433	H	OA	Cameroon: Batouri Dist., Kanyol
PCH Herfield 305	H	A	Cameroon: Batouri Dist., Meyoss
PCH Herfield 336	H	OA	Cameroon: Batouri Dist., Meyoss
PCH Herfield 378	H	A	Cameroon: Batouri Dist., Meyoss
PCH Herfield 990	F	A	Cameroon: Batouri Dist., Meyoss
PCH Herfield 999	H	A	Cameroon: Batouri Dist., Meyoss
PCH Herfield 232	H	OA	Cameroon: Batouri Dist., Obala
PCH Herfield 410	F	YA	Cameroon: Batouri Dist., Obala

PCN Herfield 625	H	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 645	H	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 680	H	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 691	F	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 792	F	YA	Cameroon: Batouri Dist.. Obala
PCN Herfield 793	F	OA	Cameroon: Batouri Dist.. Obala
PCN Herfield 832	H	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 836	H	A	Cameroon: Batouri Dist.. Obala
PCN Herfield 904	E	OA	Cameroon: Batouri Dist.. Obala
PCN Herfield 906	H	OA	Cameroon: Batouri Dist.. Obala
<i>Hiopithecus talapoin</i>			
BN 1977.861	F	YA	W. Africa
BN 1977.867	F	A	W. Africa
AIUZ 7572	H	A	Rio Muni
AIUZ 7676	H	A	Rio Muni
AIUZ 7674	F	A	Rio Muni
AIUZ 7602	H	A	Rio Muni
AIUZ 7632	F	A	Rio Muni
AIUZ 7613	F	A	Rio Muni
AIUZ 7612	F	YA	Rio Muni
NNHH 399	H	A	Gabon
PCN Herfield 665	F	-	no info
<i>Erythrocebus patas</i>			
KHN OH 4284	F	A	Kenya: Tigoni Primate Research Center
KHN OH 5093	H	A	no info
<i>Erythrocebus patas pyrrhonotus</i>			
NNHH 34709	F	A	Kenya: Wasin Gishu District
NNHH 34712	H	A	Kenya: Wasin Gishu District
NNHH 34713	H	YA	Kenya: Wasin Gishu District
NNHH 34714	H	OA	Kenya: Wasin Gishu District
<i>Macaca arctoides</i>			
FMHH 105683	H	A	Thailand: Trang Province; Ban Palian
BN 1882.11.18.5	H	VO	Burma: Meplay Valley; Thoungyan R.
<i>Macaca assamensis</i>			
FMHH 99631	H	A	Thailand: Kamphaengphaet Province
<i>Macaca thibetana</i>			
NNHH 258651	H	A	China: Szechwan. Wen Chuan
NNHH 258649	H	OA	China: Szechwan. Wen Chuan
NNHH 254800	H	YA	China: Szechwan. Wen Chuan
NNHH 241163	H	OA	China: Szechwan. Wen Chuan
<i>Macaca sylvanus</i>			
NNHH 476785	H	OA	Morocco: Meknes Prov.. Azrou
RHHH 24585	H	A	Barbary
BN 1858.4.5.1	H	YA	no info
RHHH 24577	H	A	no info
RHHH 24578	F	OA	no info

