

## MORPHOLOGY OF THE HUMERUS AND FEMUR IN AFRICAN MANGABEYS AND GUENONS: FUNCTIONAL ADAPTATION AND IMPLICATIONS FOR THE EVOLUTION OF POSITIONAL BEHAVIOR

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**ABSTRACT** The morphology of the humerus and femur was examined in three mangabey species (*Cercocebus albigena*, *Cercocebus torquatus*, *Cercocebus galeritus*) and three guenon species (*Cercopithecus mitis*, *Cercopithecus mona*, *Cercopithecus aethiops*). *Cercocebus albigena*, *Cercopithecus mitis* and *Cercopithecus mona* are strictly arboreal whereas *Cercocebus torquatus*, *Cercocebus galeritus* and *Cercopithecus aethiops* are more frequently utilize terrestrial substrates. Morphological differences, which presumably reflect different positional behaviors, were found within both *Cercocebus* and *Cercopithecus* genera. The arboreal *Cercocebus albigena* differs from the more terrestrial *Cercocebus torquatus* and *Cercocebus galeritus* in having more mobile joints and more gracile bones. In *Cercocebus torquatus* and *Cercocebus galeritus*, joint movements tends to be restricted to the parasagittal plane emphasizing the economy of parasagittal excursion of the limbs. Similar tendencies were observed between the arboreal *Cercopithecus mitis* and *Cercopithecus mona* and the semi-terrestrial *Cercopithecus aethiops*. However, the morphological distinctions, associated to arboreality vs. terrestriality, are not identical between *Cercocebus* and *Cercopithecus*. Semi-terrestrial mangabeys exhibit stronger adaptations for terrestriality by comparison with the semi-terrestrial guenon. While the postcrania of the arboreal mangabey seem to be adaptive for deliberate movements in trees, those of the arboreal guenons suggest more rapid and agile activities. In addition, the arboreal *Cercopithecus mona* exhibits features related to leaping, which are not found in the more deliberately moving *Cercopithecus mitis*.

Despite these differences, the common morphotype of the humerus and femur in the Cercopithecinae is exhibited in both *Cercocebus* and *Cercopithecus*, contrasting with the morphology shown by other primates (Colobinae, Hominoidea and Cebidae). The cercopithecine morphotype is characterized by the restriction of joint movements for economical fore-aft excursions of the limbs. Both the large-bodied cebids and apes exhibit a morphotype that allows greater mobility of the joints involving axial rotations and abduction. The humerus of apes is further characterized by specializations for suspensory positional behaviors. The morphotype of the limb bones of the Colobinae differs from that of the Cercopithecinae in having less restricted joint movements. However, the morphotypes of these two subfamilies show a greater similarity to each other than to those of large-bodied cebids and apes. It is presumed that positional behaviors of ancestral cercopithecids involved parasagittal excursions of the limbs.

**Key Words:** *Cercocebus*; *Cercopithecus*; Femur; Functional morphology; Humerus; Locomotor behavior; Terrestriality.

## INTRODUCTION

Mangabeys and guenons are common primates in African forests. Mangabeys live in tropical rain forests from French Guinea to Western Uganda, and riverine forests along the Tana River in East Kenya (Napier & Napier, 1967). Habitats of guenons are more widespread in rain forest, secondary forest, montane forest, woodland savanna and open savanna, in most of sub-Saharan Africa (Napier & Napier, 1967; Lernould, 1988). Mangabeys and guenons are included in the Cercopithecinae, one of the two extant subfamilies which constitute the family Cercopithecidae (the Old World monkey). The Old World monkeys have more uniform basic morphologies than the other major groups of primates (Schultz, 1970). Locomotor modes also do not differ markedly. Both mangabeys and guenons are classified as “quadrupeds” in the basic locomotor category (Napier & Napier, 1967). Napier & Napier (1967) include them in the “branch-running-and-walking” subgroup. M.D. Rose (1973) included them in the (large size) “arboreal-branch-sitters-and-walkers” in his classification of positional behavior (locomotor and postural behaviors; see Prost, 1965). While these classifications have been accepted widely, both of the authors have pointed to variation within the positional behavior of each of these genera.

The white-cheeked mangabey (*Cercocebus albigena*) is strictly arboreal. It is observed exclusively in trees and tends to avoid heights below 10 meters (Waser, 1977, 1984). By contrast, the Tana river mangabey (*Cercocebus galeritus*) forages on the ground (Waser, 1984). Heights within 2 meters of the ground are most favored for feeding (Napier & Napier, 1967; Homewood, 1978). The white-collared mangabey (*Cercocebus torquatus*) is the most terrestrial species in the genus (Jones & Sabater Pi, 1968; Manaster, 1975). It spends considerable time during the day on the ground or in the lower levels of forests (Jones & Sabater Pi, 1968; Mitani, 1989, 1991; Napier & Napier, 1967). *Cercocebus torquatus* utilizes the lower level for moving or resting at a higher frequency than sympatric *Cercocebus albigena* and guenons (Mitani, 1989, 1991). The hand position of *Cercocebus torquatus* is digitigrade on the ground (M.D. Rose, 1973), as part of a cursorial adaptation.

Guenons are primarily arboreal and their habitats are restricted to forested environments. However, the savanna monkey (*Cercopithecus aethiops*) is uniquely adapted for a ground-living way of life (Napier & Napier, 1985). Although *Cercopithecus aethiops* has an arboreal ability (Struhsaker, 1967), they exploit broader ecological habitats including more arid environments, such as woodland and open savannas and riverine forest (Napier & Napier, 1967; Gartlan & Brain, 1968). *Cercopithecus aethiops* depend on the ground level significantly for foraging and resting (Kavanagh, 1978; M.D. Rose, 1979). The blue monkey (*Cercopithecus mitis*) lives in evergreen forest, lowland forest, gallery forest and savanna woodland (Napier & Napier, 1967). *Cercopithecus mitis* utilizes the middle to low canopy levels and seldom descends to the ground (Struhsaker, 1978), although it may descend to the ground to cross between discontinuous patches of forest (Gartlan & Brain, 1968). When *Cercopithecus mitis*

and *Cercopithecus aethiops* are sympatric, *Cercopithecus mitis* is limited to more denser areas while *Cercopithecus aethiops* occupies open and sparsely vegetated areas (Struhsaker, 1967). According to Napier & Napier (1967), the mona monkey (*Cercopithecus mona*) lives in rain forest and mainly occupies upper canopy levels during the day and middle levels at night. Gartlan & Struhsaker (1972) claim that *Cercopithecus mona* is most successful in mangrove swamp and commonly occupies the lower strata of the forests, although it is not restricted to these levels. According to Hill (1966), *Cercopithecus mona* utilizes the middle and lower storeys of the rain forest and moves actively and leaps frequently. Haddow (1951) notes that *Cercopithecus mona* characteristically shows leaping and darting movements, thus differing from *Cercopithecus mitis*. Although differences in positional behavior are likely in different habitats, *Cercopithecus mona* frequently utilizes small terminal branches (Kingdon, 1988).

Multivariate analyses reveals that mangabey and guenon species have different morphological patterns in the postcranial skeleton, which presumably reflect different positional behaviors (Manaster, 1975, 1979). The present study examines the associations between behavior and limb bone morphology in these mangabeys and guenons. A number of studies have revealed that musculoskeletal anatomy differs between closely related species with different positional behaviors and that the differences are related to diverse positional behaviors (Washburn, 1944; Oxnard, 1967; Fleagle, 1976a, 1977; Manaster, 1975, 1979; Rodman, 1979; Ward & Sussman, 1979; MacArdle, 1981; Glassman, 1983; Fleagle & Meldrum, 1988; Burr et al., 1989; Yu et al., 1993; Gebo & Sargis, 1994). A comparison of closely related species which are diverse in positional behavior, controls for those differences in morphology due to marked differences in phylogenetic heritage (Fleagle, 1977, 1979). Therefore, most anatomical differences can be simply correlated with the differences in positional behavior. Characteristics which are related to the arboreal vs. terrestrial diversification in these genera can be used to infer positional behavior of fossil monkeys.

The Cercopithecinae includes a number of species which may spend more or less time foraging on the ground. A few colobine species exhibit semi-terrestriality. In contrast, there is no New World primate which significantly utilizes the terrestrial substrate, despite of a large diversity of positional behavior (Fleagle & Mittermeier, 1980; Napier & Napier, 1967, 1985; M.D. Rose, 1973). Semi-terrestriality is a unique feature in the positional behavior of cercopithecids, particularly cercopithecines. Due to this peculiarity, the evolution of cercopithecids has been discussed with respect to the acquisition of semi-terrestriality. There are two different hypotheses concerning the original habitat of the cercopithecids, i.e., forests (e.g., Napier, 1970) or savannas (e.g., Andrews & Aiello, 1984). The postcranial plesiomorphies of cercopithecines serve as clues to their original habitat. The mangabeys and guenons represent extremes of the arboreal-to-semi-terrestrial diversification in each genus. Therefore, morphological similarities among these congeneric species most likely represent the ancestral morphotype of the humerus and femur of each genus, prior to a secondary radiation in substrate use. Their morphotypes are compared each other

and with those of other taxa (Colobinae, Hominoidea, and Cebidae), then implications for the evolution of positional behavior is discussed.

## MATERIALS AND METHODS

Characteristics of positional behavior in the examined species are summarized in Table 1. *Cercocebus albigena* is strictly arboreal, while *Cercocebus torquatus* and *Cercocebus galeritus* are more terrestrial. *Cercopithecus mitis* and *Cercopithecus mona* are basically arboreal. By contrast, *Cercopithecus aethiops* utilizes the ground significantly. For convenience, *Cercocebus torquatus*, *Cercocebus galeritus*, and *Cercopithecus aethiops* are labeled as “semi-terrestrial,” while *Cercocebus albigena*, *Cercopithecus mitis*, and *Cercopithecus mona* are called “arboreal” in the following sense. These terms do not imply that *Cercocebus torquatus*, for example, is the most semi-terrestrial of all living primates. Rather, it is more terrestrial in relation to the other mangabeys examined in the present study.

Body size is an important factor for positional behavior. Average body weights of the studied species are given in Table 2. Since body weight is variable depending on data sources, and is unavailable for some species, linear measurements of the humerus and femur are given for comparison in Appendix 1. Generally speaking mangabeys are larger than guenons. *Cercocebus albigena* is slightly smaller than *Cercocebus torquatus* and possibly *Cercocebus galeritus*. *Cercopithecus mitis* is the largest of the studied guenons. The size of male *Cercopithecus mitis* is close to that of female *Cercocebus albigena*. *Cercopithecus aethiops* and *Cercopithecus mona* are approximately the same size.

In addition to mangabeys and guenons, nine different genera of anthropoid were also studied for comparative purposes. Table 3 lists the examined species (*Papio* spp., *Colobus guereza*, *Presbytis melalophos*, *Nasalis larvatus*, *Pan troglodytes*, *Hylobates lar*, *Alouatta* spp., *Cebus* spp., *Ateles* spp.) and their positional habits.

The examined specimens for the present study are housed in British Museum (Natural History) (London, U.K.), Dokkyo University School of Medicine (Mibu, Japan), Japan Monkey Centre (Inuyama, Japan), National Museums of Kenya (Nairobi, Kenya), Powell-Cotton Museum (Birchington, U.K.), Primate Research Institute, Kyoto University (Inuyama, Japan), Royal Museum of Central Africa (Tervuren, Belgium) and Sumatra Nature Study Center, University of Andalas (Padang, Indonesia) (Appendix 2). In most cases, adult specimens were used for the study. However, to improve the sample size, a few young adults of *Cercopithecus aethiops* and *Cercopithecus mona*, in which epiphyseal lines were not completely lost, were included. When including these young specimens in the analysis, the general size and overall morphologies were checked to verify a more or less adult condition. Pathologically affected and very old individuals were not included. Except for *Cebus* and *Ateles*, the sexes are analyzed separately to control for sexual difference due to body size and sexual dimorphism

**Table 1.** Characteristic of the positional behavior of the studied species.

<i>Cercocebus albigena</i>	Strictly arboreal; uses higher canopy level ; moves deliberately on large branches ; no leaping.
<i>Cercocebus galeritus</i>	Occupies lower stratum ; uses the ground for foraging; walks deliberately on branches.
<i>Cercocebus torquatus</i>	Spends considerable time on the ground or lower stratum; arboreal only for eating and sleeping.
<i>Cercopithecus aethiops</i>	Spends considerable time on the ground; keeps extreme arboreal ability for escape.
<i>Cercopithecus mitis</i>	Uses middle or low stratum; comes down to the ground in the forest patches.
<i>Cercopithecus mona</i>	Occupies upper canopy, lower or middle level stratum; moves actively, using leaping and darting gaits.

Sources: Gartland & Brain, 1968; Gartland & Struhsaker, 1972; Haddow, 1951; Hill, 1966; Homewood, 1978; Jones & Sabater Pi, 1968; Kavanagh, 1978; Manaster, 1975; Mitani, 1989, 1991; Napier & Napier, 1967, 1985; Rollinson & Martin, 1981; M.D. Rose, 1979; Struhsaker, 1967; Struhsaker, 1978; Waser, 1977, 1984.

**Table 2.** Body weights of mangabeys and guenons (kg).

species	sex	Butynski	Hill	Jungers	Napier	Haltenorth & Diller
		(1988)	(1966)	(1985)	(1981)	(1980)
<i>Cercocebus albigena</i>	m	10.0	8.8	9.0	7.3	6.0-11.0
	f	7.0	6.0	6.4	5.7	4.0-7.0
<i>Cercocebus torquatus</i>	m	-	-	-	10.8	7.0-12.5
	f	-	-	-	-	4.5-7.0
<i>Cercocebus galeritus</i>	m	10.2	-	-	-	7.0-13.0
	f	5.4	-	-	-	4.5-7.0
<i>Cercopithecus mitis</i>	m	6.9	-	-	7.4	5.0-7.0
	f	4.2	-	-	4.2	3.5-4.5
<i>Cercopithecus mona</i>	m	-	4.6	-	2.7	4.5-7.5
	f	-	-	-	-	2.5-4.0
<i>Cercopithecus aethiops</i>	m	5.1	-	5.4	4.6	3.5-7.7
	f	3.5	-	3.6	3.3	2.5-5.3

that may arise from behavioral differences. In *Cebus* and *Ateles*, the sexes are pooled due to the small sample sizes. Male specimens of *Pan troglodytes* and female specimens of *Nasalis larvatus*, *Hylobates lar* and *Alouatta* are not included. However, given the marked morphological differences between these genera and mangabeys and guenons, pooling does not affect the comparisons significantly.

Ten and twelve measurements were measured in the humerus and femur, respectively

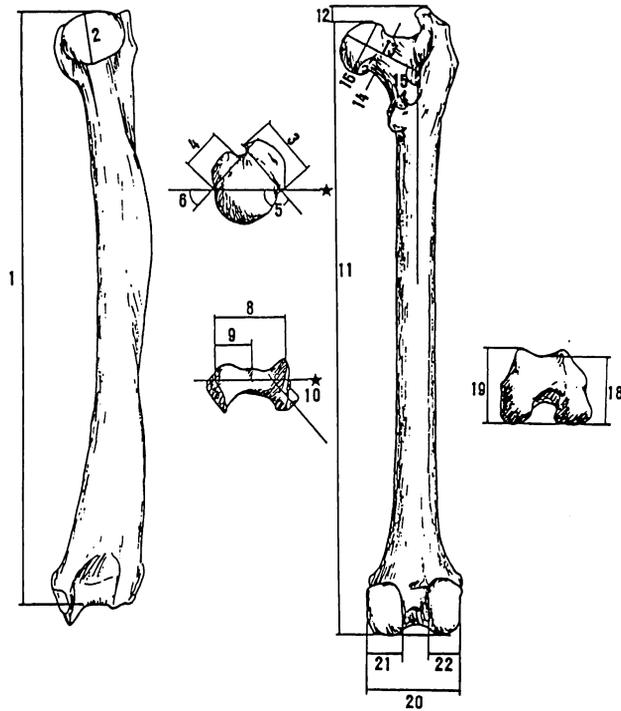
**Table 3.** Characteristics of positional behavior in anthropoids.

species (N)	positional behavior
<i>Papio</i> spp. (5 males, 3 females)	terrestrial walking and running, cursorial locomotion
<i>Colobus guereza</i> (15 males, 15 females)	arboreal quadrupedal walk, leaping, quadrumanous climbing
<i>Presbytis melalophos</i> (15 males, 18 females)	arboreal, frequent leaping, arm-swinging
<i>Nasalis larvatus</i> (1 male)	arboreal quadrupedal walk
<i>Pan troglodytes</i> (3 females)	knuckle walk, palm walk, unimanual arm hanging, vertical climbing
<i>Hylobates lar</i> (2 males)	suspensory behaviors, ricochetel brachiation, quadrumanous climbing
<i>Alouatta</i> spp. (2 males, 18 females)	arboreal quadrupedal walking, quadrumanous climbing, bridging
<i>Cebus</i> spp. (3 males, 5 females)	arboreal quadrupedal walking, quadrumanous climbing
<i>Ateles</i> spp. (3 males, 3 females)	suspensory behaviors, quadrumanous climbing

N: number of examined skeletal specimens.

Sources of positional behavior: Fleagle, 1976a, 1976b, 1977; Gebo, 1992; Hunt, 1992; Mittermeier, 1978; Morbeck, 1977; Napier & Napier, 1985; Rose, 1977.

(Fig. 1). Humeral measurements and their definitions are as follows. (1) Humeral length: minimum distance from the most proximal point on the head to the most distal point on the trochlea. (2) Humeral head diameter: proximodistal diameter of the humeral head on the posterior aspect. (3) Greater tuberosity diameter: maximum diameter of the greater tuberosity measured at right angle to the proximal shaft axis. (4) Lesser tuberosity diameter: maximum diameter of the lesser tuberosity measured at right angle to the proximal shaft axis. (5) Greater tuberosity angle: projected angle intersected by the border line of the greater tuberosity and the horizontal trochlear axis. (6) Lesser tuberosity angle: projected angle intersected by the border line of the lesser tuberosity and the horizontal trochlear axis. (7) Circumference of the mid-humeral shaft: shaft circumference at the mid length of the humerus. (8) Width of the distal articular surface: distance from the most lateral point of the capitulum to the medial margin of the trochlea, measured anteriorly. (9) Capitulum width: distance from the most lateral point of the capitulum to the lateral trochlear ridge measured anteriorly. (10) Retroflexion angle of the medial epicondyle: projected angle made by the posterior reflection of the medial epicondyle and the horizontal trochlear axis.



**Fig. 1.** Measurements of the humerus and femur. For description of measurements, see text pp. 6-8. Lines with an asterisk indicate the horizontal trochlear axis.

Femoral measurements are as follows. (11) Femoral length: minimum distance from the proximal surface of the head to the line connecting the distal aspects of the femoral condyles. (12) Greater trochanter height: distance from the tip of the greater trochanter to the proximal surface of the head, measured vertically with respect to the shaft axis. (13) Femoral neck length (including head length): distance from the intertrochanteric crest to the proximomedial surface of the femoral head along the neck axis. (14) Femoral neck diameter: maximum diameter of the neck at the mid-length of the neck measured vertical to the neck axis. (15) Femoral neck-shaft angle: angle intersected by the shaft axis and the neck axis. (16) Femoral head diameter: maximum diameter of the femoral head measured in the frontal plane. (17) Circumference at the mid-femoral shaft: shaft circumference at the mid-length of the femur. (18) Depth of the distal epiphysis of the femur: distance from the lowest point on the patellar surface to the vertical plane which passes through the posterior aspect of the femoral condyles. (19) Patellar surface rim height: distance from the most anteriorly projected point on the lateral patellar rim to the vertical plane which passes through the posterior aspect of the femoral condyles. (20) Bicondylar width: distance between the lateral margin of the lateral condyle and the medial margin of the medial condyle

on the posterior aspect. (21) Width of the medial condyle: mediolateral width of the medial condyle on the posterior aspect. (22) Width of the lateral condyle: mediolateral width of the lateral condyle on the posterior aspect.

Linear lengths were measured using digital sliding calipers, to the nearest tenth of mm. Diaphyseal circumferences were measured using a tape to the nearest half of mm. Angles were measured on photographs which were taken vertically with respect to the projected plane.

For size standardization, ratios of two length measurements were calculated. In most cases, articular dimension or bone length was taken as the denominator. The tibuberosity angle was calculated from the greater tuberosity angle and lesser tuberosity angle. Eleven indices and four angles were used in the analysis (Table 4).

Statistical and scaling analyses were carried out by StatView (Abacus Concepts, Inc. Berkeley) on a Macintosh personal computer. Means and standard deviations were calculated. T-tests were performed to test statistical significance at the 5% level.