<i>Macaca nenestrina leonina</i>			
AMNH 011091	F	A	India: Dhappa
<i>Macaca nenestrina nenestrina</i>			
MCZ 035602	F	A	Borneo: Camp Abai
MCZ 035631	F	YA	Borneo: Camp Abai
MCZ 035670	H	A	Borneo: Camp Abai
MCZ 035687	F	YA	Borneo: Camp Abai
STA 6959	F	A	Sumatra
RNH 049874	H	YA	Sumatra
RNH 3562	H	A	Sumatra
RNH 049874	H	A	E Sumatra: Aru Bay
RNH 049696	F	A	E Sumatra: Katenan River
RNH 049691	H	-	E Sumatra: Katenan River
RNH 11748	F	YA	NE Sumatra: Deli
<i>Macaca nigra</i>			
RNH 049874	H	A	Celebes
RNH 3325	H	A	Celebes
RNH 049874	F	OA	Celebes: Batjan
BM 1896.6.24.5	H	A	Celebes: Lipuang
<i>Macaca tonkeana</i>			
AMNH 153400	F	YA	Celebes: Togian Is., Malenge
AMNH 153402	H	YA	Celebes: Togian Is., Malenge
AMNH 153401	H	YA	Celebes: Togian Is., Malenge
<i>Macaca fascicularis</i>			
FMNH 099651	H	A	Thailand: Uthai Thani Prov., Kata Taek
<i>Macaca fascicularis fascicularis</i>			
AMNH 103654	F	OA	Borneo: Sampit Parit (Tjenpago)
MCZ 035658	F	YA	Borneo: Camp Abai
MCZ 035651	F	YA	Borneo: Camp Abai
MCZ 035724	F	A	Borneo: Camp Abai
MCZ 037663	F	YA	Borneo: Camp Abai
MCZ 035736	H	A	Borneo: Camp Abai
MCZ 035727	F	A	Borneo: Camp Abai
MCZ 037414	H	A	Borneo: Mt. Kinabalu
MCZ 037352	F	A	Borneo: Mt. Kinabalu
MCZ 037349	F	YA	Borneo: Mt. Kinabalu
MCZ 037407	H	A	Borneo: Jesselton
MCZ 057836	H	A	Borneo: Jesselton
<i>Macaca fascicularis philippinensis</i>			
FMNH 065451	F	A	Philippines: Negros Is., Anio Kabongahan
FMNH 062902	H	A	Philippines: Palawan, Puerto Princesa
FMNH 062276	H	VO	Philippines: Luzon, Abra Massisiat
FMNH 062274	F	OA	Philippines: Luzon, Abra Massisiat
FMNH 062275	H	A	Philippines: Luzon, Abra Massisiat
FMNH 061026	H	OA	Philippines: Mindanao, Mainit
FMNH 065450	H	A	Philippines: Kabungahan

<i>Macaca fuscata</i>		
UMNH 020936	H A	Japan
UMNH Nfu a	H A	Japan
UMNH Nfu b	H YA	Japan
<i>Macaca mulatta</i>		
PAL 210	H A	Physical Anthropology Laboratory
PAL 216	H A	Physical Anthropology Laboratory
PAL 213	H A	Physical Anthropology Laboratory
PAL 144	H A	Physical Anthropology Laboratory
PAL 179	F A	Physical Anthropology Laboratory
PAL 214	F A	Physical Anthropology Laboratory
PAL 168	F A	Physical Anthropology Laboratory
PAL 204	F A	Physical Anthropology Laboratory
PAL 181	F A	Physical Anthropology Laboratory
PAL 212	F A	Physical Anthropology Laboratory
PAL 49	F A	Physical Anthropology Laboratory
AS 97	F OA	no info
AS 932	F A	no info
AS 908	F A	no info
AS 1650	H A	no info
AS 1704	H A	no info
AS 1836	H A	no info
AS 1641	H A	no info
AS 1705	H A	no info
AS 1753	H A	no info
<i>Cercocebus albigena johnstoni</i>		
AMNH 052596	F A	Zaire: Akenge
AMNH 052598	H A	Zaire: Akenge
AMNH 052603	H A	Zaire: Akenge
AMNH 052627	H A	Zaire: Niapu
UMNH 000187	F A	Uganda: Mabira Forest
UMNH 000250	F A	Uganda: Mabira Forest
UMNH 000257	F A	Uganda: Mabira Forest
UMNH 000258	F A	Uganda: Mabira Forest
UMNH 000249	F A	Uganda: Mabira Forest
UMNH 000206	F A	Uganda: Mabira Forest
UMNH 000252	F A	Uganda: Mabira Forest
UMNH 000164	F OA	Uganda: Mabira Forest
UMNH 000159	F OA	Uganda: Mabira Forest
UMNH 000116	H A	Uganda: Mabira Forest
UMNH 000163	H A	Uganda: Mabira Forest
UMNH 000193	H A	Uganda: Mabira Forest
UMNH 000178	H A	Uganda: Mabira Forest
UMNH 000177	H A	Uganda: Mabira Forest
UMNH 000188	H A	Uganda: Mabira Forest

UWHT 000114	H	OA	Uganda: Nabira Forest
UWHT 000191	H	OA	Uganda: Nabira Forest
UWHT 000076	H	OA	Uganda: Nabira Forest
UWHT 000157	H	OA	Uganda: Nabira Forest
<i>Cercocebus albigena opdenboschi</i>			
TER 15647	H	A	?Zaire: Mwilambongo
<i>Cercocebus galeritus agilis</i>			
AMNH 052641	H	A	Zaire: Akenge
AMNH 081250	H	A	Zaire: Akenge
TER 36971	H	A	Zaire: PNG Kpaika
TER 23497	H	-	Zaire: Léopoldville
TER 23495	H	YA	Zaire: Léopoldville
TER 23496	F	A	Zaire: Léopoldville
TER 6000	H	A	Zaire: NE Uele
PCN Merfield 22	F	A	Cameroon: Batouri Dist.. Obala
PCN Merfield 181	H	A	Cameroon: Batouri Dist.. Pang
PCN Merfield 422	F	A	Cameroon: Batouri Dist.. Meyoss
PCN Merfield 573	H	OA	Cameroon: Batouri Dist.. Lelo
<i>Cercocebus galeritus galeritus</i>			
AMNH 054280	F	A	Kenya: Tana River
<i>Cercocebus torquatus torquatus</i>			
PCN Merfield 59	H	A	Cameroon: Yabassi Dist.
PCN Merfield 69	H	OA	Cameroon: Yabassi Dist.
PCN Merfield 71	H	A	Cameroon: Yabassi Dist.
PCN Merfield 77	F	A	Cameroon: Yabassi Dist.
PCN Merfield 80	H	A	Cameroon: Yabassi Dist.
PCN Merfield 81	F	A	Cameroon: Yabassi Dist.
PCN Merfield 84	F	A	Cameroon: Yabassi Dist.
PCN Merfield 102	F	A	Cameroon: Yabassi Dist.
PCN Merfield 115	H	A	Cameroon: Yabassi Dist.
PCN Merfield 39	H	OA	Cameroon: Yabassi Dist.
BH 1938.7.7.2	H	A	Cameroon: Yabassi Dist.. Nkan River
BH 1938.7.7.3	H	A	Cameroon: Yabassi Dist.. Nkan River
BH 1938.7.7.5	F	A	Cameroon: Yabassi Dist.. Nkan River
BH 1938.7.7.4	F	A	Cameroon: Yabassi Dist.. Nkan River
BH 1938.12.6.1	F	A	Cameroon: Yabassi Dist.. Nkan River
NHS 4 694	H	-	Cameroon: Campo, Bongola
NHS 4 693	H	-	Cameroon: Campo, Bongola
PCN CAN I 18	H	A	Cameroon: Belai
<i>Papio leucophaeus</i>			
NHS 38322	H	OA	Cameroon: Mfakwu
BH 1949.82	H	YA	Cameroon: Yabassi Dist.. Ndokyan Hills
NHS 1 559	F	YA	W Africa
AMNH HL b	F	A	Africa