Since the present study is concerned with animals whose body sizes are within a relatively narrow range (Table 2, Appendix 1), isometric relationships were presumed for most measurements of bones. However, to control for allometric relationships between measurements, two measurements (numerator and denominator of index) are logarithmically transformed and the least square regression was calculated based on average values in Old World monkeys (Fig. 7a-k). Each species is plotted separately by sex. Only a male sample is plotted for *Nasalis*. The regression equation and  $R^2$  (r squared) are given in each figure. 95% confidence limit of the predicted y-value was also calculated and indicated as curved lines in each figure. The obtained regression was tentatively considered as the general scaling trend in the Old World monkey and the Percentage Predicted Error, PPE (Smith, 1980; Jungers, 1985) was calculated, except for the regression in which correlation coefficient is low. If the scaling trend differs largely from isometry, the PPE analysis may produce different results from the index. On the other hand, if the scaling trend is close to isometry, the PPE will produce a similar result to the index.

## RESULTS

### I. Morphology of the Humerus in Mangabeys and Guenons

The greater and lesser humeral tuberosities serve as the insertion sites for the rotator cuff muscles. The morphology of the humeral tuberosities (height, size, orientation) reflects the functions of these muscles. The semi-terrestrial *Cercocebus galeritus* has a very superiorly projecting greater tuberosity (Fig. 2c). It expands laterally, as in *Papio* (Fig. 2g). The projection of the greater tuberosity is not marked in the semi-terrestrial *Cercocebus torquatus*, however, the tuberosity is expanded laterally,

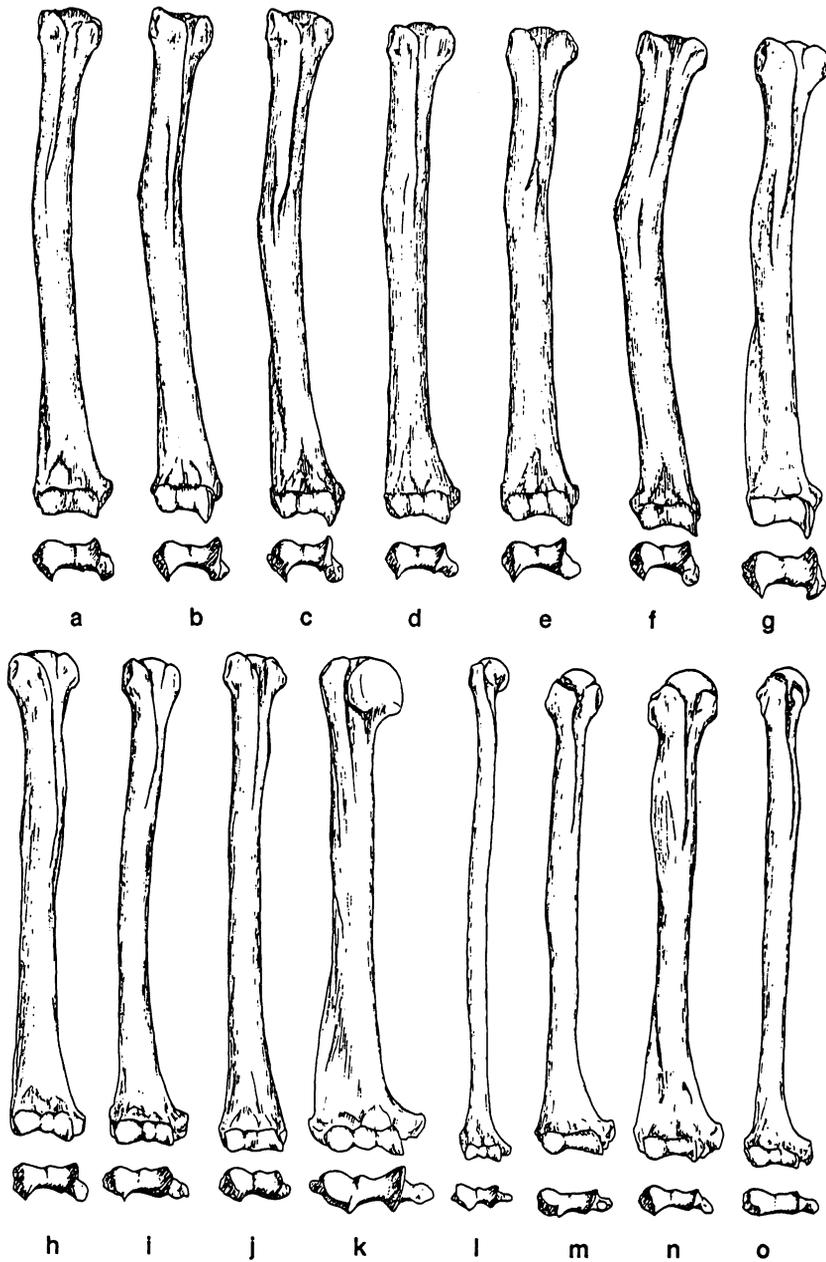
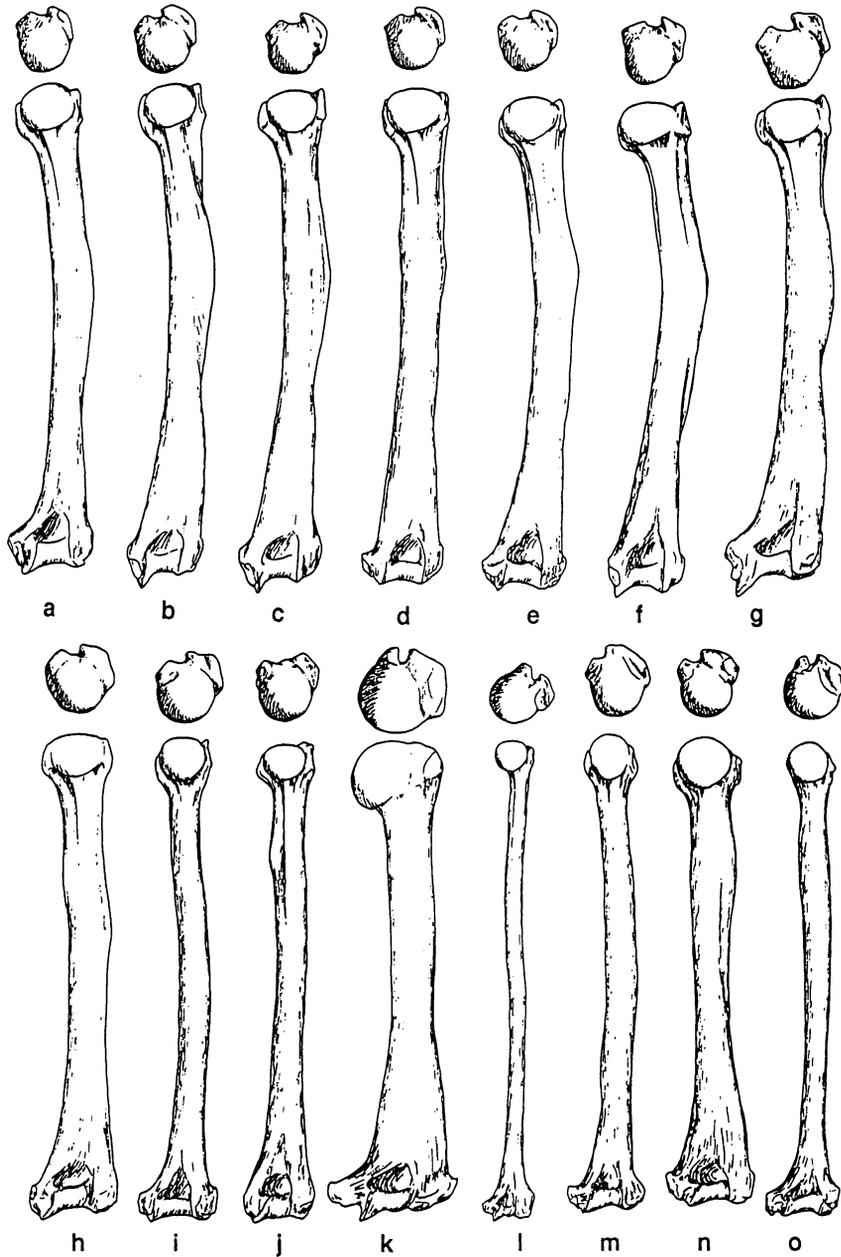


Fig. 2. Right humeri of anthropoid taxa (anterior and inferior). a: *Cercocebus albigena*; b: *Cercocebus torquatus*; c: *Cercocebus galeritus*; d: *Cercopithecus mitis*; e: *Cercopithecus mona*; f: *Cercopithecus aethiops*; g: *Papio hamadryas*; h: *Colobus guereza*; i: *Presbytis melalophos*; j: *Nasalis larvatus*; k: *Pan troglodytes*; l: *Hylobates lar*; m: *Alouatta seniculus*; n: *Cebus capucinus*; o: *Ateles paniscus*. All specimens are drawn to the same proximodistal length.



**Fig. 3.** Right humeri of anthropoid taxa (posterior and superior). a: *Cercocebus albigena*; b: *Cercocebus torquatus*; c: *Cercocebus galeritus*; d: *Cercopithecus mitis*; e: *Cercopithecus mona*; f: *Cercopithecus aethiops*; g: *Papio hamadryas*; h: *Colobus guereza*; i: *Presbytis melalophos*; j: *Nasalis larvatus*; k: *Pan troglodytes*; l: *Hylobates lar*; m: *Alouatta seniculus*; n: *Cebus capucinus*; o: *Ateles paniscus*. All specimens are drawn to the same proximodistal length.

as in *Cercocebus galeritus* (Fig. 2b, 3b). The anteroposterior diameter of the greater tuberosity is more than 90% of the humeral head diameter in *Cercocebus torquatus* (index 1). This value is significantly larger than that of *Cercocebus albigena* ( $p=.0001$  in males,  $p=.0026$  in females). The diameter of the greater tuberosity is about 87% of the head diameter in *Cercocebus albigena*. In *Cercocebus albigena*, the greater tuberosity does not project as high as in *Cercocebus galeritus* (Fig. 2a, 3a). The tuberosity is not laterally expanded (Fig. 2a).

The lesser tuberosity diameter of mangabeys is about 65% of the humeral head diameter (index 2) and the tuberosity lies below the level of the humeral head (Fig. 3a-c). The shape and size of the lesser tuberosity are less variable than those of the greater tuberosity. The relative diameter of the lesser tuberosity is larger in female *Cercocebus torquatus* than in female *Cercocebus albigena* ( $p=.0285$ ). However, such a difference is not evident in males.

The greater tuberosity of *Cercopithecus aethiops* and *Cercopithecus mona* forms a sharp projection on the anterolateral side of the humeral head (Fig. 3e, f). The projection is lower in *Cercopithecus mitis* than in *Cercopithecus aethiops* and *Cercopithecus mona* (Fig. 3d). The diameter of the greater tuberosity (index 1) tends to be larger in *Cercopithecus aethiops* than in *Cercopithecus mitis* and *Cercopithecus mona* although the difference is significant only in males ( $p=.0156$  with *Cercopithecus mitis*,  $p=.0054$  with *Cercopithecus mona*). The lesser tuberosity also projects higher and is larger in diameter in *Cercopithecus aethiops* than in *Cercopithecus mitis* and *Cercopithecus mona* (Fig. 3d, index 2). The lesser tuberosity of male *Cercopithecus aethiops* is significantly larger in diameter than that of *Cercopithecus mitis* ( $p=.0123$ ) and *Cercopithecus mona* ( $p=.008$ ). Since the lesser tuberosity diameter is particularly large in *Papio*, a terrestrial quadruped (index 2), a larger lesser tuberosity suggests an important role for *m.subscapularis* in quadrupedalism on the ground.

The greater tuberosity is situated on the anterolateral side of the head in mangabeys (angle 1). There is no significant difference in its location in mangabey species. It is located more anteriorly than that of colobines, apes and larger cebids, but less than that of *Papio*. The greater tuberosity angle of guenons is similar to that of colobines. The greater tuberosity is rotated most anteriorly in *Cercopithecus aethiops*. The location of the tuberosity in *Cercopithecus mona* is intermediate between *Cercopithecus aethiops* and *Cercopithecus mitis*. The greater tuberosity angle is significantly larger in male *Cercopithecus aethiops* than in male *Cercopithecus mitis* ( $p=.007$ ) and *Cercopithecus mona* ( $p=.046$ ). The difference is less clear in female comparisons. Female *Cercopithecus aethiops* have a larger angle than female *Cercopithecus mitis*, but no significant difference exists between female *Cercopithecus aethiops* and *Cercopithecus mona*.

The capabilities for axial rotation are significantly affected by the bituberosity angle (M.D. Rose, 1989). However, there is no difference in the bituberosity angle (angle 2) in mangabeys and guenons. The average values for the three species of mangabeys range from 68° to 73°, and 65° to 70° in the examined guenons.

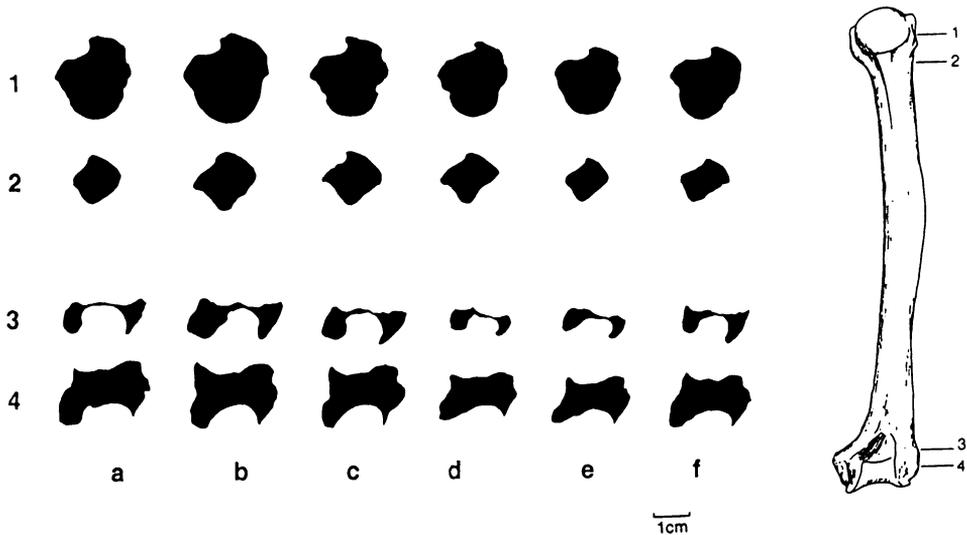


Fig. 4. Cross sections of the humerus at various levels. a: *Cercocebus albigena*; b: *Cercocebus torquatus*; c: *Cercocebus galeritus*; d: *Cercopithecus mitis*; e: *Cercopithecus mona*; f: *Cercopithecus aethiops*. Numerics indicate section levels.

The humeral head is less convex in cercopithecines in comparison with living apes and larger cebids (Fig. 2, 3; also see Gebo et al., 1988; Harrison, 1989; M.D. Rose, 1989). The humeral head is nearly hemispherical in mangabeys and guenons rather than a proximodistally elongated ovoid as seen in the New World climber (Fig. 2m; also see Schön Ybarra & Schön, 1988). Although these conditions are common in most cercopithecines, the humeral head of *Cercopithecus aethiops* exhibits some different features. The anteroproximal aspect of the head tends to be flat in comparison with other guenons. In posterior view the head is an inferomedial to superolaterally elongated ovoid (Fig. 3f), differing from that of *Cercopithecus mitis* and *Cercopithecus mona* (Fig. 3d, e).

The surgical neck of the humerus bears ridges which accommodate the insertions for muscles; *m.teres major* on the medial aspect, *m.deltoideus* on the lateral aspect, and *m.pectoralis major* on the anterior aspect. Posteriorly, a vertical buttress supports the humeral head (Fig. 4). The ridge for *m.teres major*, the deltotriceps crest (lateral corner), the deltopectral crest (anterior corner), and the buttress for the head are well developed in *Cercocebus torquatus* and *Cercocebus galeritus* (Fig. 4, second row). The cross-sectional shape of the neck is rhomboidal in these mangabeys (Fig. 4b, c). In contrast, these ridges are less marked and the cross-sectional shape of the surgical neck is round in *Cercocebus albigena* (Fig. 4a). The cross section of the neck is rhomboidal in guenons. However, the neck of *Cercopithecus aethiops* exhibits a more

flattened cross-sectional shape as compared with that of *Cercopithecus mitis* and *Cercopithecus mona* (Fig.4f). The buttress for the head is situated more medially as the distal pole of the head is rotated medially and the deltopectoral plane flares out laterally.

The proximal third of the humeral shaft of the cercopithecines is bowed anterolaterally, with the deltopectoral plane flaring eminently. The shaft curvature is emphasized in the semi-terrestrial mangabeys and guenon. The bowing is more developed in *Cercocebus torquatus* and *Cercocebus galeritus* than it is in *Cercocebus albigena* (Fig. 2, 3) Similarly, the shaft of *Cercopithecus aethiops* humerus is bowed more than that of *Cercopithecus mitis* and *Cercopithecus mona*.

Among mangabeys, averages of the circumference at mid-shaft in percent of humeral length range between 20% and 24% (index 3). Male *Cercocebus torquatus* have a larger robusticity index for the humeral shaft than male *Cercocebus albigena* ( $p=.0004$ ). Among guenons, averages range from 21% to 24%. There is no significant difference in the robusticity index except for females of *Cercopithecus mona*, which have a particularly thin shaft .

The distal part of the medial keel, and the posterior part of the lateral keel of the trochlea are protuberant in cercopithecines, particularly in the relatively terrestrial ones (Fig.2, 4; also see M.D. Rose, 1988; Harrison, 1989). These developed keels resist shearing and axially rotational forces at the elbow joint (Jenkins, 1973; M.D. Rose, 1988). There is a marked difference in the shape of the trochlear keels between the semi-terrestrial *Cercocebus torquatus* and *Cercocebus galeritus* on the one hand and the arboreal *Cercocebus albigena* on the other (Fig. 2, 4). The lateral and medial trochlear keels of *Cercocebus torquatus* and *Cercocebus galeritus* projects prominently on the posterior and anterodistal aspects, respectively. The prominent lateral trochlear keels continues to the lateral wall of the olecranon fossa. The trochlear keels of the studied guenons are developed to a lesser degree than those of *Cercocebus albigena*, but they are still marked as compared with colobines and New World monkeys (Fig. 3d-f).

The capitulum size and shape (breadth, roundness) vary, reflecting differences in humeroradial joint function (flexion-extension, pronation-supination). Capitulum width (including the *zona conoidea*) in relation to total articular surface width (index 4) is significantly larger in *Cercocebus albigena* in comparison with *Cercocebus torquatus* ( $p=.0024$  in males,  $p=.0285$  in females) and *Cercocebus galeritus* ( $p=.0017$  in males,  $p=.026$  in females). The capitulum of *Cercocebus albigena* is mediolaterally wide and relatively flattened (Fig. 2a). Among the guenons, female *Cercopithecus mitis* have a narrower capitulum than female *Cercopithecus aethiops* and *Cercopithecus mona*. This difference is not significant in males.