Papio sphinx			
ANHH 089357	F	A	Caneroon: Hfane
ANHH 089358	F	A	Caneroon: Hfane
ANHH 089365	F	A	Caneroon: 6 mi N of Cumba
ANHH 089367	F	YA	Caneroon: 6 mi N of Cumba
ANHH 170364	H	VO	Caneroon: Bafia
ANHH 170366	H	YA	Caneroon: Bafia
BH 1930.12.15.9	H	A	?Caneroon
RHHH 24582	F	YA	Gabon
Papio anubis			
KHH OH 3144	F	A	Kenya: Baringo
BH 1972.127	H	A	Kenya: Central Prov.. Kedong Escarpment
Papio anubis anubis			
NNHH 236976	H	A	Uganda: Budongo Forest
NNHH 239743	[H]	[A]	Uganda: Budongo Forest
TER 1285	H	A	?Zaire: (Uele) Bafuka, W of Muangara
TER 6149	H	A	Congo
TER 9331	H	A	?Zaire: Gona, Lake Kivu
TER 6317	F	OA	?Zaire: N of Kisenyi
Papio anubis doguera			
STA HO 4 2	F	A	Ethiopia: Modjoseun
STA AH 2 86	H	A	Ethiopia: Djan Djan Schoa
STA AHII 85	H	A	Ethiopia: Djan Djan
STA BuU 71	H	A	Ethiopia: BulbuUa Anissi
STA BuU 72	H	A	Ethiopia: BuU lla Anissi
Papio anubis neumanni			
NNHH 384233	H	OA	Kenya: Mau Harok
NNHH 384223	H	YA	Kenya: Mau Harok, Site A
NNHH 384228	F	YA	Kenya: Mau Harok, Site A
NNHH 384229	H	YA	Kenya: Mau Harok, Site A
NNHH 384234	H	A	Kenya: Mau Harok, Site B
NNHH 384235	F	OA	Kenya: Mau Harok, Site B
Papio anubis tessellatus			
ANHH 051380	H	YA	Zaire: Akenge
Papio cynocephalus			
BH 1972.129	H	A	Kenya: Coast Prov., Kwale
BH 1962.7.6.13	H	A	Kenya: Tsavo Park, Mazinga Hill, Voi
Papio cynocephalus cynocephalus			
KHH OH 5178	H	A	Kenya: Welcone Trust Research Lab., Kabete
KHH OH 5067	H	A	Kenya: Welcone Trust Research Lab., Kabete
KHH OH 5072	H	A	Kenya: Welcone Trust Research Lab., Kabete
KHH OH 5064	H	A	Kenya: Welcone Trust Research Lab., Kabete
KHH OH 5053	H	A	Kenya: Southwest Prinate Research Center
KHH OH 3183	H	A	Kenya: Southwest Prinate Research Center
KHH OH 3185	F	A	Kenya: Southwest Prinate Research Center
KHH OH 3187	F	A	Kenya: Southwest Prinate Research Center

KNH OH 3190	F	A	Kenya: Southwest Primate Research Center
KNH OH 3175	F	A	Kenya: Southwest Primate Research Center
KNH OH 3199	F	A	Kenya: Kibvezi
KNH OH 3198	M	A	Kenya: Loitokitok
KNH OH 3005	F	A	Kenya: Kwale
KNH OH 3006	F	A	Kenya: Kwale
KNH OH 5065	M	A	no info
KNH OH 5070	M	A	no info
KNH OH 5089	F	A	no info
Papio hamadryas			
STA HA 8 3	M	-	Ethiopia: Harar
STA HA 8 41	M	-	Ethiopia: Erresfal near Harar
STA HA 8 39	F	-	Ethiopia: Erresfal near Harar
AIUZ 6932	F	A	Ethiopia: 5 km from Dire Dana
AIUZ 6934	M	A	Ethiopia: 5 km from Dire Dana
STA HA 8 83	M	-	Ethiopia
STA HA 840	M	A	no info
Papio ursinus			
AMNH 216251	M	YA	Mozambique
AMNH 216247	F	A	Mozambique: Alvez de Lina Camp
AMNH 216250	F	A	Mozambique: Inhanhara, Zihave, Rio Sava
STA 153-67	F	A	S Africa
STA 213 67	M	A	S Africa: Vrolijkheid
Papio ursinus ruacana			
BH 1862.6.26.1	M	A	Angola: Benguela near Cuio Bay
BH 1862.6.26.2	F	OA	Angola: Benguela near Cuio Bay
NHS 16 790	M	YA	SW Africa: N'Ordl. Otjivarongo
Theropithecus gelada			
AMNH 201008	M	YA	Ethiopia
STA 202	M	-	Ethiopia: Enta Selanie, Erylwa
STA DB 9/55	F	-	Ethiopia
STA DB 9 60	M	-	Ethiopia
STA 201	M	-	Ethiopia: Haliale Tigre
Colobus angolensis angolensis			
TER 28674	M	A	Zaire: Kekese (Kasai)
Colobus angolensis cottoni			
TER 25476	M	A	Kenya: Territory Mombasa, Epulu
Colobus angolensis palliatus			
BH 1972.158	F	A	Kenya: Coast Province, Kwale, Mrina Hill
BH 1938.4.21.2	F	A	Tanzania: E Usanbara Mts.
Colobus angolensis ruwenzorii			
MMNH 268946	F	A	Tanzania: Bukoba
MMNH 268947	F	A	Tanzania: Bukoba

<i>Colobus guereza caudatus</i>			
TER 2155	M	A	BBA: Mokini Forest (Front. Angl. Allen.)
TER 2157	F	A	BBA: Mokini Forest (Front. Angl. Allen.)
<i>Colobus guereza guereza</i>			
STA AN 2-66	M	-	Ethiopia: Gudella Schoa
STA AN 139	M	-	Ethiopia: Gudella Schoa
STA AN 138	M	-	Ethiopia: Gudella Schoa
STA AN 68	M	-	Ethiopia: Gudella Schoa
<i>Colobus guereza kikuyensis</i>			
NNHH 163122	F	A	Kenya: Mt. Kenya
NNHH 099468	F	OA	Kenya: Aberdare Range
NNHH 027711	M	A	Kenya: Kijabe
NNHH 452621	M	A	Kenya: Mkinangop
KNH OH 3078	M	A	Kenya: Thomson's Falls
KNH OH 3070	F	A	Kenya: Thomson's Falls
KNH OH 3073	F	A	Kenya: Thomson's Falls
KNH OH 3045	F	A	Kenya: Thomson's Falls
KNH OH 3071	M	A	Kenya: Thomson's Falls
KNH OH 3091	F	A	Kenya: Thomson's Falls
KNH OH 3092	F	A	Kenya: Thomson's Falls
KNH OH 3008	M	A	Kenya: Thomson's Falls
<i>Colobus guereza natschiei</i>			
NNHH 452632	F	-	Kenya: Mt. Elgon
BH 1972.149	M	A	Kenya: Kaptagat, near Mt. Elgon, Uasin Gishu
BH 1972.148	F	A	Kenya: Kaptagat, near Mt. Elgon, Uasin Gishu
NNHH 452636	F	YA	Kenya: Wandu Dist.
<i>Colobus guereza occidentalis</i>			
NNHH 052206	M	A	Zaire: Avakubi
NNHH 052248	M	-	Zaire: Paradje
NNHH 052229	M	A	Zaire: Paradje
NNHH 052240	M	A	Zaire: Paradje
NNHH 052241	F	A	Zaire: Paradje
NNHH 052223	F	A	Zaire: Paradje
TER 5896	F	A	Zaire
NNHH 268509	M	-	Uganda: Toro Bwanbe
<i>Colobus polykomos polykomos</i>			
NNHH 477321	F	A	Ivory Coast: Niebe
GOT D 1651	M	-	Liberia: Peloken
GOT F 2530	F	A	Liberia: HLC Camp
GOT A 981	M	A	Liberia: Freemanstown
<i>Colobus vellerosus</i>			
RHHH CPV a	M	YA	Ghana
NNHH 1017	M	A	zoo in Sierra Leone
<i>Colobus satana</i>			
PCH Herfield 174	F	A	Cameroon: Batouri Dist.
PCH CAN II 40	M	A	Cameroon: Mouth of N'Yong River
BH 1856.12.29.1	M	A	No data