The flexors of the wrist and digits originate at the medial epicondyle. The medial epicondyle has greater degree of posterior reflection (retroflexion) in *Cercocebus torquatus* and *Cercocebus galeritus* as compared with *Cercocebus albigena* (angle 3). This difference is not significant in males due to the large variations ( $p=.591$  between

**Table 4.** Indices and angles of the humerus and femur. Upper: average; middle: standard deviation; lower: range.

species	sex	N	index 1	index 2	angle 1	angle 2	index 3	index 4
<i>Cercocebus albigena</i>	m	16	87.5	64.5	131.7	74.3	21.4	62.5
			2.60	4.44	7.21	6.59	1.36	2.23
				82.4-91.6	56.2-71.4	120.0-144.0	64.0-85.0	19.1-23.9
<i>Cercocebus torquatus</i>	f	11	86.0	61.0	128.3	71.9	21.1	63.7
			4.79	4.61	6.87	6.12	1.51	3.25
				77.5-95.8	52.5-67.1	113.0-136.0	61.0-83.0	18.8-24.0
<i>Cercocebus galeritus</i>	m	12	94.2	64.5	134.8	70.1	23.7	59.2
			4.42	5.18	5.95	8.35	1.70	2.90
				83.4-98.9	58.0-75.3	125.0-145.0	46.0-85.0	20.0-26.3
<i>Cercocebus galeritus</i>	f	8	93.0	66.7	129.1	67.9	22.0	60.4
			3.39	6.37	7.95	4.36	1.33	2.57
				86.5-98.0	57.9-73.5	115.0-139.0	64.0-77.0	19.7-23.9
<i>Cercocebus galeritus</i>	m	5	88.4	60.4	132.2	73.0	21.9	58.1
			3.97	3.34	3.83	5.20	1.51	2.73
				83.5-93.2	56.8-65.1	126.0-135.0	66.0-78.0	20.3-24.0
<i>Cercocebus galeritus</i>	f	4	89.4	64.4	130.0	73.3	20.5	59.1
			4.05	6.03	2.87	7.50	1.47	2.42
				84.4-94.2	59.9-73.2	126.0-132.0	66.0-83.0	18.3-21.4
<i>Cercopithecus mitis</i>	m	14	87.0	63.8	126.5	67.7	23.4	58.0
			4.11	3.80	6.56	6.56	1.49	2.98
				80.1-94.1	55.8-73.0	114.0-136.0	58.0-80.0	21.4-25.8
<i>Cercopithecus mitis</i>	f	9	88.4	60.7	127.0	70.4	22.7	57.1
			5.33	5.26	6.92	8.05	1.88	2.16
				81.9-96.5	52.2-69.2	115.0-137.0	62.0-83.0	19.9-26.4
<i>Cercoithacus mona</i>	m	12	87	62.5	128.8	67.9	23.7	60.6
			3.31	4.76	6.29	8.49	1.58	2.42
				82.9-92.4	54.3-70.1	116.0-135.0	49.0-83.0	20.8-26.6
<i>Cercoithacus mona</i>	f	4	86.0	64.4	129.0	65.3	21.0	62.4
			2.49	1.89	3.61	0.58	0.78	3.24
				83.7-88.4	62.0-66.7	126.0-133.0	65.0-66.0	20.0-21.7
<i>Cercopithecus aethiops</i>	m	10	91.3	68.8	134.7	66.2	23.8	59.3
			3.61	5.12	6.10	5.36	1.59	3.54
				83.3-95.2	61.9-77.1	123.0-143.0	59.0-73.0	21.6-26.2
<i>Cercopithecus aethiops</i>	f	16	89.2	64.0	132.0	65.6	23.2	62.2
			3.29	4.89	5.62	5.36	1.59	3.37
				83.1-94.4	55.0-74.5	124.0-149.0	45.0-79.0	20.7-26.5
<i>Papio spp.</i>	m	5	93.8	72.3	141.0	75.2	25.8	59.3
			87.3-100.0	70.4-73.6	130.0-154.0	62.0-84.0	25.1-26.6	55.7-62.0
				87.4	72.7	139.0	75.5	23.5
<i>Colobus guereza</i>	m	15	86.7-88.2	70.9-74.5	137.0-140.0	66.0-85.0	23.3-23.7	61.4-65.1
			97.0	64.1	127.1	72.4	23.1	62.6
				88.9-106.9	55.2-69.8	115.0-141.0	62.0-83.0	19.5-26.2
<i>Colobus guereza</i>	f	15	95.3	60.4	124.0	71.8	21.9	62.4
			86.9-101.8	49.5-65.5	113.0-135.0	60.0-81.0	20.4-23.6	57.2-66.3
				87.9	58.2	129.5	82.9	20.7
<i>Presbytis melalophos</i>	m	15	78.2-95.0	51.6-65.8	118.0-140.0	66.0-94.0	19.2-22.8	58.4-68.0
			86.5	57.4	129.0	77.4	21.1	62.8
				75.2-93.4	48.7-63.4	116.0-159.0	68.0-90.0	18.9-22.8
<i>Nasalis larvatus</i>	m	1	84.0	54.9	127.0	75.0	19.9	64.0
			-	-	-	-	-	-
				91.0	58.7	103.7	124.3	26.4
<i>Pan troglodytes</i>	f	3	87.5-94.0	52.1-64.5	87.0-122.0	118.0-130.0	24.6-28.2	50.5-53.8
			70.0	55.9	126.5	134.0	13.4	58.1
				68.5-71.0	53.6-58.2	115.0-138.0	130.0-138.0	13.3-13.6
<i>Alouatta seniculus</i>	m	2	84.0	52.3	118.0	64.0	21.2	57.8
			81.7-85.6	48.7-55.9	112.0-124.0	58.0-70.0	20.9-21.4	55.6-60.0
				82.6	56.3	120.0	74.6	22.0
<i>Cebus spp.</i>	pooled	8	78.2-88.6	50.0-60.2	113.0-131.0	63.0-83.0	19.3-25.8	41.1-63.4
			74.0	42.6	120.8	103.8	16.8	64.2
				69.8-79.0	35.0-66.7	110.0-129.0	96.0-117.0	16.0-17.7

Table 4. Continued.

angle 3	index 5	index 6	index 7	angle 4	index 8	index 9	index 10
45.9	1.4	11.8	52.6	127.9	18.1	82.2	85.4
6.42	0.60	0.66	4.59	3.28	0.68	4.58	5.74
34.0-57.0	0-2.1	10.3-13.2	4.8-63.4	123.0-135.0	17.1-19.1	74.7-88.9	75.6-96.7
45.1	1.2	11.6	54.7	129.1	18.2	81.3	83.7
5.14	0.72	0.78	4.61	5.37	2.85	3.39	3.07
40.0-54.0	0-2.3	10.3-13.6	47.7-60.3	120.0-136.0	17.1-20.2	77.1-87.7	77.8-88.0
51.1	2.8	12.1	56.0	129.8	20.9	84.8	85.2
7.34	0.57	1.05	4.93	3.30	1.18	4.20	6.47
40.0-62.0	1.8-3.5	10.3-13.6	49.1-66.8	125.0-137.0	19.0-22.5	77.2-90.4	73.4-100.0
51.9	1.9	12.3	57.6	129.1	20.9	83.5	82.7
5.69	0.56	0.08	4.11	3.52	1.33	2.16	4.67
45.0-60.0	0.6-2.4	11.0-13.6	51.4-63.5	125.0-134.0	19.4-22.7	80.6-86.7	77.1-89.6
49.6	2.3	12.5	52.1	126.0	19.4	83.6	89.7
6.66	1.20	0.69	2.66	6.34	1.36	5.30	4.93
43.0-58.0	0.2-3.3	11.9-13.6	48.0-54.9	117.0-133.0	17.9-20.8	78.8-92.1	82.9-96.1
56.3	2.4	11.7	60.1	129.8	18.8	82.2	81.0
5.56	0.78	1.96	7.91	4.65	1.30	1.05	4.23
48.0-60.0	1.9-3.6	10.5-14.6	49.6-67.7	125.0-136.0	17.1-20.0	80.8-83.0	77.9-87.2
45.3	2.1	13.8	49.4	127.6	20.4	86.2	86.7
8.46	0.41	0.84	3.98	4.40	0.97	3.48	5.10
26.0-55.0	1.2-2.6	12.0-15.5	43.3-56.9	118.0-135.0	18.9-22.2	81.7-93.3	77.1-93.3
41.7	2.1	13.7	50.5	122.8	20.8	83.7	87.4
6.91	0.83	1.09	4.04	8.09	0.74	5.04	6.04
33.0-54.0	0.6-3.0	11.4-14.5	45.8-59.5	110.0-135.0	19.6-21.7	76.6-93.7	77.6-95.7
41.1	2.3	12.8	52.5	127.3	20.0	90.6	88.3
5.5	0.8	0.62	2.74	4.29	0.81	3.92	4.41
34.0-50.0	0.6-3.5	11.6-13.8	47.8-57.1	118.0-132.0	18.8-21.3	83.5-95.4	77.3-94.2
41.0	2.2	11.8	56.4	125.0	20.0	88.0	87.2
3.37	0.22	0.42	3.47	3.74	1.41	2.11	6.74
36.0-43.0	1.9-2.4	11.2-12.2	51.7-59.6	120.0-129.0	18.6-21.9	86.7-91.2	81.0-94.8
51.1	2.4	12.9	53.9	122.4	20.6	89.4	85.2
7.25	0.83	0.89	2.34	7.68	1.74	2.93	4.03
40.0-62.0	1.3-3.7	11.5-14.7	51.6-58.8	111.0-135.0	17.9-23.4	84.8-93.9	79.6-92.6
49.4	2.1	13.1	51.3	123.3	20.0	86.7	85.8
6.27	0.62	1.08	4.44	5.17	1.86	3.56	5.30
42.0-63.0	1.3-3.3	11.8-15.0	44.5-58.3	115.0-135.0	15.4-22.3	81.5-107.3	76.5-100.0
52.2	3.9	14.5	50.1	125.4	23.1	79.8	78.0
41.0-59.0	2.3-4.7	14.0-15.2	48.7-54.2	122.0-134.0	22.1-25.1	76.6-82.6	71.7-87.6
49.0	2.5	14.4	53.6	124.0	21.6	83.0	74.5
48.0-50.0	2.3-2.6	13.5-15.3	50.2-56.9	121.0-127.0	21.3-21.9	82.5-83.6	74.1-75.0
30.1	1.2	13.4	52.4	117.4	20.9	78.9	90.7
24.0-40.0	0.5-2.4	12.2-15.2	47.1-61.8	109.0-124.0	18.9-23.8	73.8-83.5	85.6-99.0
35.2	0.7	13.2	51.0	119.2	20.1	81.0	89.1
31.0-42.0	0.3-1.4	12.3-14.7	47.0-56.4	112.0-126.0	18.2-21.8	76.1-90.4	77.4-98.9
35.7	1.2	10.1	64.6	115.8	17.4	78.3	90.2
30.0-40.0	0.2-2.1	8.9-10.9	55.2-76.6	109.0-125.0	16.0-19.6	70.5-84.9	82.6-98.9
34.8	1.3	10.1	63.5	115.1	17.7	80.1	87.9
20.0-42.0	0.5-1.8	9.4-10.8	59.2-67.5	110.0-124.0	16.1-18.8	74.8-86.2	80.5-97.8
17.0	1.0	12.3	55.9	126.0	20.8	81.5	91.2
-	-	-	-	-	-	-	-
21.3	-1.0	16.4	44.9	131.7	25.0	72.8	75.3
18.0-26.0	-1.4- -0.7	15.0-17.9	40.4-49.4	125.0-140.0	24.5-25.3	68.7-78.3	72.7-80.5
24.0	-1.1	11.1	43.0	137.0	15.5	73.5	69.4
18.0-30.0	-1.5- -0.8	10.7-11.5	39.7-46.3	135.0-139.0	15.2-15.7	72.9-74.0	68.4-70.3
18.5	-2.2	14.4	42.7	130.5	20.4	78.9	84.0
17.0-20.0	-3.0- -1.4	13.9-14.8	42.5-42.9	129.0-132.0	19.3-21.6	77.5-80.4	82.2-85.9
43.6	0.2	13.6	43.6	134.6	18.5	74.4	86.5
40.0-52.0	-0.7-1.0	11.9-15.4	38.2-48.9	128.0-143.0	15.7-21.2	68.2-80.0	79.1-96.7
15.5	-2.1	13.0	43.0	136.5	19.5	67.0	84.1
9.0-20.0	-3.7- -1.4	10.7-15.3	29.5-58.6	134.0-139.0	17.8-21.1	61.8-71.1	72.9-94.3

Note: index 1	greater tuberosity diameter % (measurement 3) relative to humeral head diameter (measurement 2)
index 2	lesser tuberosity diameter % (measurement 4) relative to humeral head diameter (measurement 2)
angle 1	greater tuberosity angle (°)
angle 2	bituberosity angle (°)
index 3	humeral shaft circumference at mid-length % (measurement 7) relative to humeral length (measurement 1)
index 4	capitulum width % (measurement 9) relative to distal humeral articular width (measurement 8)
angle 3	retroflexion angle of the medial epicondyle (°)
index 5	greater trochanter projection % (measurement 12) relative to femoral length (measurement 11)
index 6	femoral neck length % (measurement 13) relative to femoral length (measurement 11)
index 7	femoral neck diameter % (measurement 14) relative to femoral neck length (measurement 13)
angle 4	neck-shaft angle (°)
index 8	femoral shaft circumference at mid-length % (measurement 17) relative to femoral length (measurement 11)
index 9	distal epiphysis depth % (measurement 18) relative to femoral bicondylar width (measurement 20)
index 10	lateral condyle width % (measurement 22) relative to medial condyle width (measurement 21)
index 11	lateral rim height % (measurement 19) relative to femoral bicondylar width (measurement 20)

*Cercocebus albigena* and *Cercocebus torquatus*,  $p=.2831$  between *Cercocebus albigena* and *Cercocebus galeritus*). Female *Cercocebus albigena* has a more medially directed medial epicondyle than *Cercocebus torquatus* ( $p=.0147$ ) and *Cercocebus galeritus* ( $p=.003$ ). The medial epicondyle of *Cercocebus torquatus* is shorter than that of *Cercocebus albigena* and *Cercocebus galeritus*.

The retroflexion of the medial epicondyle is greater in the semi-terrestrial *Cercopithecus aethiops* than in the arboreal *Cercopithecus mitis* and *Cercopithecus mona* (Fig. 2d-f). The difference is not significant between male *Cercopithecus aethiops* and *Cercopithecus mitis* ( $p=.093$ ), although the difference is significant between male *Cercopithecus aethiops* and *Cercopithecus mona* ( $p=.0015$ ). Female *Cercopithecus aethiops* exhibits a larger angle compared to female *Cercopithecus mitis* ( $p=.008$ ) and *Cercopithecus mona* ( $p=.0191$ ). The size of the medial epicondyle does not differ in these guenons.

## II. Morphology of the Femur in Mangabeys and Guenons

The greater trochanter projection (index 5) represents the lever arm length of *mm.gluteus medius* and *piriformis*. The greater trochanter of *Cercocebus torquatus* and *Cercocebus galeritus* projects well above the femoral head. The difference is significant between *Cercocebus torquatus* and *Cercocebus albigena* ( $p=.0001$  in males,  $p=.031$  in females) and between *Cercocebus galeritus* and *Cercocebus albigena* ( $p=.0242$  in males,  $p=.0115$  in females). However, no difference is observed in the degree of projection of the greater trochanter in arboreal and semi-terrestrial guenons. The relative projection of guenons lies within the range of the semi-terrestrial mangabeys.

The femoral head of mangabeys is hemispherical rather than spherical (Fig. 6a-c). In *Cercocebus albigena*, the articular surface extends slightly onto the anterior and proximoposterior aspects of the neck as compared with other mangabeys. This articular extension, though not as extreme as in New World monkeys, might allow a greater range of abduction and rotation at the hip joint than in *Cercocebus torquatus* and *Cercocebus galeritus*. The femoral head of guenons is hemispherical and resembles those of *Cercocebus torquatus* and *Cercocebus galeritus*. The articular surface is most extensive on the proximoposterior aspect (Fig. 6d-f). Despite minor variations in the extent of the articular surface, no consistent difference is apparent.

The position of the fovea capitis femoris, in which the ligamentum teres inserts, is variable depending upon positional behaviors (Jenkins & Camazine, 1977; K.D. Rose, 1987; Fleagle & Meldrum, 1988). The fovea of mangabeys and guenons is located slightly posteroinferior to the center of the articular surface. There is no significant difference in this character. The shape of the fovea is a mediolaterally long ellipsoid and the depth is shallow in most of mangabeys and guenons. However, that of *Cercopithecus mona* differs in being round and deep. The depth of the fovea may suggest the development of the ligamentum teres.

The relative neck length, neck diameter and neck-shaft angle affect the mobility

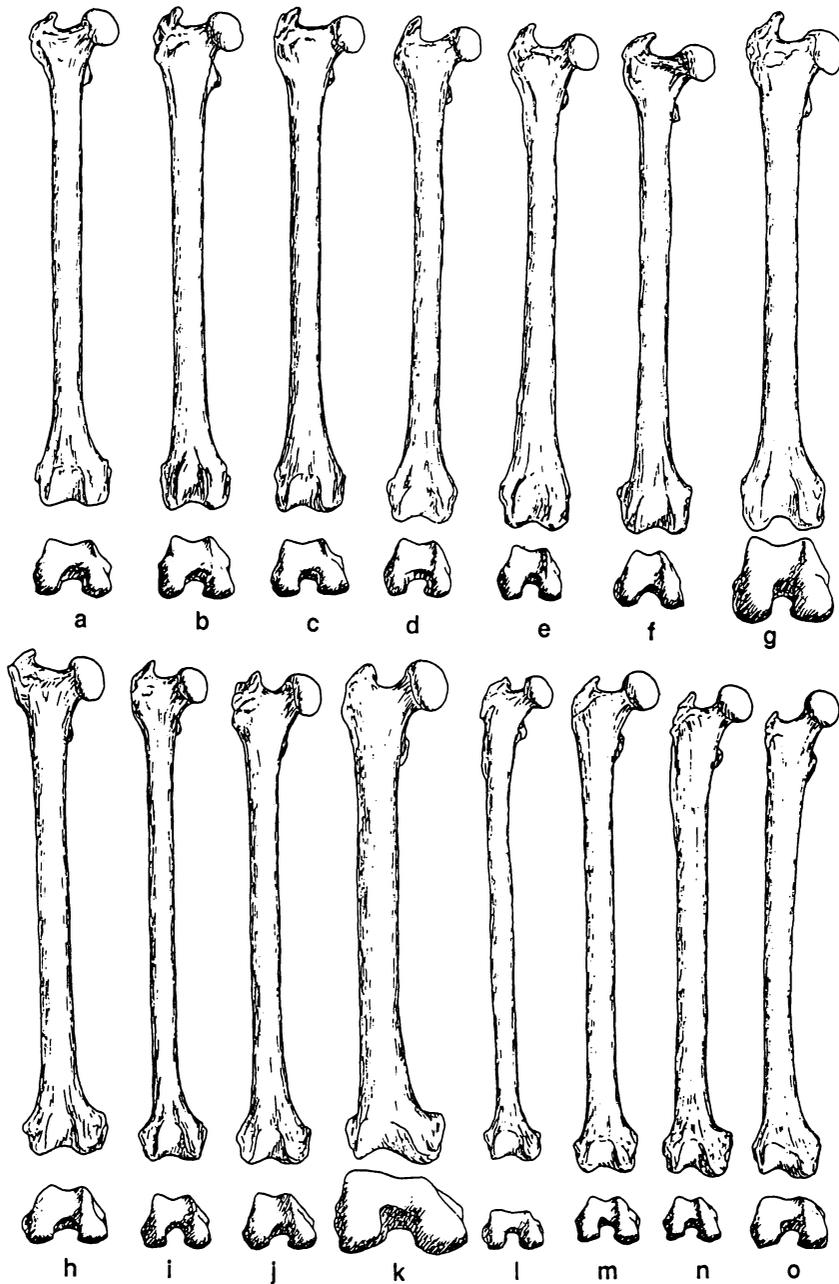


Fig. 5. Right femora of anthropoid taxa (anterior and inferior). a: *Cercocebus albigena*; b: *Cercocebus torquatus*; c: *Cercocebus galeritus*; d: *Cercopithecus mitis*; e: *Cercopithecus mona*; f: *Cercopithecus aethiops*; g: *Papio hamadryas*; h: *Colobus guereza*; i: *Presbytis melalophos*; j: *Nasalis larvatus*; k: *Pan troglodytes*; l: *Hylobates lar*; m: *Alouatta seniculus*; n: *Cebus capucinus*; o: *Ateles paniscus*. All specimens are drawn to the same proximodistal length.