Procolobus badius badius			Ivory Coast: Guitori
HNHN 477323	H	YA	Liberia: Sofore Place, St Paul's River
HNHN CBD b	H	A	Liberia: Sofore Place, St Paul's River
HNHN CBD a	F	A	Liberia: Duotown
GOT B 1918	H	A	
Procolobus badius ellioti			Zaire: Mawanbe
TER 2117	F	OA	Zaire: Route Stanleyville-Irundu
TER 18042	F	YA	
Procolobus badius oustaleti			Zaire: Paradje
HNHN 052298	H	OA	Zaire: Paradje
HNHN 052303	H	A	Zaire: Bafuka
HNHN 052287	H	A	Zaire: Ganangui
HNHN 052334	H	A	?Zaire: Uele poste de Sili
TER 1291	H	A	
Procolobus badius preussi			Cameroon: Yabassi Dist.
BN 1940.109	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 243	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 259	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 261	F	OA	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 264	F	VO	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 265	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 267	H	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 285	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 286	F	A	Cameroon: Mbokofass, NE of Yabassi
PCN Herfield 290	H	A	Cameroon: Mbokofass, NE of Yabassi
Procolobus badius rufonitratus			Zaire: Kisiki
HNHN 051811	F	YA	Kenya: Tana River
HNHN 054279	H	A	
Procolobus badius tenninckii			Gambia: Abuko Nature Reserve
BN 1982.628	F	A	Gambia: Abuko Nature Reserve
BN 1982.626	H	A	
Procolobus badius tephrosceles			Uganda: Ruahara River
BN 1901.8.9.46	H	A	
Procolobus badius tholloni			?Zaire: Moma
TER 9516	H	VO	
Procolobus verus			Ivory Coast: Niebe
HNHN 477327	F	A	Liberia: Zwedru
HNHN 477330	H	YA	Liberia: Schieffelinville, Junk River
HNHN PCV b	H	A	Liberia: Peloken
GOT B 1738	H	YA	Liberia: Duotown
GOT B 1911	H	-	Liberia: HLC Camp River Gbe
GOT F 2570	F	-	Sierra Leone: Kimbana
JFO 1984-13	H	YA	Sierra Leone: Kimbana
JFO 1984-14	F	A	Sierra Leone: Freetown (imported from)
ZHUC 580	H	OA	

<i>Hasalis larvatus</i>			
ANHH 028255	F	A	Borneo
HNHB 6017	F	A	Borneo
ANHH 103670	H	A	S Borneo: Sanpit Parit (Tjenpago)
ANHH 103671	H	A	S Borneo: Sanpit Parit (Tjenpago)
ANHH 106272	H	A	SW Borneo: Rian (Katuvaringen)
ANHH 106273	H	A	SW Borneo: Rian (Katuvaringen)
RNHH NL b	F	OA	SE coast of Borneo
RNHH NL a	H	OA	SE coast of Borneo
PNHH 068682	H	A	N Borneo: Kinabatangan Province
PNHH 068683	H	A	N Borneo: Kinabatangan Province
PNHH 068684	H	OA	N Borneo: Kinabatangan Province
MNHH CG 1301	F	A	Borneo: Sarawak, Seintubong
MNHH CG 1302	F	A	Borneo: Sarawak, Sedong
<i>Sennopithecus entellus achilles</i>			
ZNHC 607	F	A	Nepal: Walun
ZNHC 609	F	A	Nepal: Walun
ZNHC 615	H	A	Nepal: Walun
ZNHC 602	F	A	Nepal: Walun
ZNHC 608	F	A	Nepal: Walun
ZNHC 598	H	A	Nepal: Walun
ZNHC 604	F	YA	Nepal: Walun
<i>Sennopithecus entellus priani</i>			
HNHH 049701	H	-	S India: Anninalli Hills
<i>Sennopithecus entellus schistaceus</i>			
HNHH 021843	F	YA	India: Kaj Nag
<i>Sennopithecus cristata</i>			
HNHH 049695	H	OA	N Borneo: Katenan River
HCZ 035685	H	A	Borneo: Camp Abai
HCZ 035708	H	A	Borneo: Camp Abai
HCZ 037665	H	A	Borneo: Camp Abai
HCZ 035718	F	YA	Borneo: Camp Abai
HCZ 037669	F	YA	Borneo: Camp Abai
HCZ 037670	H	A	Borneo: Camp Abai
HCZ 037671	H	A	Borneo: Camp Abai
HCZ 037673	F	A	Borneo: Camp Abai
HCZ 035688	F	YA	Borneo: Camp Abai
HCZ 037675	H	YA	Borneo: Camp Abai
HCZ 035709	H	A	Borneo: Camp Abai
HCZ 037402	F	A	Borneo: Jesselton
HCZ 037404	F	YA	Borneo: Jesselton
HCZ 037392	F	A	Borneo: Jesselton
HCZ 037396	H	A	Borneo: Jesselton
HCZ 037399	H	A	Borneo: Jesselton
HCZ 037391	F	A	Borneo: Jesselton
HCZ 037398	F	YA	Borneo: Jesselton