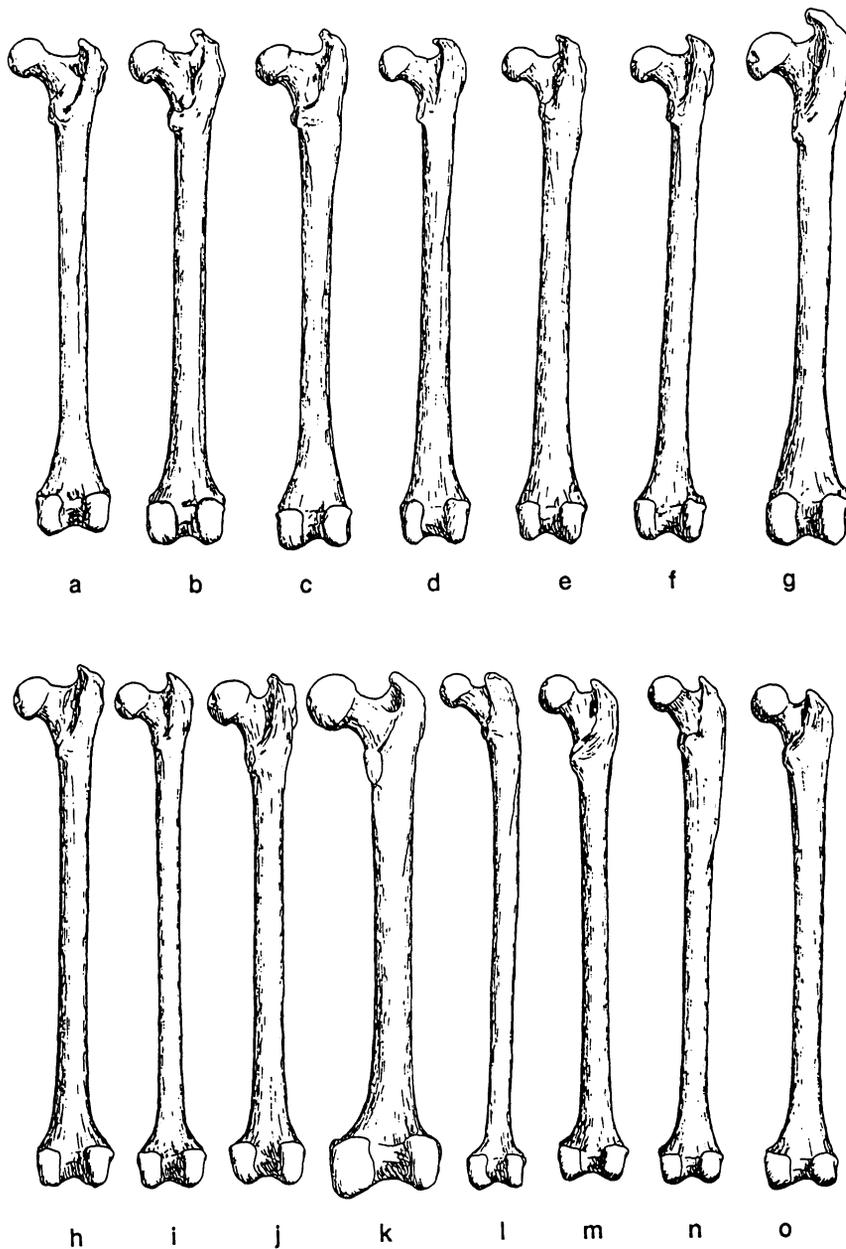


Fig. 6. Right femora of anthropoid taxa (posterior). a: *Cercocebus albigena*; b: *Cercocebus torquatus*; c: *Cercocebus galeritus*; d: *Cercopithecus mitis*; e: *Cercopithecus mona*; f: *Cercopithecus aethiops*; g: *Papio hamadryas*; h: *Colobus guereza*; i: *Presbytis melalophos*; j: *Nasalis larvatus*; k: *Pan troglodytes*; l: *Hylobates lar*; m: *Alouatta seniculus*; n: *Cebus capucinus*; o: *Ateles paniscus*. All specimens are drawn to the same proximodistal length.

of the hip joint (flexion-extension, abduction-adduction, axial rotation) and the structural strength of the femoral neck (e.g., Fleagle, 1976a; Fleagle & Meldrum, 1988). Averages for relative neck length are around 12% of the femoral length in mangabeys (index 6). Averages of the neck robusticity index (neck diameter relative to the neck length, index 7) range from 52 to 60%. There are no significant differences concerning either index among mangabeys. In the three species of guenon, the neck of *Cercopithecus mitis* is longer than that of *Cercopithecus mona* and *Cercopithecus aethiops* (index 6). The differences are significant if compared with *Cercopithecus mona* ( $p=.0062$  in males,  $p=.0095$  in females) and male *Cercopithecus aethiops* ( $p=.0174$ ) although the significance level is low in a comparison with female *Cercopithecus aethiops* ( $p=.3011$ ). The robusticity index of the neck is also lower in *Cercopithecus mitis*. *Cercopithecus mitis* shows a significantly lower value in comparison with other species except with female *Cercopithecus aethiops* ( $p=.6509$ ). Significant levels are; .0306 and .0286 with male and female *Cercopithecus mona*, respectively, .0039 with male *Cercopithecus aethiops*. *Cercopithecus mona* has a short and robust neck, differing from *Cercopithecus mitis* irrespective of the same arboreal habit. The neck-shaft angle (angle 4) may reflect modes of positional behavior (e.g., Fleagle, 1976a; Fleagle & Meldrum, 1988; but also see Ford, 1988). However, the neck-shaft angle is almost the same in mangabeys and guenons. Average values are about 125° to 130° in mangabeys and 123° to 128° in guenons.

The shaft of the femur is slender (index 8) in *Cercocebus albigena* as compared with *Cercocebus torquatus* ( $p=.0001$  in males,  $p=.0372$  in females). The robusticity index of the femoral shaft of male *Cercocebus albigena* is also lower than that of male *Cercocebus galeritus* ( $p=.0060$ ) although the difference is not significant when comparing the females ( $p=.3625$ ). There are no significant differences between the arboreal and semi-terrestrial guenons. Variational range overlaps and the averages range from 20.0 to 20.8%.

A mediolaterally wide epiphysis ensures the knee joint stability during axial rotatory movements, whereas an anteroposteriorly deep knee joint is mainly designed for flexion-extension in the parasagittal plane. Although the distal femur in *Cercocebus albigena* seems relatively wider than in *Cercocebus torquatus* and *Cercocebus galeritus*, there is no significant difference (index 9). Guenons have a deeper knee joint in general if compared with mangabeys. The knee joint of male *Cercopithecus mitis* is mediolaterally wider than that of both *Cercopithecus mona* ( $p=.0061$ ) and *Cercopithecus aethiops* ( $p=.0306$ ). In females, however, the differences are not significant ( $p=.1407$  with *Cercopithecus mona*,  $p=.088$  with *Cercopithecus aethiops*).

The width of the lateral condyle relative to the medial condyle reflects the degree of abduction of the femur. When abduction is emphasized, the medial condyle transmits more weight (Preuschoft, 1970). This condition may cause the lateral condyle to become narrower relative to the medial condyle (index 10). Among mangabey and guenon species, there is no difference in the proportion of the relative width of the lateral condyle. All species show a slightly narrower lateral condyle relative to the

medial one (78% to 88%).

The patellar surface of *Cercocebus torquatus* is narrow and deeply excavated and the rim of the patellar surface is raised (Fig. 5b). By contrast, the patellar surface of *Cercocebus albigena* is wider and shallower (Fig. 5a). The morphology of the patellar surface of *Cercocebus galeritus* is like that of *Cercocebus albigena* (Fig. 5c). The patellar surface is wider than that of *Cercocebus torquatus* and the rims of the patellar surface are only moderately raised. The elevation of the lateral rim (index 11) is significantly greater in *Cercocebus torquatus* than in *Cercocebus albigena* ( $p=.0059$  in males,  $p=.0207$  in females) whereas there is no significant difference between *Cercocebus albigena* and *Cercocebus galeritus* ( $p=.6489$  in males,  $p=.8578$  in females).

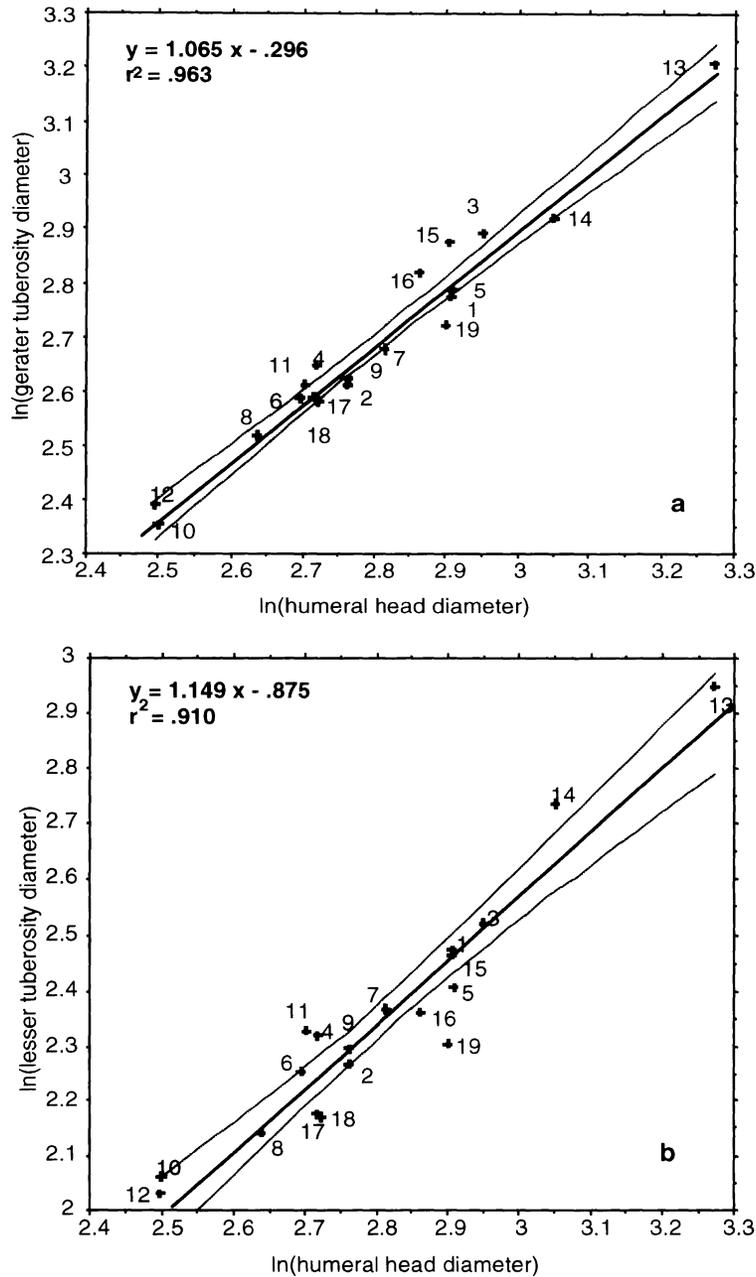
The lateral rim of the patellar surface is elevated moderately in guenons. The proximolateral margin of the patellar surface is especially raised in *Cercopithecus mona* (Fig. 5e) as is in *Presbytis* and *Colobus* (Fig. 5i, j). The patellar surface of *Cercopithecus mona* tends to be extensive proximolaterally. The relative elevation of the lateral rim is particularly large in male *Cercopithecus mona* (index 11).

### III. Allometric Analysis within Cercopithecids

Fig. 7a-k indicate the scaling of humeral and femoral measurements in Old World monkeys. All of the plots exhibit highly significant correlation. In most cases,  $r$  squared values are more than 0.83, except for the plot depicting femoral length versus greater trochanter projection (Fig. 7e), and femoral length versus neck length (Fig. 7f). In general, scaling trends are close to isometry. However, there are a few exceptions. The diameter of the lesser tuberosity scales slightly positively relative to femoral head diameter ( $k=1.149$ , Fig. 7b). Negative allometry is seen in the diameter of the femoral neck relative to neck length ( $k=.855$ , Fig. 7g), and condyle depth relative to bicondylar width ( $k=.848$ , Fig. 7i). Significant correlation is not observed between the length of the femur and trochanter projection. Thus, the greater trochanter height is not included in the PPE analysis.

Since most of the scaling trends are close to isometry, there is few discrepancies between results of PPE analysis and bivariate index (Table 5). For example, in the scaling of the greater tuberosity diameter on the head diameter, *Cercocebus torquatus* and *Cercocebus galeritus* have a larger PPE than *Cercocebus albigena*. Similarly, PPEs of male and female *Cercopithecus aethiops* are larger than those of *Cercopithecus mitis* and *Cercopithecus mona*.

Subtle discrepancies are also noted. The PPE of neck diameter is quite small in female *Cercopithecus aethiops*. The robusticity index of the neck is larger in female *Cercopithecus aethiops* than is in male *Cercopithecus mitis* (index 7), but the PPE is larger in male *Cercopithecus mitis*. The neck of female *Cercopithecus aethiops* is rather gracile if its smaller body size is taken into account. Due to the negative allometric relation, the depth to the width ratio of the distal epiphysis of the femur tends to be smaller as size increases. However, in this case no marked allometric effect is recognized



**Fig. 7a-k.** Logarithmical scaling of the measurements. Curved lines beside the regression line represent 95% confidence limit of the predicted value. 1: male *Cercocebus albigena*; 2: female *Cercocebus albigena*; 3: male *Cercocebus torquatus*; 4: female *Cercocebus torquatus*; 5: male *Cercocebus galeritus*; 6: female *Cercocebus galeritus*; 7: male *Cercopithecus mitis*; 8: female *Cercopithecus mitis*; 9: male *Cercopithecus mona*; 10: female *Cercopithecus mona*; 11: male *Cercopithecus aethiops*; 12: female *Cercopithecus aethiops*; 13: male *Papio*; 14: female *Papio*; 15: male *Colobus guereza*; 16: female *Colobus guereza*; 17: male *Presbytis melalophos*; 18: female *Presbytis melalophos*; 19: male *Nasalis larvatus*.

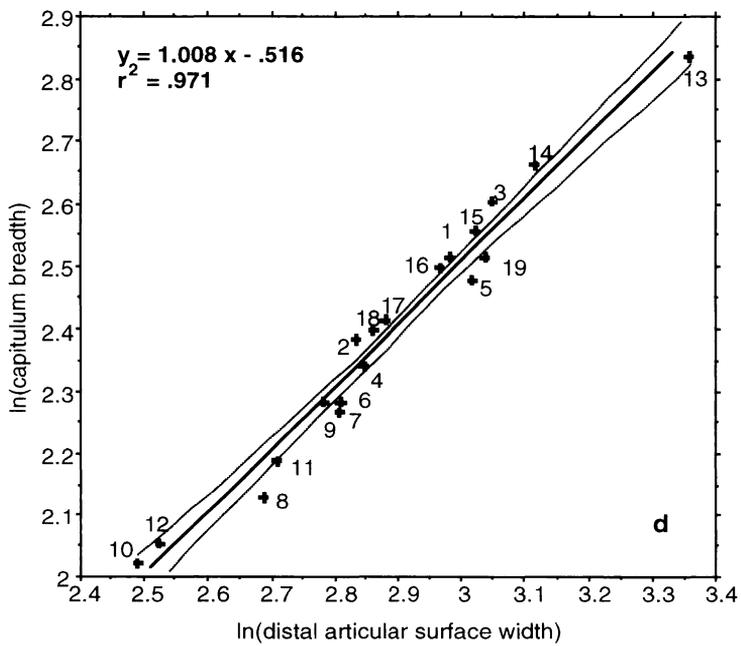
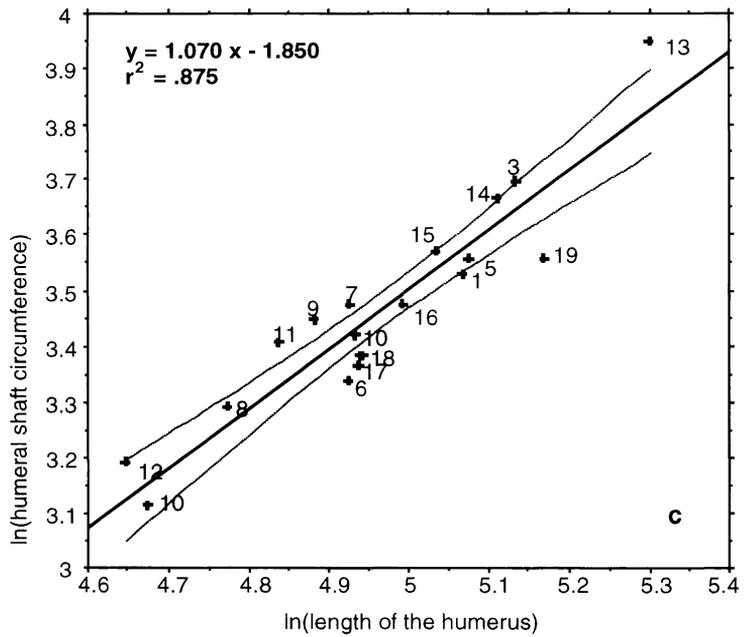


Fig. 7c-d.

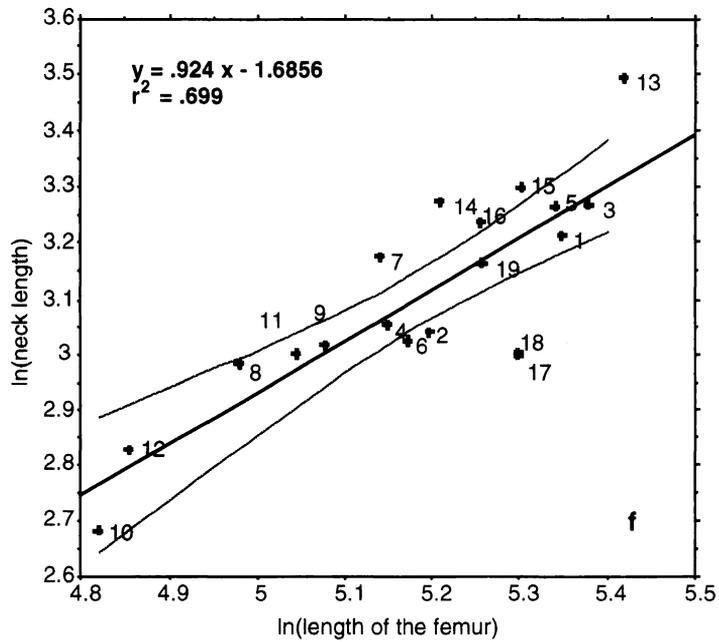
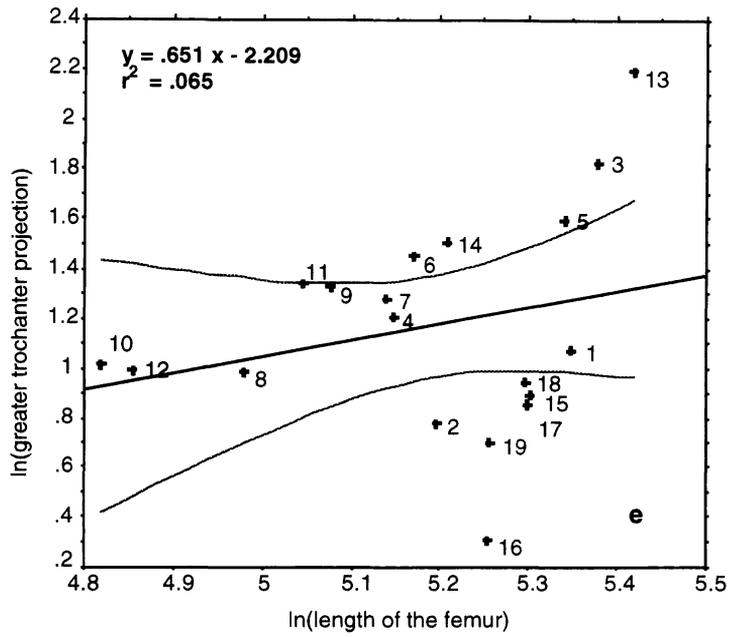


Fig. 7e-f.

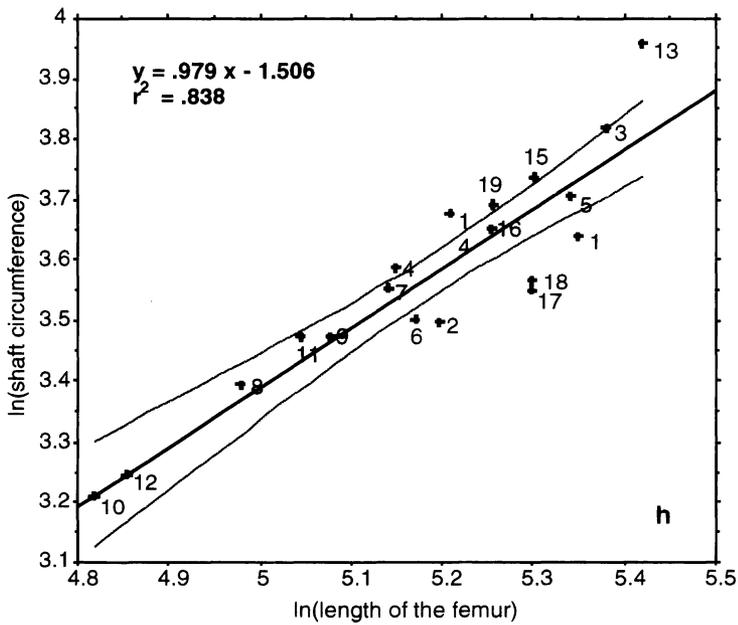
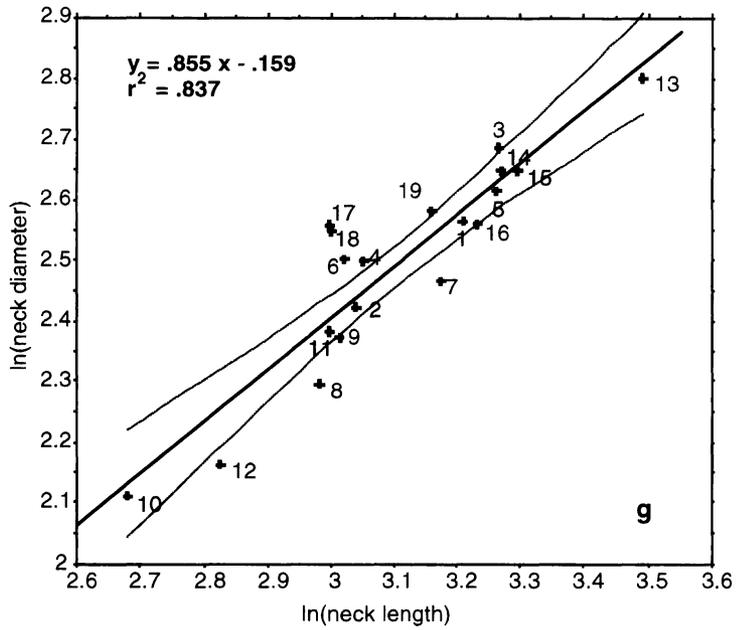


Fig. 7g-h.