HCZ 037400	F	OA	Borneo: Jesselton
HCZ 037394	H	A	Borneo: Jesselton
<i>Sennopithecus cristata cristata</i>			
NNHH 240014	F	OA	China: Hainan
NNHH 240009	F	OA	China: Hainan
<i>Sennopithecus cristata pyrrhus</i>			
NNHH 154928	F	YA	Java: Depok
NNHH 156305	H	YA	Java: Tjibodas
<i>Sennopithecus obscura</i>			
FNHH 105686	F	OA	Thailand: Trong Province. Ban Palian
FNHH 105652	H	-	Thailand: Krabi Province. Ban Thop Plik
BH 1971.751	F	A	Malaya: Pahang, Mt. Benan Base Camp
BH 1971.737	F	OA	Malaya: Perak. Bukit Merah
BH 1971.736	F	A	Malaya: Perak. Bukit Merah
BH 1971.734	H	YA	Malaya: Perak. Bukit Merah
BH 1971.733	H	YA	Malaya: Perak. Bukit Merah
BH 1971.729	H	A	Malaya: Perak. Bukit Merah
BH 1971.721	F	A	Malaya: Parit. Changkat Cheko
BH 1971.720	F	A	Malaya: Parit. Changkat Cheko
BH 1971.722	H	YA	Malaya: Parit. Changkat Cheko
RNHH PO b	H	YA	Sumatra: Lahat
RNHH PO a	F	OA	Sumatra: Lahat
<i>Sennopithecus obscura flavicauda</i>			
NNHH 049440	H	OA	Thailand: Chong, Trang
<i>Sennopithecus obscura obscura</i>			
NNHH 049641	H	VO	Malaya: Pahang, Rungpin River
<i>Presbytis aygula</i>			
STA 6956	F	A	Sumatra
Sta 6957	F	A	Sumatra
<i>Presbytis aygula aygula</i>			
RNHH PAA a	H	A	Java
RNHH PAA b	H	YA	Java
RNHH PAA c	F	A	Java
NNHH 156299	H	OA	Java: Tjiboda, Mt. Gede
<i>Presbytis frontata</i>			
RNHH PF a	H	A	S Borneo: Poulu-Lanpy
<i>Presbytis frontata frontata</i>			
NNHH 198831	H	A	Borneo: Djanbajan River
NNHH 198833	F	OA	Borneo: Djanbajan River
NNHH 198832	F	-	Borneo: Djanbajan River
<i>Presbytis hosei</i>			
HCZ 037370	F	A	Borneo: Mt. Kinabalu
<i>Presbytis hosei sabana</i>			
FNHH 068697	H	YA	N Borneo: Sandakan Dist., Sapagaya Forest Res.
FNHH 068695	H	YA	N Borneo: Kinabatangan Dist., Little Kretan R.
FNHH 068693	F	YA	N Boreno: Kinabatangan Dist., Little Kretan R.

<i>Presbytis nelalophos chrysonelas</i>			Borneo: Sarawak. Bini Baran River
NNNH CG 1305	M	A	
<i>Presbytis nelalophos fenoralis</i>			Sumatra: Mount Ophir
NNNH PHS b	F	A	Sumatra: Haut Padang
NNNH PHS c	M	YA	
<i>Presbytis nelalophos ferruginous</i>			Sumatra: Padang Bovenlanden, Goenoeng Sago
NNNH 5024	F	A	Sumatra: Padang
NNNH PHF a	M	A	Sumatra: Batang-Singalang
NNNH PHF b	F	YA	
<i>Presbytis nelalophos nelalophos</i>			Sumatra: Nyalo. Tarussan Bay
NNNH 049749	M	-	
<i>Presbytis nelalophos siamensis</i>			Sumatra: Palembang
NNNH PHS a	F	A	
<i>Presbytis rubicunda chryseus</i>			M Borneo: Kinabatangan Dist.. Little Kretan R.
NNNH 068685	F	A	M Borneo: Kinabatangan Dist.. Little Kretan R.
NNNH 068688	M	YA	M Borneo: Kinabatangan Dist.. Little Kretan R.
NNNH 068689	F	YA	
<i>Presbytis rubicunda rubicunda</i>			Borneo: Camp Abai
MCZ 035654	F	A	Borneo: Camp Abai
MCZ 035639	F	A	Borneo: Camp Abai
MCZ 035667	M	A	Borneo: Camp Abai
MCZ 035653	M	A	Borneo: Camp Abai
MCZ 035648	F	YA	Borneo: Camp Abai
MCZ 035638	M	YA	Borneo: Camp Abai
MCZ 035637	M	A	Borneo: Camp Abai
MCZ 035601	M	A	Borneo: Camp Abai
MCZ 035624	F	YA	Borneo: Camp Abai
MCZ 035630	M	A	Borneo: Camp Abai
MCZ 035570	F	A	Borneo: Camp Abai
MCZ 035577	F	A	Borneo: Camp Abai
MCZ 035596	M	YA	Borneo: Camp Abai
MCZ 035599	F	A	Borneo: Camp Abai
MCZ 035616	M	A	Borneo: Camp Abai
MCZ 035650	F	YA	Borneo: Camp Abai
NNNH 033537	M	A	M Borneo: 8 mi W of Sandakan Dist.
NNNH 033540	M	YA	M Borneo: W of Sandakan
NNNH 068692	F	OA	M Borneo: Sandakan Dist.. Sapagaya Forest Res.
<i>Pygathrix nemaeus nemaeus</i>			Vietnam: Quang Nam Prov.. Mt. Sontra
NNNH 356576	M	O	Vietnam: Quang Nam Prov.. Mt. Sontra
NNNH 356577	M	YA	Vietnam: Quang Nam Prov.. Mt. Sontra
NNNH 357628	M	VO	

Pygathrix nanaeus nigripes

PHNH 046514	M	OA	Vietnam: Ban Me Thuot
PHNH 046513	F	YA	Vietnam: Ban Me Thuot
NNNH 257997	M	OA	Vietnam: Bien Hoa Province
NNNH 257998	F	YA	Vietnam: Bien Hoa Province
NNNH 256917	F	A	Vietnam: Bien Hoa Province, Prang

Pygathrix roxellanae roxellanae

NNNH 268897	F	A	China: Szechwan, Wen Chuan
NNNH 268895	F	A	China: Szechwan, Wen Chuan
NNNH 268894	F	YA	China: Szechwan, Wen Chuan
NNNH 268390	F	VO	China: Szechwan, Wen Chuan
NNNH 268828	F	YA	China: Szechwan, Wen Chuan
NNNH 268887	M	A	China: Szechwan, Wen Chuan
NNNH 268886	F	YA	China: Szechwan, Wen Chuan

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