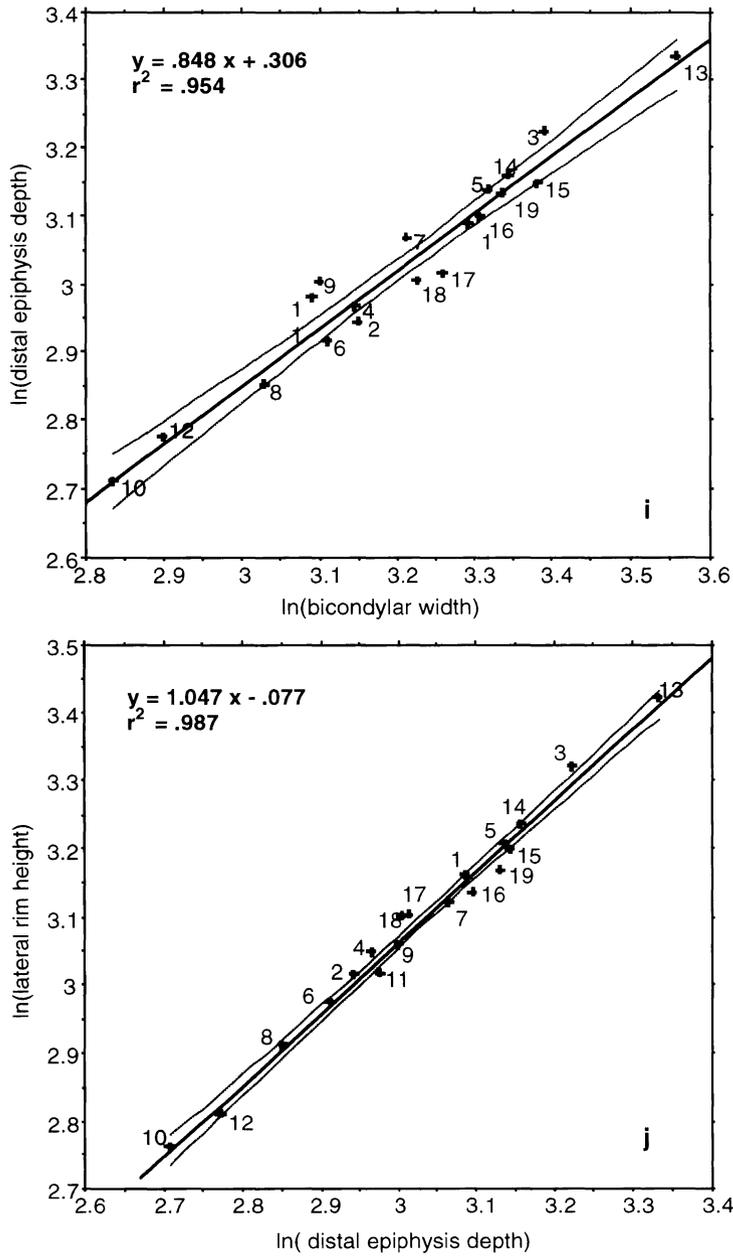


Fig. 7i-j.

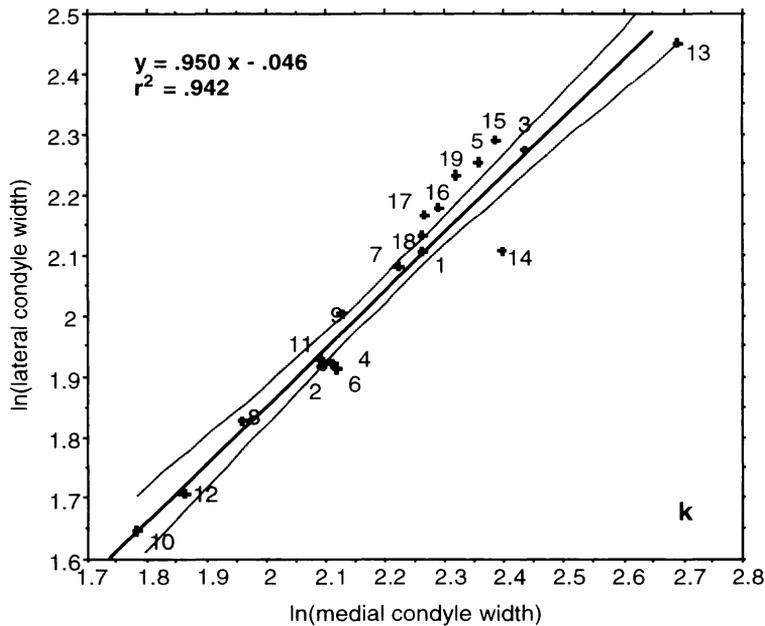


Fig. 7k.

in the result of the PPE analysis. Both *Cercocebus albigena* and *Cercopithecus mitis* exhibit a negative deviation from the scaling trend. In general, when interpreting functional morphology of mangabeys and guenons, allometric factors, even if they exist, can be mostly neglected mostly because of the relatively small size differences in these forms.

#### IV. Comparison of the Humerus and Femur with Non-cercopithecine Taxa

The humeral head of the mangabey and guenon as well as that of *Papio* is less convex and mediolaterally wide in contrast to the round or bulbous and proximodistally elongated shape seen in New World climbers (Fig. 3; Gebo et al., 1988; Harrison, 1989; Rose M.D., 1989). The humeral head of *Cercopithecus aethiops* and *Papio* is particularly flattened anteriorly (M.D. Rose, 1989). The condition in colobines is similar to that of most mangabeys and guenons with the exception of *Presbytis melalophos*, whose humeral head is relatively round (Fig. 3).

The bituberosity angle (angle 2) in cercopithecines including *Papio* overlaps those of colobines (about 72°) except *Presbytis melalophos* (around 80°). *Alouatta* and *Cebus* also have a similar value (about 60° to 80°). *Ateles*, *Pan*, and *Hylobates* exhibit values much larger than these primates (more than 100°; also see Harrison, 1989; Rose, M.D., 1989; Schön Ybarra & Schön, 1988).

The greater tuberosity projects above or is at the same level of the humeral head in

**Table 5.** Percent Predicted Error (PPE) calculated from the logarithmic least square regression in Fig. 7.

species	sex	a greater tuberosity diameter	b lesser tuberosity diameter	c humeral shaft robusticity	d capitulum breadth	f femoral neck length	g femoral neck diameter	h femoral shaft circumfer- ence	i femur distal epiphysis depth	j femoral condyle width ratio	k patellar surface rim height
<i>C.albigena</i>	m	-2.7	0.3	-4.7	2.3	-4.4	-2.0	-8.8	-1.1	0.1	0.6
	f	-3.3	-3.4	-5.7	4.2	-7.2	-2.3	-8.2	-3.4	-2.5	1.3
<i>C.torquatus</i>	m	4.6	0.4	5.1	-3.6	-1.7	5.0	5.8	4.5	0.5	2.4
	f	4.5	7.3	-1.1	-0.8	-2.0	5.6	5.3	-0.7	-4.7	2.0
<i>C.galeritus</i>	m	-1.5	-5.6	-2.6	-4.9	1.5	-1.9	-1.9	1.6	5.5	0.4
	f	0.6	3.1	-8.0	-3.2	-6.3	7.8	-5.6	-3.0	-4.7	0.6
<i>C.mitis</i>	m	-2.8	0.1	5.3	-5.1	11.8	-8.2	2.6	3.6	1.7	-1.4
	f	0.3	-1.7	3.1	-6.2	7.0	-9.2	2.2	-2.5	0.8	0.8
<i>C.mona</i>	m	-3.2	-1.1	7.3	-0.7	1.2	-4.7	0.7	6.8	2.5	-0.3
	f	-1.7	5.7	-3.9	1.9	-8.1	-2.8	-0.1	-0.5	-0.8	0.4
<i>C.aethiops</i>	m	3.0	9.8	7.9	-3.2	2.7	-2.6	3.6	5.0	-1.0	-2.0
	f	2.1	2.9	7.0	2.6	3.0	-9.0	-0.1	0.6	-1.3	-1.4

both cercopithecines and colobines (Fig. 2, 3). In *Pan*, the greater tuberosity is almost at the same level as the humeral head. In *Hylobates*, *Ateles*, *Alouatta* and *Cebus*, the greater tuberosity lies below the humeral head. This feature is relatively weak in *Cebus*. The articular surface of the distal humerus is uniform in guenons. The trochlear keels are not developed as markedly as is in *Papio* and semi-terrestrial mangabeys, but are distinct in comparisons with colobines, larger cebids and apes (Fig. 2; also see Napier & Davis, 1959; Ford, 1988; M.D. Rose, 1988; Schön Ybarra & Schön, 1988; Harrison, 1989). On the other hand, the humeroulnar joint of semi-terrestrial mangabeys and *Papio* exhibits structural adaptations for joint stability. The trochlear keels of colobines are reduced as compared with cercopithecines (Fig. 2). *Nasalis* is an extreme regarding this feature. *Presbytis melalophos* has a pronounced lateral trochlear keel as much as in guenons, however, the medial keel is very diminished. Its articular surface is mediolaterally wider in relation to the anteroposterior diameter of the trochlea as compared with cercopithecines (Fig. 2). The development of the trochlear keels of New World monkeys does not differ from that of colobines. However, the trochlea and capitulum are wider mediolaterally in New World monkeys than in colobines (Fig. 2). The trochlea of *Pan* and *Hylobates* has a relatively well developed trochlear keel. The gutter is developed between the trochlea and capitulum to receive the side of the radial head (Fig. 2; Sarmiento, 1985; M.D. Rose, 1989). This type of elbow joint is not observed in Old and New World monkeys. The medial epicondyle is quite large and projects medially.

Although the size and retroflexion of the medial epicondyle vary in cercopithecines, the medial epicondyle is short and relatively retroflexed in comparison to other taxa (Fig. 2). The average of the retroflexion angle (angle 3) is more than 30° in cercopithecines. The medial epicondyle of *Papio* and *Cercopithecus aethiops* is reduced in size and more posteriorly directed than in other cercopithecines. The medial epicondyle of colobines is less retroflexed than in cercopithecines (30-35°), although the size of the medial epicondyle is variable (largest in *Presbytis melalophos* and very diminished in *Nasalis*). In large-bodied cebids and apes, the medial epicondyle is quite large and projected medially (less than 20°) although moderate retroflexion is observed in *Cebus* (44°).

The greater trochanter extends above the head in the studied mangabeys and guenons by 2% of the femoral length except in *Cercocebus albigena*. This value is the largest of all the examined species except *Papio*, which has a particularly high greater trochanter. A relatively high greater trochanter is a common feature of the Cercopithecinae. The greater trochanter of colobines extends moderately above the femoral head (index 5, Fig. 5). Although the projection is less than in cercopithecines, both cercopithecines and colobines differ markedly from larger cebids and apes in this character. The greater trochanter of larger cebids and apes rarely projects beyond the femoral head (index 5, Fig. 5).

The head of the femur is a hemisphere in both cercopithecines and colobines. The neck-shaft angle is small (angle 4). By contrast, the femoral head of larger cebids

and apes is a sphere rather than a hemisphere (Fig. 6; Schön Ybarra & Schön, 1988). The head and neck is directed more proximally than in cercopithecines and colobines.

The distal femur in cercopithecines generally exhibits anteroposteriorly deep femoral condyles and a narrow and proximodistally long patellar groove (Fig. 5). In *Papio*, the knee joint is relatively wider than in guenons and mangabeys. The patellar groove of *Papio* is relatively wide. However, these features seem secondary specializations for improving knee joint stability, associated with a large body size. The patellar rims in *Papio* are parallel and raised anteriorly. The distal femur in colobines is mediolaterally wider than in cercopithecines, overlapping the range of larger cebids (index 9). However, the joint is mediolaterally symmetrical compared to that of larger cebids (e.g., *Alouatta*, *Ateles*), in which the medial condyle is displaced medially (Fig. 5). Regarding the symmetrical condition, the morphotype of the knee joint in colobines is close to that of cercopithecines. The distal femur of larger cebids is also mediolaterally wide, especially in *Ateles*. The medial condyle deviates medially from the center of the patellar surface, the medial rim of which is raised more prominently than the lateral rim (Fig. 5). In *Pan* and *Hylobates*, the distal femur is mediolaterally wide. The patellar surface is also wide. The medial deviation of the medial condyle is emphasized in *Pan*, as it is in *Ateles*. *Alouatta* and *Cebus* differ from apes in their narrow patellar surface.

## DISCUSSION

### I. Function of the Humerus and Femur

#### 1. Humeral Tuberosities

The humeral tuberosities accommodate insertions for the rotator cuff muscles; *mm. supraspinatus* and *infraspinatus* on the greater tuberosity, and *m. subscapularis* on the lesser tuberosity. In most cursorial mammals and terrestrial primates the greater tuberosity is quite large and projects proximally above the humeral head (Fleagle & Simons, 1982). A highly projected greater tuberosity is recognized in the terrestrial *Papio* (Fig. 3g).

The greater tuberosity of *Papio* is large in diameter (Table 4, index 1) and projected laterally from the humeral head (Fig. 2g). Jolly (1967) claims that the proximal projection of the greater tuberosity increases the moment arm for *m. supraspinatus* to enable powerful and well-controlled movements at the glenohumeral joint for joint stabilizing and arm protraction. The projection of the greater tuberosity is relatively low in arboreal primates, like some colobines, New World monkeys and apes (Fig. 2, 3). In most of these species, the greater tuberosity diameter is small as compared with more terrestrial species (index 1). Though the index is largest in the arboreal *Colobus guereza*, the greater tuberosity of *Colobus guereza* lies at the lower level as compared with other colobines (Fig. 3h). Since a lower greater tuberosity shortens the lever arm for

*m.supraspinatus* in the retracted position, it may enable a fast protraction of the forelimb (Jolly, 1967). EMG studies by Larson & Stern (1989, 1992) revealed that the *m.supraspinatus* of primates acts as a joint stabilizer rather than a protractor during walking or galloping on the level surface. These authors explain that a relatively low greater tuberosity in arboreal primates is correlated with the greater mobility of the glenohumeral joint at the expense of the lever arm length of *m.supraspinatus* (Larson & Stern, 1989, 1992). Arm-raising is frequently observed in arboreal locomotor activities (Schön Ybarra & Schön, 1988) and in postural activities particularly (Morbeck, 1977; M.D. Rose, 1979).

The semi-terrestrial *Cercocebus torquatus* and *Cercocebus galeritus* exhibits a greater tuberosity similar to that of *Papio*. Although the superior projection of the greater tuberosity is less marked in *Cercocebus torquatus*, the tuberosity is expanded laterally (Fig. 2b, 3b), and the anteroposterior diameter of the greater tuberosity is significantly larger than that of *Cercocebus albigena*. Thus, *Cercocebus torquatus* and *Cercocebus galeritus* may have a relatively longer lever arm for *m.supraspinatus* and more developed rotator cuff muscles. In contrast, the diameter of the greater tuberosity is relatively small in *Cercocebus albigena*. The greater tuberosity of *Cercocebus albigena* neither projects as highly as is in *Cercocebus galeritus* (Fig. 2a, 3a) nor expands laterally (Fig. 2a). These conditions suggest that *Cercocebus albigena* has a greater shoulder joint mobility than in *Cercocebus torquatus* and *Cercocebus galeritus*.

The shape and size of the lesser tuberosity is less variable than that of the greater tuberosity. Although there is a size difference in the lesser tuberosity between females of *Cercocebus torquatus* and *Cercocebus albigena*, such a difference is not evident in males. *M.subscapularis* probably has a more uniform function through the range of postures and behaviors exhibited by mangabeys than do the muscles inserting on the greater tuberosity.

The greater tuberosity of the semi-terrestrial *Cercopithecus aethiops* is large in diameter and markedly projects superior to the head of the humerus. As in the semi-terrestrial mangabeys, the greater tuberosity of *Cercopithecus aethiops* is probably adapted for powerful protraction of the arm or stabilization of the shoulder joint as compared with the relatively small and virtually non-projecting greater tuberosity of *Cercopithecus mitis*. The lesser tuberosity of *Cercopithecus aethiops* also tends to project high. The diameter is larger than that of *Cercopithecus mitis* and *Cercopithecus mona*. Since the lesser tuberosity diameter is particularly large in *Papio* (Table 4, index 2), the development of *m.subscapularis* might be correlated with quadrupedal progression on the ground. The greater tuberosity of the arboreal *Cercopithecus mona* forms a sharp projection on the anterolateral side of the humeral head, differing from *Cercopithecus mitis*, although its diameter is not particularly large. This configuration may suggest that powerful and well-controlled recruitment of *m.supraspinatus* is required in *Cercopithecus mona*.

As well as the superior projection, the positioning of the greater tuberosity also affects the lever arm length of *m.supraspinatus* and *infraspinatus* (Jolly, 1967). In

arboreal quadrupeds, the tuberosities are positioned closer along the side of the articular surface (Fleagle & Simons, 1982). This tendency is shown in Table 4 (angle 1). Humeral tuberosities that are located alongside of the head provide widespread insertions for the rotator cuff muscles. Therefore, the muscles can act to stabilize the shoulder joint effectively through a range of forelimb position. By contrast, an anteriorly positioned greater tuberosity is often combined with a projection of the greater tuberosity. This condition lengthens the lever arm of the *mm.supraspinatus* and *infraspinatus* (Fleagle & Simons, 1982). The greater tuberosity angle (angle 1) is largest in *Papio* (Fig. 3).

While there is no interspecies difference in the orientation of the greater tuberosity among mangabeys, the semi-terrestrial *Cercopithecus aethiops* has a more anteriorly positioned greater tuberosity than the other guenons. This positioning of the greater tuberosity in *Cercopithecus aethiops* might suggest a specialization for economical forelimb excursion in the parasagittal plane.

The morphological differences of the humeral tuberosities indicate that there are different functional adaptations corresponding to either arboreal or semi-terrestrial habitats. In more terrestrial species, the rotator cuff muscles are more developed and have longer lever arms, whereas in more arboreal species shoulder joint mobility is optimized. However, the arboreal *Cercopithecus mona* exhibits the higher projection of the greater tuberosity than *Cercopithecus aethiops*. The shoulder joint of *Cercopithecus mona* may be modified to gain a greater power. This condition resemble that of *Presbytis melalophos*. The greater tuberosity of *Presbytis melalophos* projects proximally but is small in diameter (Fig. 2i, index 1). *Presbytis melalophos* is known to engage in frequent leaping and arm-swinging (Fleagle, 1977). Quadrupedal branch walking and leaping in *Cercopithecus mona* may require large muscle force as much as in ground walking and running in *Cercopithecus aethiops*.

## 2. Humeral Head

The shape of the articular surface of the humeral head closely correlates with shoulder joint mobility (e.g., Schön Ybarra & Schön, 1988; M.D. Rose, 1989). Movements of the humeral head on the glenoid cavity are restricted by the humeral tuberosities. The bituberosity angle affects the range of axial rotation and abduction-adduction of the humerus significantly. A larger bituberosity angle which is combined with inflation of the humeral head increases joint mobility (M.D. Rose, 1989). The bituberosity angle (angle 2) is quite large in apes and the suspensory *Ateles* whereas it is smaller in Old World monkeys and non-suspensory New World monkeys (Fig. 3). The humeral head is less convex in cercopithecines in comparison with *Pan*, *Hylobates* and large-bodied cebids (Fig. 2, 3; also see Gebo et al., 1988; Harrison, 1989; M.D. Rose, 1989). The humeral head is nearly a hemisphere in mangabeys and guenons rather than a proximodistally elongated ovoid as seen in the New World climber (Fig. 2m, also see Schön Ybarra & Schön, 1988). Thus, extreme arm protraction-retraction is unlikely in these cercopithecines.

In the examined cercopithecines, only *Cercopithecus aethiops* exhibits a few differences regarding the humeral head morphology. The flattened anteroproximal aspect of the head limits the mobility of the glenohumeral joint when the arm is fully protracted, because the capabilities for axial rotation and abduction-adduction are restricted. Once the shoulder joint is stabilized, the scapula and humerus can act as a unit and the powerful scapulothoracic muscles can be used to produce the propulsive force at the beginning of the stance phase (M.D. Rose, 1989). In posterior view, the head has an ovoid shape which is elongated in the inferomedial to superolateral direction (Fig. 3f). Therefore, axial rotations of the humerus in the retracted position may be more restricted in *Cercopithecus aethiops* compared with *Cercopithecus mitis* and *Cercopithecus mona*.

### 3. Surgical Neck

The cross-sectional shape of the surgical neck is rhomboidal in the semi-terrestrial mangabeys (Fig. 4b, c). In contrast, the cross section of the surgical neck is a more or less round shape in *Cercocebus albigena* (Fig. 4a). Since the rhomboidal shape is caused by the development of ridges which accommodate insertions for muscles of the arm (*mm. teres major*, *deltoideus*, and *pectoralis major*) and the vertical buttress for humeral head (Fig. 4), it is likely that *Cercocebus torquatus* and *Cercocebus galeritus* have a more developed muscular system in this region. Besides the body size difference, intensive activities may be involved more frequently in the semi-terrestrial mangabeys than in the arboreal mangabey.

In *Cercopithecus aethiops*, the cross section of the neck is distinctively flattened. The asymmetrical shape in *Cercopithecus aethiops* may be functionally adaptive to bear unidirectional forces rather than torsions and bending forces acting in various directions (Schön Ybarra & Schön, 1988). The fore-aft excursion may be most dominantly involved in the shoulder joint during terrestrial activities.

### 4. Shaft of the Humerus

The shaft of the humerus in cercopithecines exhibits a developed bowing. The deltopectral plane flares eminently. This curvature lengthens the moment arms for *mm. deltoideus* and *pectralis major* and enables the powerful and economical excursion of the forelimb. The flaring of the deltopectral plane accommodates a larger insertion area for these muscles. In contrast to cercopithecines, the humeral shaft is straight in living apes and *Ateles* (Fig. 2, 3). The greater shaft bowing in the semi-terrestrial mangabeys and guenon suggest the significance of recruiting these muscles for terrestrial cursorial movements.

Burr et al. (1989) noted that the shafts of the humerus and femur have a greater structural rigidity in terrestrial than in arboreal macaque. In general, highly terrestrial primates tends to exhibit a higher robusticity index of the humerus. For example, *Papio* has a larger shaft circumference in relation to humeral length than do the arboreal colobines (index 3). On the other hand, the shaft is thin in brachiating

primates (e.g., *Hylobates*, *Ateles*). In mangabeys, the semi-terrestrial *Cercocebus torquatus* tends to have more robust humerus than the arboreal *Cercocebus albigena*. Guenons have similarly robust humerus irrespective of different modes of positional behavior. Since the robusticity index of arboreal guenons is comparable to that of semi-terrestrial mangabeys, arboreal activities in *Cercopithecus mitis* and *Cercopithecus mona* probably produce higher stress than in *Cercocebus albigena*.

### 5. Humeroulnar Joint

The humeroulnar joint experiences shearing and rotational forces during the support phase of quadrupedal progression (Jenkins, 1973; M.D. Rose, 1988; Harrison, 1989). The elevation of the trochlear keels effectively resists these forces when the elbow is partially flexed (Jenkins, 1973; M.D. Rose, 1988). During higher speed gaits, the humeroulnar joint needs to be stabilized in extended or semi-flexed positions. By contrast, trochlear keels are relatively low in exclusively arboreal monkeys (e.g., *Alouatta*) without the rigid guide of the elbow joint in the anteroposterior direction (Fig. 2m; also see Schön Ybarra & Schön, 1988).

When the elbow is extended or partially flexed, the medial surface of the lateral keel assumes an extensive contact with the proximolateral extension of the articular surface of the trochlear notch of the ulna. The pronounced trochlear keels of *Cercocebus torquatus* and *Cercocebus galeritus* provide a higher joint stability which excludes rotational movements of the ulna. By contrast, the trochlear keels of *Cercocebus albigena* are reduced, suggesting a relatively low joint stability. The trochlear keels of the studied guenons is not as markedly developed as in mangabeys. It may provide sufficient joint stability for medium sized primates which adopt relatively agile quadrupedal movements in both arboreal and semi-terrestrial habitats.

### 6. Humeroradial Joint

Capitular size and shape reflect the mobility of the humeroradial joint (pronation and supination). Colobines and *Ateles* have a mediolaterally wide and round capitulum, which allows rotations of the radial head freely during partial flexion of the elbow (Fig. 2). Arboreal substrates are not only horizontal but also diagonal or vertical (Grand, 1968). A greater pronation-supination capability is required for grasping variably positioned substrates. *Pan*, *Cebus*, and *Alouatta* have a relatively narrow capitulum in relation to a very wide trochlea. The trochlea in these species are especially developed for the stability at the humeroulnar joint and their capitulum may be wide enough for pronation and supination. The relatively wide and moderately round capitulum of *Cercocebus albigena* suggests free pronation-supination movements in a partially flexed position. On the other hand, a relatively narrow and round capitulum in *Cercocebus torquatus* and *Cercocebus galeritus* might be suitable to keep the forearm pronated in the semi-flexed position. Capitular shape is less variable in guenons, where the relative width and convexity of the capitulum are generally uniform. The humeroradial joints of guenons are not as different from those of mangabeys as

is the humeroulnar joint.

### 7. Medial Epicondyle

Flexors of the wrist and digits originate from the medial epicondyle of the humerus. A short and posteriorly flexed medial epicondyle, as seen in terrestrial mammals (see *Papio*, Fig. 2g), is beneficial in reducing the medial torques which are caused by the activities of the flexors in the fully pronated position (Jolly, 1967; Jenkins, 1973). Jolly (1967) claims that the reduced size of the medial epicondyle in terrestrial primates is related to the relative reduction of the flexor muscle masses. He explains that wrist and digits flexion is less important in terrestrial movements than in climbing and branch walking, in which chiropodial grasping plays a significant role (Jolly, 1967). On the other hand, a large and medially directed medial epicondyle in arboreal primates (Fig. 2k-o; also see Schön Ybarra & Schön, 1988) provides a longer lever arm for the flexors through different pronated-supinated positions (Fleagle, 1988). The roles of the wrist and digital flexors are important in holding supports during climbing or branch walking (Morbeck, 1979; Schön Ybarra & Schön, 1988). The semi-pronated posture is usually required in such behaviors (Sarmiento, 1985).

The retroflexed epicondyle of *Cercocebus torquatus*, *Cercocebus galeritus* and *Cercopithecus aethiops* probably reduces the torques caused by the flexor masses which originates there during the pronograde progression on the ground. *Cercocebus torquatus* has a relatively short medial epicondyle as compared to both *Cercocebus galeritus* and *Cercocebus albigena*. If a small sized medial epicondyle is correlated with the reduction of the flexor masses, it is suggested that *Cercocebus torquatus* is specialized for a more semi-terrestrial style of life than *Cercocebus galeritus*. On the other hand, a long medial epicondyle of *Cercocebus albigena* support the inference that developed flexors of the wrist and digits are necessary for larger sized primates to climb the trees or to walk on the branches (Manaster, 1975).

## II. Morphology of the Femur

### 1. Greater Trochanter

The upper part of the greater trochanter provides a lever arm for *mm.gluteus medius* and *piriformis*. Thus, a higher projection of the greater trochanter seen in semi-terrestrial forms (e.g., Fig. 5g) allows the muscles to produce a greater force (Howell, 1944), whereas a less projecting one (e.g., Fig. 5m- o) allows greater mobility at the hip joint. The latter type is favored in climbing or scansorial activities (Walker, 1974) and for branch walking in which the thigh is often in an abducted position (Grand, 1968; Schön Ybarra & Schön, 1988). The higher trochanter of *Cercocebus torquatus* and *Cercocebus galeritus* would enable greater propulsive forces to be developed when thigh excursion occurs in the parasagittal plane. On the other hand, the lower greater trochanter of the arboreal *Cercocebus albigena* would allow a larger degree of hip abduction at the expense of the leverage of *mm.gluteus medius* and *piriformis*.

Both arboreal and semi-terrestrial guenons also have a relatively high greater trochanter, as do the semi-terrestrial mangabeys. The high projection of the greater trochanter limits hip joint abduction. This situation might be disadvantageous in arboreal *Cercopithecus mitis* and *Cercopithecus mona*. However, a recent kinesiological study indicates that hip joint abduction does not occur in the branch walking of some cercopithecines (Meldrum, 1991). If this is also true for these guenons, the projection of the greater trochanter may not compromise their branch walking.

## 2. Femoral Head

The shape of the articular surface of the femoral head is closely correlated with habitual joint position (Jenkins, 1972; Jenkins & Camazine, 1977). An extensive articular surface allows a larger mobility at the hip joint (Fig. 6l, m, o). The posteroproximal articular surface extension has been explained as allowing a wider range of femoral abduction or extension during activities such as climbing or leaping (Fleagle, 1976a; Jenkins & Camazine, 1977; K.D. Rose, 1987; Ford, 1988; Schön Ybarra & Schön, 1988). In general, the femoral head is hemispherical in most catarrhines, in particular *Papio* (Fig. 6g), whereas it is close to a sphere in cebids (Fig. 6m, o).

Since the femoral head of mangabeys is hemispherical rather than spherical (Fig. 6a-c), movements at the hip joint are involved mainly in a parasagittal plane. However, the slightly extensive articular surface of *Cercocebus albigena* may allow a relatively large range of abduction and axial rotation, though not extreme as is in New World monkeys. The femoral head of guenons is uniform and resembles that of *Cercocebus torquatus* and *Cercocebus galeritus*. Probably, both the arboreal and semi-terrestrial guenons share a similar hip joint mechanism irrespective of different positional habits.

The position of the fovea capitis femoris is considered to be related with femoral posture in locomotor and postural behaviors (Jenkins & Camazine, 1977). The fovea is situated on the center of the femoral head in cursorial animals, reflecting an adducted position of the femur, whereas it is more proximally positioned in ambulatory or scansorial animals, due to a habitually abducted limb position (Jenkins & Camazine, 1977; K.D. Rose, 1987; Fleagle & Meldrum, 1988). The fovea capitis of *Presbytis melalophos*, a prominent leaper (Fleagle, 1976a, 1977), is located inferiorly from the center of the articular surface, presumably reflecting hindlimb excursion in the adducted position (Fig. 6i). On the other hand, that of *Alouatta* is more superiorly situated (Fig. 6m). This condition reflects a more versatile use of the hindlimb in *Alouatta*. Most cercopithecines have a fovea which is located slightly posteroinferior to the center of the articular surface. The femur is likely to be positioned slightly abducted and laterally rotated. Neither extreme abduction nor adduction of the hip joint seems likely.

Although there is no difference in the location of the fovea, *Cercopithecus mona* has a round and deep fovea, differing from ellipsoidal and shallow one in other cercopithecines. Since the ligamentum teres inserts here, this feature may indicate a pronounced development of the ligament. Although the ligamentum teres itself does not contribute to joint stability, this ligament is tightened during ricochet

leaping, as seen in *Tarsius* (Grand & Lorenz, 1968). The fovea of *Presbytis melalophos* is often deeply excavated as compared with other langur species (*personal observation*). The fovea of *Cercopithecus mona* might suggest a great range of flexion-extension at the hip joint.

### 3. Femoral Neck

A short femoral neck is adaptive for activities in which the neck is highly stressed (Fleagle & Meldrum, 1988). Prominent leapers (e.g., *Presbytis melalophos*, *Pithecia pithecia*) have a shorter neck than in non-leaping primates (Fig. 6i; also see Fleagle, 1976a and Fleagle & Meldrum, 1988). On the other hand, a longer neck promotes a greater degree of thigh abduction, which is required in branch walking and climbing (Schön Ybarra & Schön, 1988). It also provides longer moment arms for muscles of the hip joint, although structural strength may be sacrificed.

Although there is no significant differences in relative neck length and robusticity among mangabeys, the arboreal *Cercopithecus mitis* has a longer and more gracile neck than in *Cercopithecus mona* and *Cercopithecus aethiops*. The long neck allows a wide range of movements at the hip joint. By contrast, the arboreal *Cercopithecus mona* has a short and robust neck, differing from the arboreal *Cercopithecus mitis*. It can be presumed that hindlimb usages are different between *Cercopithecus mitis* and *Cercopithecus mona*. Abduction at the hip joint may be involved more frequently in the former while intensive excursions in the parasagittal plane may be dominant in the latter.

Leapers often exhibit an acute neck-shaft angle (angle 4) combined with a short neck. This situation is correlated with a more adducted femoral position. On the other hand, arboreal quadrupedal walkers have a bluntly angled and relatively long neck which allows a greater abduction of the femur (Fleagle, 1976a; Fleagle & Meldrum, 1988). Table 4 shows that leaping *Colobus guereza* (Fig. 6h) and *Presbytis melalophos* (Fig. 6i) exhibit an acute neck-shaft angle as compared with New World anthropoid (Fig. 6m-o) and *Hylobates* (Fig. 6l). The angle of most quadrupedal cercopithecines are in-between these two extremes. The highly terrestrial *Papio* has an angle of 125°, which is in the range of mangabeys and guenons. There is no difference in the neck-shaft angle in mangabeys and guenons. This angle may not be affected significantly by locomotor behaviors in these cercopithecines.

### 4. Femoral Shaft

As is in the humerus, terrestrial cursorial locomotion requires a greater structural rigidity of the femoral shaft due to high speed gaits (Burr et al., 1989). In fact, the femur of *Papio* has a greater robusticity index (index 8). The semi-terrestrial mangabeys have more robust femoral shaft than the arboreal mangabey. On the other hand, such a distinction is not seen in guenons. The robusticity index of guenons is equivalent to that of semi-terrestrial mangabeys. This suggests that agile running and leaping on branches may require structural strength of femur in arboreal guenons to the same

degree much as in the semi-terrestrial guenon for ground running.

### 5. Femoral Condyles

An anteroposteriorly deep knee joint tends to restrict the joint mobility to the parasagittal plane. This configuration enhances the economy of flexion-extension of the knee. This type of joint is typically seen in cursorial digitigrade mammals (Tardieu, 1981). In contrast, a mediolaterally wider knee joint accommodates a larger contact area on the tibial plateau in various degrees of knee rotation. This type of knee joint is adaptive for maneuvers in which knee rotations are involved and is found in ambulatory plantigrade mammals (Tardieu, 1981). The mediolaterally wide knee joint of *Cercopithecus mitis* may suggest knee rotations are involved more frequently in the arboreal activities. However, the knee joint of *Cercopithecus mona* is relatively deep. Therefore, flexion-extension may be more dominant function at the knee joint in *Cercopithecus mona*.

The medial and lateral femoral condyles of leapers have a similar mediolateral width, whereas the medial condyle is wider than the lateral condyle in arboreal quadrupedal walkers (Fleagle, 1976a; Fleagle & Meldrum, 1988). According to these authors, the adducted femoral position in leaper introduces even loads on both the medial and lateral condyles. The abducted and laterally rotated position of the femur in arboreal quadrupeds results in a larger load on the medial side of the knee joint (Fleagle, 1976a; Fleagle & Meldrum, 1988). However, there is no difference in the proportion of the femoral condyle between the examined species of mangabey and guenon. The lateral condyle is slightly narrow relative to the medial condyle. Even *Papio* has a particularly narrow lateral condyle in relation to the medial one. Although an allometric relationship may exist in the size of the medial and lateral condyles, cursorial movements on the ground might require a different function from that of arboreal leaping.

### 6. Patellar Surface

Leapers have a patellar surface which is proximally extended with a pronounced lateral rim (Walker, 1974; Fleagle, 1976a; Fleagle & Meldrum, 1988). This condition is typically seen in *Presbytis melalophos* (Fig. 5i). The proximal extension of the patellar surface reflects a higher range of knee extension. The prominent lateral margin of the patellar surface correlates with the powerful contraction of the quadriceps (Fleagle, 1976a).

The patellar surface of *Cercocebus torquatus* is narrow and deeply excavated. The patellar rims are anteriorly raised. This condition prevents the dislocation of the patella during intensive knee flexion-extension. In contrast to *Cercocebus torquatus*, the wider and shallower patellar surface of *Cercocebus albigena* suggests wide range of movements at the knee joint including not only flexion-extension, but also rotation and abduction (K.D. Rose, 1987). The relatively low patellar rim suggests less developed knee extensors in *Cercocebus albigena* as compared with *Cercocebus torquatus*. The

patellar surface of *Cercocebus galeritus* is wider than that of *Cercocebus torquatus* and the patellar surface rims are only moderately raised. Probably, knee function is similar to *Cercocebus albigena*. The knee joint of *Cercocebus torquatus* seems more specialized for powerful cursorial movements in comparison with the joint of *Cercocebus albigena* and *Cercocebus galeritus*, even though the depth of the femoral condyles do not differ. *Cercopithecus mona* differs from other guenons in the raised proximolateral rim and proximal extension of the patellar surface. These features are associated with leaping habits (Fleagle, 1976a; Walker, 1974; Fleagle & Meldrum, 1988). In addition, *Cercopithecus mona* has deep femoral condyles. Thus, *Cercopithecus mona* may engage in leaping or agile arboreal movements relatively frequently.

### III. Diversity of Humeral and Femoral Morphology in Mangabeys and Guenons

Various functional morphologies of the humerus and femur are evolved within the *Cercocebus* and *Cercopithecus* genera. Since phylogenetic factors are minimal in the morphology of congeneric species (Fleagle, 1977), these differences, more than likely reflect different positional behaviors. The present study is, in this sense, an experiment for inferring the relationship between the positional behaviors (ie., arboreality and semi-terrestriality) and skeletal anatomy. In addition, it allows for comparisons between two genera of the relationship of behavior to morphology.

Fleagle (1976a) compared skeletal anatomy of two sympatric Malaysian leaf monkeys (*Presbytis obscura* and *Presbytis melalophos*). *Presbytis obscura* moves quadrupedally along large boughs while *Presbytis melalophos* often leaps between branches and engages in the forelimb suspension more frequently. He found numerous distinctions in the postcranial skeleton which are related to the difference in locomotor behavior between the two. Later, Fleagle & Meldrum (1988) recognized similar morphological differences between two New World pitheciines, one which engaged more often in leaping than the other. This shows a convergence caused by similar functional necessities and confirms the association between leaping habit and a number of specialized morphological features.

It is widely accepted that there are definite associations between strata preference and anatomy in primates. Generally speaking, terrestrially specialized primates tend to have a larger body size than arboreal primates because they are free from the constraint of substrate size. The increased body size is closely tied with behavioral characteristics in terrestrial habitats, such as great protection from predators, large home range, and long foraging time (e.g., M.D. Rose, 1974, 1979; Clutton-Brock & Harvey, 1977; Foley, 1987). Fast cursorial movements on the ground causes the robusticity of the skeletal system in specialized semi-terrestrial primates (Burr et al., 1989). The economy of cursorial movements is an important factor in terrestrial locomotion (Rodman, 1979). Limbs are adducted and extended, and their movements are restricted to the parasagittal planes (Roberts, 1974). A large stride and fast excursion of the limbs elaborates the economy of movements. The joints of the limbs have a

restricted, hinge-like mobility (Hildebrand, 1974). The restriction the joint mobility in turn increases the structural strength of the joint and saves on the energetic cost of stabilizing the joints.

On the other hand, arboreal primates are constrained in their body size, due to the necessity for maintaining balance on supports (Napier, 1967; Cartmill, 1985). Thus, large arboreal primates either move deliberately in trees, or they are specialized for below-branch activities. A distinctive feature of arboreal primates is their great joint mobility. Arboreal supports are unstable and variable in shape and direction (Fleagle, 1976b; Grand, 1984). Various limb positions and movements are required in both postural and locomotor behaviors. Highly mobile joints are required in order to maintain a grasp on supports (Grand, 1968; Mendel, 1976; Morbeck, 1977; Schön Ybarra & Schön, 1988). Limbs are flexed to lower the center of gravity close to the substrate so as to maintain a stable body balance reducing the moment arm around the supporting branch (Napier, 1967; Grand, 1968; M.D. Rose, 1974). Hands and feet are semi-pronated or inverted to grasp the supports. Structural adaptations for these functions are typically seen in larger cebids. These include a globular and extensive humeral head projecting above the humeral tuberosities, minimally developed trochlear keels, moderately round and wide capitulum, long and medially oriented medial epicondyle, lower projection of the greater trochanter, spherical shape of the head and asymmetrically developed femoral condyles (Ford, 1988; M.D. Rose, 1988, 1989; Schön Ybarra & Schön, 1988).

Although these tendencies are clear across the broad primate taxa, departures from these trends are apparent if confined to the species in the present study. For example, the semi-terrestrial *Cercopithecus aethiops* is not one of the larger species of guenons (Table 2, Appendix 1). *Cercopithecus aethiops* maintains an extreme ability for climbing trees (Struhsaker, 1978). Some mangabeys and guenons do not always display flexed and abducted limb posture when branch walking, instead they extend and adduct the limbs, moving the limbs primarily in the parasagittal plane (Meldrum, 1991).

When a species assumes a different positional behavior, structural adaptations to the past behavior are required to serve the new behavior. However, phyletic inertia constrains a species to develop specific modes of positional behavior. If the new behavior induces only similar stresses to the postcrania as those required in the past behavioral pattern, skeletal modification may not occur. Even though the new behavioral pattern introduces different stresses, skeletal modifications may differ in different groups. If past functional adaptation can serve the new stresses, skeletal modifications will be unlikely, or at least minor. Only when the past adaptation can not cope with new stresses, significant modifications will be developed. In addition, with difference in inherited morphology, different structural modifications may develop in different phyletic groups. Therefore, various behavioral and structural solutions to the same habitat are likely. To establish proper behavior-morphology associations, it will be necessary to analyze stresses to the postcrania in locomotor behaviors and to survey such associations in various living taxa confirming how much degree of the convergence

**Table 6a.** Character states of the humerus in mangabeys.

		<i>C.albigena</i>	<i>C.torquatus, C.galeritus</i>
greater tuberosity	h1	moderately projected	well projected ( <i>C.galeritus</i> )
	h2	diameter small	moderate ( <i>C.torquatus</i> ) diameter large laterally expanded
	h3	no difference in orientation	
lesser tuberosity	h4	no difference in projection	
	h5	no difference in diameter	
humeral head	h6	no difference in bituberosity angle	
	h7	no difference in sphericity	
surgical neck	h8	round cross section	rhomboidal cross section
shaft	h9	curvature weak	marked
	h10	circumference small	large
	h11	lateral & medial keels reduced	pronounced
humeral joint	h12	capitulum wide and flattened	narrow and round
medial epicondyle	h13	no difference in retroflexion angle	
	h14	long	short ( <i>C.torquatus</i> ) long ( <i>C.galeritus</i> )

**Table 6b.** Character states of the femur in mangabeys.

		<i>C.albigena</i>	<i>C.torquatus, C.galeritus</i>
greater trochanter	f1	proximally less projected	more projected
femoral head	f2	articular surface extensive	less extensive
	f3	no difference in fovea capitis shape	
neck	f4	no difference in length and diameter	
shaft	f5	circumference small	large
distal epiphysis	f6	no difference in a-p depth	
femoral condyles	f7	no difference in relative breadth	
patellar surface	f8	wide	narrow ( <i>C.torquatus</i> ) wide ( <i>C.galeritus</i> )
	f9	no difference in proximal extension	
	f10	lateral rim weakly elevated	elevated ( <i>C.torquatus</i> ) weakly elevated ( <i>C.galeritus</i> )

**Table 6c.** Character states of the humerus in guenons.

		<i>C.mitis, C.mona</i>	<i>C.aethiops</i>
greater tuberosity	h1	moderately projected ( <i>C.mitis</i> ) well projected ( <i>C.mona</i> )	well projected
	h2	diameter smaller	diameter larger
	h3	anterolaterally oriented	more anteriorly oriented
lesser tuberosity	h4	less projected	well projected
	h5	diameter smaller	diameter larger
humeral head	h6	no difference in bituberosity angle	
	h7	hemispherical	flattened
surgical neck	h8	rhomboidal, mediolaterally symmetry	rhomboidal, asymmetry
	h9	curvature weak	marked
humero-ulnar joint	h10	no difference in circumference	
	h11	no difference in trochlear keels	
humero-radial joint	h12	capitulum narrow ( <i>C.mitis</i> ) wide ( <i>C.mona</i> )	wide
	h13	posteromedially directed	more posteriorly directed
medial epicondyle	h14	no difference in size	

**Table 6d.** Character states of the femur in guenons.

		<i>C.mitis, C.mona</i>	<i>C.aethiops</i>
greater trochanter	f1	no difference in projection	
femoral head	f2	no difference in articular surface extension	
	f3	fovea capitis shallow ( <i>C.mitis</i> ) circular and deep ( <i>C.mona</i> )	shallow
neck	f4	long ( <i>C.mitis</i> ) short and robust ( <i>C.mona</i> )	short and robust
	f5	no difference in circumference	
shaft	f6	wide ( <i>C.mitis</i> ) deep ( <i>C.mona</i> )	deep
	f7	no difference in relative breadth	
distal epiphysis	f8	no difference in width	
	f9	no extension ( <i>C.mitis</i> ) proximally extended ( <i>C.mona</i> )	no extension
	f10	lateral rim not elevated ( <i>C.mitis</i> ) elevated ( <i>C.mona</i> )	weakly elevated

occurs. If morphological convergence does not occur, phyletic heritage needs to be analyzed.

Morphological characters which reflect either arboreal or semi-terrestrial activities are summarized in Table 6. The semi-terrestrial *Cercocebus torquatus* and *Cercocebus galeritus* differ from the arboreal *Cercocebus albigena* in 10 out of 24 characters (h2, h8, h9, h10, h11, h14, f1, f2, f5, f10 and h1, h2, h8, h9, h10, h11, h12, f1, f2, f5), respectively. In the *Cercopithecus* genus, the semi-terrestrial *Cercopithecus aethiops* differs from the arboreal *Cercopithecus mitis* and *Cercopithecus mona* in 11 characters (h1, h2, h3, h4, h5, h7, h8, h9, h12, h13, f6 and h2, h3, h4, h5, h7, h8, h9, h13, f4, f9, f10, respectively).

In general, habitat preferences correlate with morphological character states. Both *Cercocebus torquatus* and *Cercocebus galeritus* are distinguished from the arboreal *Cercocebus albigena* in 9 characters (h2, h8, h9, h10, h11, h12, f1, f2, f5). The semi-terrestrial *Cercopithecus aethiops* differs from the arboreal *Cercopithecus mitis* and *Cercopithecus mona* in eight characters (h2, h3, h4, h5, h6, h7, h8, h13). These morphological diversifications are presumably introduced by differentiation in positional behavior within the *Cercocebus* and *Cercopithecus* genera.

The behavior-morphology associations represent some similarity between the *Cercocebus* and *Cercopithecus* genera. More terrestrial species show a large greater tuberosity diameter (h2), developed ridges at the humeral surgical neck (h8) and enhanced humeral shaft curvature (h9). However, the other characters might not always indicate strata preferences if applied to different taxa.

Some characters do not indicate differences in positional behavior. These may be conservative traits and weak indicators of strata preference in cercopithecines. In mangabeys they include orientation of the greater tuberosity (h3), shape and size of the lesser tuberosity (h4, h5), humeral head shape (h6, h7), retroflexion of the medial epicondyle (h13), shape of fovea capitis femoris (f3), femoral neck length and diameter (f4), depth of the femoral condyle (f6), size ratio of the lateral and medial femoral condyles (f7) and proximal extent of the patellar surface (f9). In guenons, these characters include bituberosity angle (h6), shaft robusticity of the humerus and femur (h10, f5), development of the trochlear keels (h11), size of the medial epicondyle (h14), projection of the greater trochanter (f1), extent of the articular surface of the femoral head (f2), size ratio of the lateral and medial femoral condyles (f7) and patellar surface width (f8).

Although the character states are in general similar between *Cercocebus torquatus* and *Cercocebus galeritus*, the former differs from the latter regarding four characters (h1, h14, f8, f10). Similarly, *Cercopithecus mona* differs from *Cercopithecus mitis* in seven characters (h1, h12, f4, f3, f6, f9, f10). It is better to interpret the differences as indicating that these mangabeys and guenons engage in different modes of positional behavior in the semi-terrestrial and arboreal habitats, respectively.

In summary, mangabeys and guenons developed different morphological features which are related to diverse modes of positional behavior. Partly, the morphological

differences are parallel with the semi-terrestrial-to-arboreal diversification across broad taxa of primates. However, this is not always true. Even in the comparison between mangabeys and guenons, the intrageneric variation is not necessarily identical. Although these genera are close in phylogeny, the semi-terrestrial-to-arboreal radiation has been developed in subtly different ways. Morphological distinctions between *Cercocebus torquatus* and *Cercocebus galeritus*, and those between *Cercopithecus mitis* and *Cercopithecus mona* demonstrate that even congeneric species living in a similar habitat may have evolved different modes of positional behavior. The arboreal versus semi-terrestrial dichotomy is not sufficient to comprehend the positional behavior of these cercopithecines. The next section details characteristics of functional morphologies of the humerus and femur in these cercopithecines and discusses the correlation with positional behavior.

#### IV. Functional Morphology and its Correlation with Positional Behavior

The humerus and femur of *Cercocebus albigena* are characterized by features indicating a greater mobility of the joints and a general gracility of the musculoskeletal system. The joints are minimally restricted in their movements and the articular surfaces are relatively extensive, allowing a larger freedom of movement (h1, h11, h12, f1, f2, f8, f10), the flexors of the wrist and digits have a long lever arm throughout the range of pronation-supination (h14), muscular or ligamentous insertions are weakly developed (h2, h8, h9), lever arms for muscles are generally short (h1, h2, h9, f1) and the diaphyses are thin (h10, f5).

Napier & Napier (1967) described the locomotion of *Cercocebus albigena* as somewhat deliberate in trees with a high frequency of slow walking. In a study of captive specimens, Rollinson & Martin (1981) also recognized the relatively slow and deliberate gaits of mangabeys in comparison with *Cercopithecus* species. According to Jones & Sabater Pi (1968), mangabeys tend to move about the branches of trees with considerable caution. They avoid jumping across gaps and tend to move along the stout branches even when escaping. Probably, the deliberate movements are a result of the larger body size (Table 2, Appendix 1) because a larger size makes the arboreal substrates more unstable and the risk of falling greater (Cartmill & Milton, 1977). A larger body size also increases risk of injury when falling (Cartmill & Milton, 1977). It has been recognized that body size is deeply correlated with locomotor pattern and utilization of substrate (e.g., M.D. Rose, 1974; Ripley, 1979; Fleagle & Mittermeier, 1980; Aiello, 1981; Fleagle, 1985). Agile arboreal activities such as leaping or arm-swinging are unlikely in the habitual locomotor repertoires of *Cercocebus albigena*. The morphologies of the humerus and femur of *Cercocebus albigena* probably represent the functional complex of a relatively large-sized branch walker in the Old World which moves relatively slowly and deliberately.

*Cercocebus torquatus* and *Cercocebus galeritus* differ from *Cercocebus albigena* in having emphasized joint stability and restricted freedom of joint movements (h11,

h12, f1, f2). They also differ in having robustly built shafts (h10, f5), stronger development of muscles (h2, h8), and longer lever arms for muscle (h2, h9, f1). These morphologies resemble those of *Papio* (e.g., Jolly, 1967) and are interpreted as terrestrial adaptations. Since mangabeys have a relatively close relationship with baboons (Szalay & Delson, 1979), their terrestrial features may be a retention from their common ancestor.

*Cercocebus galeritus* differs from *Cercocebus torquatus* in a few characters. The patellar surface of *Cercocebus galeritus* is mediolaterally wide and does not show a marked elevation of the lateral rim (f8, f10) whereas the patellar surface of *Cercocebus torquatus* is mediolaterally narrow and deeply excavated. The condition of *Cercocebus galeritus* suggests a larger rotational capability while that of *Cercocebus torquatus* implies intensive flexion-extension in the parasagittal plane. *Cercocebus galeritus* moves deliberately in trees, and walks rather than runs (Manaster, 1975). They tend to be more arboreal than *Cercocebus torquatus* (Manaster, 1975). The differences at the knee joint may be explained by different positional behaviors.

The humerus of *Cercopithecus aethiops* is distinct from those of both *Cercopithecus mitis* and *Cercopithecus mona* in showing the large and superiorly projected humeral tuberosities (h2, h4, h5), a more anterior location of the greater tuberosity (h3), a less convex humeral head (h7), a greater flattening of the humeral neck (h8), a greater humeral shaft curvature (h9), and a more posteriorly reflected medial epicondyle (h13). The flattened and ovoid head, anteriorly located greater tuberosity, and flatness of the humeral neck may be a derived functional complex to stabilize the shoulder joint during parasagittal excursion of the forelimb. Other features (h3, h4, h13) are concerned with the long moment arm for the shoulder muscles and the habitually pronated forearm. All of these features are related to economical excursion of the forelimb on a level surface. This function is adaptive for the economy of foraging and effective predator avoidance.

Gebo & Sargis (1994) recently revealed morphological differences concerning limb bones among various guenons and Patas monkey. They found *Cercopithecus aethiops* differs from *Cercopithecus mitis* regarding nine indices out of twenty-six and interpreted those differences as specialization for terrestrial environment in *Cercopithecus aethiops*. Some of them are explained as functional adaptation for terrestriality (e.g., reduced joint mobility, increased stride length) while the rests can not (Gebo & Sargis, 1994). They claim that limb bones of *Cercopithecus aethiops* are more intermediate if compared with those of *Cercopithecus lhoesti*, one of the terrestrially inclined guenons as much as *Cercopithecus aethiops* (Gebo & Sargis, 1994). The present study differs from Gebo & Sargis (1994) in recognizing more terrestrial specialization in *Cercopithecus aethiops*. Some of the features recognized in the present study are common with those of *Cercopithecus lhoesti* noted by Gebo & Sargis (1994), for example, well projected humeral tuberosities, inferomedial to superolaterally elongated ovoid humeral head, and greater curvature of the humeral shaft. The incongruity of the two studies may come from different sampling of *Cercopithecus aethiops*.

The morphological specialization of *Cercopithecus aethiops* are more developed in the humerus than in the femur. This fact implies that the forelimb function differs significantly between arboreal and terrestrial locomotor behaviors. Because forelimbs decide the direction of progression, a greater range of mobility would be required in the three dimensional arboreal space while the forelimb excursion is more restricted on the ground. By contrast, hindlimb seems to serve the propulsive force in a similar manner in both arboreal and terrestrial habitat in *Cercopithecus*.

This also suggests that the postcranial differentiation of guenons is relatively small as compared with that of mangabeys since the examined mangabeys exhibits significant differences in femur morphology as well. The relatively small body size of guenons may allow versatile positional behavior without marked postcranial modification. The tribe Papionini, which includes *Cercocebus*, has evolved more terrestrial specialization than Cercopithecini (Szalay & Delson, 1979). Thus, when *Cercocebus albigena* returned to the forests, greater modifications might have been necessary.

*Cercopithecus mitis* is characterized by a more mobile glenohumeral joint (h1, h2, h3, h4, h5, h7), relatively weak muscular and ligamentous insertions on the humerus (h1, h9), a larger capability for pronation-supination in the forearm (h13), and capability for axial rotation at the knee joint (f6). Some of these features are the same as those differentiating between arboreal and semi-terrestrial mangabeys. They include a larger range of joint mobility (h1, h2) at the shoulder joint and a relatively short moment arm for the shoulder muscles (h1, h9). However, there are differences between the two character sets. The humerus and femur of *Cercopithecus mitis* do not show the slenderness of the shaft (h10, f5), wider capitulum of the humerus (h12), lower greater trochanter of the femur (f1) and lower patellar rim (f8). As noted above, *Cercopithecus mitis* moves on the arboreal settings in a more active and agile manner than *Cercocebus albigena* (Jones & Sabater Pi, 1968). As evidenced by the relatively robust shaft of long bones and minor modifications for thigh abduction, postcrania of *Cercopithecus mitis* are adapted for relatively agile branch-walking and running in which the limb excursions occur primarily in the parasagittal plane.

The arboreal *Cercopithecus mona* also differs from *Cercopithecus aethiops* in a number of characters. Although *Cercopithecus mona* resembles *Cercopithecus mitis* in many characters, *Cercopithecus mona* has distinct features which are observed in neither *Cercopithecus mitis* nor *Cercopithecus aethiops* (f3, f9, f10). Among these features, the shape of the patellar surface is of interest. The patellar surface is extended proximally and the lateral rim is elevated. This type of the patellar surface is characteristically seen in the leapers (Fleagle, 1976a; Fleagle & Meldrum, 1988). In addition, the deeper femoral condyles (f6), differing from *Cercopithecus mitis*, suggest efficiency of flexion-extension at the knee. The deep and round fovea capitis femoris might suggest the extreme extension and flexion of the hip joint (Grand & Lorenz, 1968). These differences in the femur are correlated with the characteristic locomotor behavior of *Cercopithecus mona*. *Cercopithecus mona* frequently displays leaping and darting (Haddow, 1951). *Cercopithecus mona* is a relatively small species among guenons

(Table 2; Napier & Napier, 1985). The highly active movements of *Cercopithecus mona* (Haddow, 1951; Hill, 1966) are probably a consequence of smaller body size. In discontinuous lower levels of forests, relatively small animals would frequently need to cross gaps by leaping (Fleagle & Mittermeier, 1980). Smaller animals can leap longer than larger ones if the leap distance is standardized by the body size and they can find stable supports for their weight more easily. A femur which is adapted for leaping and rapid cursorial movements suggests these activities are an important locomotor repertoire in *Cercopithecus mona*. Gebo & Sargis (1994) also indicated differences in limb bones between *Cercopithecus mitis* and *Cercopithecus ascanius*, which engages in leaping more frequently, and suggested behavioral inferences.

#### V. Morphotype of the Humerus and Femur in the Cercopithecinae

Although the studied mangabeys and guenons represent variations of postcranial morphologies which reflect their different habitats, they share morphological similarities when compared with more remote taxa (e.g., Colobinae, Hominoidea, and Cebidae). Such similarities are likely to represent the basic morphotype of the Cercopithecinae. This morphotype is presumed to be related to a primary locomotor adaptation of this subfamily.

Both cercopithecines and colobines show a similar morphotype of proximal humerus in general. The less convex and mediolaterally wide humeral head suggests that the primary functions of the glenohumeral joint are protraction-retraction of the arm and abduction-adduction and axial rotation in the partially retracted position. The superiorly projected humeral tuberosities are not adequate for extreme protraction of the arm. As well as the developed humeral tuberosities, the narrow bituberosity angle and flatness of the articular surface suggests that the humeral head in the Cercopithecinae and Colobinae is not suitable for rotational abilities of the fully protracted arm. Rather, the shoulder joint is kept stabilized when the arm is protracted (M.D. Rose, 1989). *Cercopithecus aethiops* and *Papio* have developed this mechanism in having the anteriorly flattened humeral head. Their shoulder joint appears specialized for economical parasagittal excursion of the forelimb. The humeral head of *Presbytis melalophos* is relatively round and its bituberosity angle is slightly high. This condition can be considered as a specialized feature for arboreal agility (Fleagle, 1976a, 1977), since other colobines show a greater similarity to general cercopithecine rather than *Presbytis melalophos*.

The cercopithecine and colobine morphotype of the proximal humerus is contrasted with that of apes and New World larger cebids. The very round humeral head and lower humeral tuberosities in larger cebids (*Alouatta*, *Cebus*) which are not specialized for suspensory behaviors enable extreme protraction and retraction of the arm. Since the bituberosity angle is relatively small, the axial rotation at the shoulder joint would occur only in a moderate degree when the arm is fully protracted. Suspensory *Ateles* and apes share a similar morphotype of the proximal humerus with *Alouatta* and *Cebus*.

However, they have a greater capability of rotation at the glenohumeral joint when the arm is fully protracted, as indicated by their larger bituberosity angle. In addition, a globular head allows an extreme range of arm protraction.

Cercopithecines have more developed trochlear keels than colobines, larger cebids and apes (Napier & Davis, 1959; Ford, 1988; M.D. Rose, 1988; Schön Ybarra & Schön, 1988; Harrison, 1989). The developed trochlear keels provide rigid guides for the ulna during flexion-extension of the elbow. Among cercopithecines, *Papio* and semi-terrestrial mangabeys have developed this joint mechanism further. This development is related to a larger body size and cursorial activities in terrestrial habits. The relatively short and posteriorly reflected medial epicondyle is common in most of cercopithecines relative to other taxa. These features do not suggest extreme specialization for either arboreal, or cursorial terrestrial activities. The medial epicondyle of *Papio* and *Cercopithecus aethiops*, which is smaller in size and more strongly retroflexed is an adaptation to keep the forearm fully pronated during quadrupedal behavior on the ground. Colobines exhibit less developed trochlear keels than cercopithecines. This tendency is marked regarding the medial keel. As well as less developed trochlear keels, the mediolaterally wide articular surface indicates that pronation-supination movements are more frequently involved in positional behavior in arboreal settings. The less retroflexed medial epicondyle of colobines suggests more frequent use of semi-pronated posture of the forearm in colobines than is in cercopithecines. The distal humerus of New World monkeys exhibits more emphasized capability pronation-supination movements. Large-bodied cebids have a mediolaterally more wider articular surface and quite large and medially projected medial epicondyle. Semi-pronated posture of the forearm and frequent pronation-supination movements may be significant in quadrumanous climbing or brachiation. The trochlea of *Pan* and *Hylobates* is uniquely modified, even differing from *Ateles*. The developed gutter on the articulation gives a greater joint stability throughout pronated-supinated position of the forearm and prevents the dislocation of the radial head (Sarmiento, 1985; M.D. Rose, 1988). The large and medially projected medial epicondyle suggests significant roles of the flexors of the wrist and digits in various position of pronation-supination. These structures are adaptive for brachiation and other suspensory positional behaviors.

The proximal projection of the greater trochanter correlates with the ability of abduction at the hip joint. On the other hand, the high greater trochanter inhibits extreme thigh abduction. Therefore, hip joint mobility in cercopithecines and colobines is relatively limited due to the relatively high greater trochanter. However, the muscles inserting here are given longer lever arms to abduct or rotate the thigh, and to keep the hip joint stabilized. The hemispherical head indicates extensive rotations or abduction are not habitual joint movements in cercopithecines and colobines. In contrast to cercopithecines and colobines, the hip joint in large-bodied cebids and apes provides a greater mobility including extensive abduction and rotations. Since the greater trochanter is usually lower than the femoral head, higher degree of abduction

is possible. In addition, a spherical rather than hemispherical head of the femur assumes extensive contact with the acetabulum through various positions of hip joint, especially abduction and rotations.

The distal femur in cercopithecines lacks functional specialization for rotator capabilities. The epiphysis is anteroposteriorly deep and the patellar groove is narrow and proximodistally long. These are interpreted to be adapted for flexion-extension in the parasagittal plane. Their knee joint is most like a uniaxial hinge joint. On the other hand, the knee joint of large-bodied cebids suggests larger rotational abilities. Though there are some difference between *Ateles* on the one hand and *Alouatta* and *Cebus* on the other, large-bodied cebids commonly exhibits a mediolaterally wide joint and a medially deviated medial condyle. This condition may be an adaptation maintaining lateral body balance when the knee is laterally rotated and partially flexed as seen in typical arboreal quadrupedal posture of New World monkeys (Meldrum, 1991). The knee joint of apes emphasizes this tendency. The joint is mediolaterally wide and asymmetrical. In addition, the wide patellar surface provides extensive contact area to resist the dislocation. Probably, joint stability when the knee is rotated and flexed is more elaborated than in large-bodied cebids. The condition of colobines is in-between the two poles. However, the relatively symmetrical shape of the joint suggests that its primary function is flexion-extension in the parasagittal plane rather than flexion-extension combined with rotation. However, the moderately wide epiphysis may suggest that the knee joint of colobines experiences more rotations during flexion-extension on arboreal supports than in cercopithecines.

Comparing with Colobinae, Hominoidea, and Cebidae, the limb joints of Cercopithecinae exhibits more restriction of mobility to simple parasagittal limb excursion (M.D. Rose, 1983). This in turn enhances the economy of cursorial locomotion. This morphotype is more emphasized in mangabeys and *Papio* than in guenons. This difference can be considered as a specialization of the tribe Papionini that differs from that of Cercopithecini.

The humerus and femur in Colobinae are in general similar to those of the Cercopithecinae. However, joint restrictions are slightly reduced in the Colobinae. This is indicated by the weakly developed trochlear keels, less projecting greater trochanter and mediolaterally wider knee joint. These structures allow relatively free pronation-supination at the elbow, flexion-extension of the hip joint combined with thigh abduction, and knee rotation, respectively.

The morphotype of large-bodied cebids and apes differs drastically from that of the Cercopithecinae. The joint morphologies suggest much greater ability for axial rotations of the arm, pronation-supination at the elbow, thigh abduction and lateral rotations, and knee rotations. Such a functional complex is perhaps adaptive for both quadrumanous and vertical climbing (Schön Ybarra & Schön, 1988). In addition, *Pan*, *Hylobates* and *Ateles* share the humeral characters reflecting specialized suspensory positional habits (e.g., larger bituberosity angle). Apes have further elaborate the elbow joint to keep the stability during various positions of pronation-supination

uniquely in anthropoids.

## VI. Evolution of Positional Behavior in Old World Monkeys

Strasser(1988) shows that the cercopithecids share derived pedal bone features which are adaptive for cursorial locomotion on the ground, rather than grasp-climbing or suspension. Cercopithecines are characterized further by extra foot stabilizing mechanism which are absent in colobines (Strasser,1988). The evidence of the pedal bone morphology coincides with that of the long bones in the present study which indicates the general restriction of the joint mobility to fore-aft limb excursions in the Cercopithecinae and less but still marked restriction in the Colobinae.

The morphotypes of Cercopithecinae and Colobinae are quite different from that of New World large-bodied cebids. The difference in postcranial morphology is correlated with a difference in positional behavior. Many authors agree that Old World monkeys predominantly adopt above-branch activities in arboreal settings rather than below-branch activities, unlike large-bodied cebids (M.D. Rose, 1973, 1974; Morbeck, 1977; Aiello, 1981). No cercopithecoid whose body size is equivalent to that of large-bodied cebids (5-10 kg) is specialized for below-branch activities. M.D. Rose(1973) noted that arboreal positional behavior in semi-terrestrial cercopithecines is similar to that of the arboreal cercopithecines. Rollinson & Martin (1981) suggested the relative uniformity concerning locomotor activities in arboreal and semi-terrestrial cercopithecines. Meldrum(1991) found that both semi-terrestrial and arboreal cercopithecines walk on the branches with the limbs extended and less abducted. This mode differs from the typical arboreal quadrupedal movements seen in the New World monkeys, where the limbs are kept flexed and abducted (Meldrum,1991). In addition, the early arboreal anthropoid (e.g., *Aegyptopithecus*) was presumed to engage in slow quadrupedal gaits (Fleagle & Simons, 1982). The positional behavior displayed by Old World monkeys is a rather derived pattern.

There are two opposite hypothesis concerning the evolutionary history of positional behavior in Old World monkeys. Napier (1967, 1970) argued that ancestral cercopithecids were arboreal and that more terrestrial habits of the living cercopithecines are derived. He claims that colobines are essentially arboreal and that it is unlikely that the colobines have evolved from a ground-living stock (Napier, 1970). However, the present study contradicts with this argument regarding the similarity of morphotype of the humerus and femur between cercopithecines and colobines.

Cant(1988) presented an interpretation of the evolution of cercopithecoid positional behavior, utilizing observations of the positional behavior of *Macaca fascicularis*. He suggests that rapid running along substrates has selected for the postcranial specializations of the cercopithecids. *Macaca fascicularis* frequently engages in rapid movements along substrates in the wild (Cant, 1988). During rapid locomotion along substrates, the chiropodia are placed below the body, the limbs are less abducted and the limb excursions occur in the parasagittal plane. The joints must be extended rather than

flexed during rapid running.

However, the tribe Papionini, which includes *Macaca*, exhibits greater terrestrial adaptation than the Cercopithecini. Thus, it is not clear if the rapid arboreal running is primitive rather than secondary derived. Further comparative data on substrate use in Cercopithecini, Colobinae and platyrrhine are required to solve this problem. In addition, ecological backgrounds remain obscure as to why rapid running along substrates should have developed in the early cercopithecids (e.g., forest structure, niche separation from apes).

Andrews(1982) and Andrews & Aiello(1984) presented another hypothesis. These authors claim that the ancestral condition of the catarrhines was forest habitat and that early cercopithecoids were evolved in savanna habitats after the recession of the forests. In this scenario, today's forest living Old World monkeys are presumed to have experienced the secondary behavioral shift toward arboreality. These authors hypothesize that the primitive savanna adaptation restricted the repertory of positional behavior exclusively to above branch activities after cercopithecids reentered to the forests (Andrews, 1982; Andrews & Aiello, 1984). Recent morphological and paleoenvironmental studies seem to support the semi-terrestrial habit of early cercopithecoid (Benefit, 1987; Strasser & Delson, 1987; Leakey, 1988; Pickford & Senut, 1988; Strasser, 1988; Harrison, 1989; McCrossin & Benefit, 1992).

The restriction of the joint movements to the parasagittal plane would be adaptive both for arboreal rapid running on branches, and terrestrial walking and running. Therefore, it can not be concluded which of these hypotheses is appropriate from the evidence of humeral and femoral morphologies. If fossil postcrania of earliest cercopithecids are found, clues to this problem may be obtained. However, there are various patterns of movements in both arboreal and semi-terrestrial cercopithecines associated to various functional morphologies in their postcranial skeleton. It is difficult to find simple correlation between locomotor behavior and postcranial morphology. Further morphological studies, combined with observations of quadrupedal activities, may allow comprehensive interpretations of locomotor behavior to be made.

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**Appendix 1.** Linear measurements of the humerus and femur. Upper: average; middle: standard deviation; lower: range.

species	sex	N	measurement 1	measurement 2	measurement 3	measurement 4	measurement 7	measurement 8
<i>Cercocebus albigena</i>	m	16	159.0	18.3	16.0	11.8	34.0	19.7
			7.39	0.93	0.78	0.86	2.31	1.01
				140.2-174.0	16.4-19.9	14.4-17.4	10.4-13.7	29.0-38.0
	f	11	140.1	15.8	13.6	9.6	29.4	17.0
			5.62	0.68	0.56	0.72	1.50	0.52
				129.0-150.0	14.3-16.8	12.4-14.6	8.4-10.8	26.0-31.0
<i>Cercocebus torquatus</i>	m	12	169.6	19.1	18.0	12.4	40.2	20.9
			3.45	0.79	0.68	0.79	3.00	1.22
				164.8-176.0	17.8-20.3	17.0-19.6	10.9-13.8	34.0-45.0
	f	8	138.8	15.2	14.1	10.2	30.5	17.2
			6.21	0.47	0.57	0.95	1.58	0.74
				125.0-146.8	14.4-15.9	12.8-14.6	8.6-11.4	28.0-32.0
<i>Cercocebus galeritus</i>	m	5	160.0	18.3	16.2	11.1	35.0	20.5
			4.00	0.59	0.89	0.66	2.10	1.41
				154.0-166.0	17.6-19.0	14.7-17.2	10.5-12.3	32.0-37.0
	f	4	137.5	14.8	13.2	9.52	28.1	16.6
			3.84	0.67	0.59	0.51	1.52	0.95
				132.0-142.0	13.8-15.6	12.4-13.9	8.8-10.1	26.0-30.0
<i>Cercopithecus mitis</i>	m	14	137.7	16.7	14.5	10.6	32.2	16.6
			6.81	0.95	1.00	0.74	2.40	1.05
				121.0-150.6	14.8-18.5	12.6-16.0	8.7-11.9	29.0-37.0
	f	9	118.3	14.0	12.4	8.5	26.8	14.7
			5.00	0.83	1.06	0.96	1.83	0.94
				110.0-125.6	12.4-15.4	10.5-13.8	7.1-10.1	24.0-29.0
<i>Cercopithecus mona</i>	m	12	131.7	15.9	13.7	9.9	31.3	16.2
			0.25	0.67	0.66	0.85	2.66	1.12
				123.3-146.8	14.4-16.8	12.9-15.1	8.7-11.2	28.0-37.0
	f	4	107.3	12.2	10.5	7.8	22.5	12.1
			4.24	0.46	0.53	0.11	1.12	0.49
				101.5-111.7	11.7-12.9	10.0-11.4	7.7-8.0	21.0-24.0
<i>Cercopithecus aethiops</i>	m	10	126.3	14.9	13.6	10.3	30.1	15.1
			8.69	1.24	1.11	1.05	3.27	1.14
				113.0-139.5	13.1-16.2	12.0-14.9	8.6-11.9	26.5-35.0
	f	16	104.3	12.2	10.9	7.6	24.3	12.5
			6.09	0.88	0.76	0.98	2.70	1.02
				93.0-114.0	10.7-13.6	9.7-12.5	4.6-8.5	20.5-29.0
<i>Papio spp.</i>	m	5	200.4	26.4	24.7	19.1	51.8	28.7
			190.0-214.0	24.4-28.4	23.7-25.7	17.7-20.2	49.0-57.0	27.9-30.0
				165.9	21.2	18.5	15.4	39.0
<i>Colobus guereza</i>	m	15	156.0-175.5	20.3-22.0	17.6-19.4	14.4-16.4	37.0-41.0	21.0-24.1
			153.7	18.3	17.7	11.7	35.5	20.6
				145.3-165.0	16.6-19.5	15.6-19.4	9.6-13.2	29.0-41.0
	f	15	147.5	17.5	16.7	10.6	32.3	19.5
			137.0-159.5	16.7-18.6	15.2-18.1	9.0-11.8	29.0-35.0	17.3-21.5
				139.3	15.1	13.3	8.8	28.9
<i>Presbytis metalophos</i>	m	15	129.0-152.3	14.1-16.7	11.7-14.3	7.3-10.4	27.0-33.0	16.8-19.5
			139.8	15.2	13.2	8.8	29.4	17.5
				127.0-146.9	14.1-16.5	10.6-14.4	7.4-9.8	27.0-32.0
<i>Nasalis larvatus</i>	m	1	175.7	18.2	15.2	10.0	35.0	21.1
			-	-	-	-	-	-
				287.3	36.4	33.2	21.3	75.7
<i>Pan troglodytes</i>	f	3	273.0-296.0	35.3-38.2	30.9-35.9	19.9-23.1	72.0-78.0	38.6-44.2
			219.5	17.4	12.2	9.7	29.5	18.2
				214.0-225.0	16.5-18.3	11.3-13.0	9.6-9.8	29.0-30.0
<i>Hylobates lar</i>	m	2	148.9	18.6	15.6	9.8	31.5	19.6
			144.7-153.1	18.6-18.7	15.2-16.0	9.1-10.4	31.0-32.0	18.5-20.7
				107.4	14.2	12.2	8.0	25.7
<i>Cebus spp.</i>	m	4	98.6-119.0	13.1-16.2	10.8-14.2	6.7-9.6	21.0-29.0	15.4-16.8
			106.5	13.6	10.9	7.7	21.9	13.6
				94.0-114.0	13.3-13.9	10.4-11.3	7.4-8.0	20.0-23.5
<i>Ateles paniscus</i>	m	3	201.0	20.0	15.0	9.4	33.3	19.1
			198.0-205.0	19.8-20.1	14.1-15.8	7.0-13.4	32.0-35.0	18.3-20.5
				180.3	18.4	13.2	7.1	30.8
			175.0-186.0	18.1-18.9	12.7-13.8	6.5-7.8	30.0-31.5	17.4-18.9

Appendix 1. Continued.

measurement 9	measurement 11	measurement 12	measurement 13	measurement 14	measurement 16	measurement 17	measurement 18
12.3	210.7	2.9	24.8	13.0	16.6	38.1	21.9
0.51	9.17	1.23	1.58	0.93	0.87	2.08	0.96
11.3-13.1	190.0-222.0	-0.5-4.5	22.0-28.2	11.0-14.4	14.3-17.9	34.0-42.0	19.5-23.3
10.8	180.8	2.2	20.9	11.2	14.7	33.0	19.0
0.55	7.37	1.20	1.32	0.95	0.59	1.54	1.00
9.8-11.8	168.0-191.0	-0.5-4.0	19.1-24.4	9.4-12.6	13.5-15.6	29.0-34.5	17.5-20.9
12.3	217.1	6.2	26.2	14.6	18.4	45.5	25.1
0.50	7.22	1.28	1.94	1.14	0.69	2.84	0.95
11.5-13.2	201.5-227.0	4.0-8.0	22.6-29.0	12.5-16.3	16.5-19.3	41.0-49.0	23.0-26.4
10.4	172.2	3.3	21.1	12.2	15.3	36.1	19.4
0.51	6.38	0.93	0.80	0.57	0.38	2.40	0.75
9.4-11.2	160.0-181.0	1.0-4.0	19.2-21.8	11.1-13.1	14.6-15.9	33.0-41.0	18.1-20.4
11.9	208.8	4.9	26.1	13.6	17.2	40.6	23.0
0.95	4.45	2.27	0.89	0.88	0.93	2.60	1.54
10.5-13.2	202.0-215.0	0.5-7.0	24.8-27.5	11.9-14.2	15.8-18.4	37.5-44.0	21.3-25.5
9.8	176.2	4.2	20.6	12.2	14.6	33.1	18.4
0.32	5.76	1.03	2.35	0.51	0.28	1.88	0.58
9.4-10.2	168.0-184.0	3.5-6.0	18.9-24.6	11.4-12.8	14.3-14.9	31.0-35.0	17.5-19.1
9.6	170.9	3.6	23.9	11.8	15.0	34.9	21.5
0.79	8.45	0.65	1.87	0.78	0.82	2.09	1.26
8.0-10.8	151.0-188.0	2.0-4.5	20.0-27.2	10.7-12.9	13.4-16.4	31.0-38.5	19.2-23.0
8.4	145.4	2.7	19.7	9.9	12.7	29.7	17.3
0.65	7.67	1.15	1.63	0.53	0.65	1.63	1.09
7.2-9.5	132.8-158.0	1.0-4.5	16.8-22.7	9.0-10.8	11.3-13.4	27.0-32.0	15.6-19.0
9.8	160.4	3.8	20.4	10.7	13.4	32.2	20.1
0.59	6.86	1.15	1.24	0.79	0.81	1.57	0.99
8.8-11.0	152.0-178.0	1.0-5.5	18.4-22.8	9.8-12.0	12.1-15.1	29.0-35.0	18.9-22.7
7.5	123.9	2.8	14.6	8.2	10.4	24.8	15.0
0.39	5.53	0.25	0.98	0.60	0.42	1.92	0.35
6.9-7.9	115.0-129.0	2.5-3.0	12.9-15.3	7.5-9.0	9.9-10.9	23.0-28.0	14.5-15.5
8.9	155.3	3.8	20.1	10.8	13.2	32.2	19.6
0.70	11.72	1.46	2.00	1.02	1.12	3.92	1.58
7.8-9.8	137.0-174.0	2.0-6.5	17.3-23.5	9.3-12.3	11.2-15.0	26.0-39.0	17.1-21.9
7.8	128.4	2.7	16.9	8.7	11.0	25.7	16.0
0.69	8.10	0.85	1.68	0.78	0.99	3.11	1.84
6.7-8.8	113.5-144.0	1.5-4.5	14.4-21.1	7.3-9.7	9.6-12.7	20.5-32.0	13.2-22.1
17.0	225.8	8.9	32.9	16.4	22.7	52.2	28.0
16.2-17.8	215.0-235.0	5.0-11.0	31.0-35.7	15.6-17.4	20.8-24.3	49.0-59.0	25.3-31.1
14.3	183.0	4.5	26.4	14.1	18.7	39.5	23.5
12.9-15.7	174.0-192.0	4.0-5.0	26.0-26.7	13.4-14.8	18.3-19.0	37.0-42.0	22.6-24.4
12.9	201.0	2.4	27.0	14.1	18.1	42.0	23.2
11.0-14.1	190.0-220.0	1.0-5.0	24.6-29.6	13.1-15.7	16.1-19.2	36.0-46.5	20.8-25.3
12.1	191.6	1.4	25.4	12.9	16.9	38.5	22.1
11.1-13.2	184.0-209.0	0.5-3.0	23.2-27.7	11.7-13.9	15.6-18.2	34.0-42.0	20.4-26.5
11.2	200.3	2.3	20.0	12.9	15.6	34.8	20.4
10.1-12.4	189.0-211.5	0.5-4.5	18.1-22.3	11.7-14.4	14.1-16.7	32.0-38.0	18.3-22.8
11.0	200.1	2.6	20.1	12.8	15.7	35.3	20.2
10.3-11.9	192.0-208.0	1.0-3.5	19.1-21.6	11.3-13.9	14.7-16.7	33.0-37.0	19.2-20.8
13.5	192.0	2.0	23.6	13.2	17.8	40.0	22.9
-	-	-	-	-	-	-	-
22.0	284.3	-3.0	46.7	20.8	29.8	71.2	38.7
19.5-23.8	271.0-292.0	-4.0- -2.0	40.7-52.0	20.1-21.3	27.7-31.0	66.5-74.0	34.5-41.8
10.6	197.5	-2.2	21.9	9.4	15.2	30.5	17.4
10.0-11.2	191.0-204.0	-3.0- -1.5	20.5-23.4	9.3-9.5	14.8-15.7	30.0-31.0	16.7-18.2
11.3	157.0	-3.5	22.5	9.6	14.0	32.0	17.6
11.1-11.5	148.0-166.0	-5.0- -2.0	21.9-23.1	9.3-9.9	13.8-14.2	-	-
8.3	134.7	0.8	19.3	8.5	10.8	26.0	14.9
6.9-9.2	127.0-145.0	0.5-1.5	17.6-22.4	6.8-10.0	9.7-12.3	20.0-30.0	13.4-16.4
8.2	134.6	-0.1	17.5	7.6	10.5	24.0	13.6
7.7-8.7	118.0-144.0	-1.0-0.5	16.8-18.2	7.0-8.2	9.7-11.0	22.0-26.0	12.2-14.2
12.4	208.0	-5.5	26.8	10.4	16.3	38.7	19.1
11.1-14.0	201.0-218.0	-7.5- -3.0	22.0-30.8	9.1-11.8	16.1-16.6	36.5-42.0	18.9-19.4
11.5	188.0	-3.0	24.7	11.2	16.0	38.3	19.0
10.7- 12.1	185.0- 194.0	-4.0- -2.5	21.6- 26.7	10.4- 12.4	15.6- 16.4	36.0- 40.0	17.2- 22.5

## Appendix 1. Continued.

species	sex	N	measurement 19	measurement 20	measurement 21	measurement 22
<i>Cercocebus albigena</i>	m	16	23.5	26.9	9.6	8.2
			0.77	1.11	0.88	0.59
			21.8-24.6	25.1-29.0	7.9-11.9	6.7-9.0
	f	11	20.4	23.4	8.1	6.8
			0.81	1.04	0.71	0.59
			18.9-21.6	21.3-25.1	6.9-9.2	5.7-7.8
<i>Cercocebus torquatus</i>	m	12	27.6	29.6	11.4	9.7
			1.16	1.29	0.93	0.68
			25.7-29.4	26.7-31.5	9.9-12.9	8.7-11.4
	f	8	21.0	23.2	8.3	6.8
			0.72	0.77	0.60	0.48
			19.7-21.9	21.9-24.3	7.6-9.6	6.0-7.4
<i>Cercocebus galeritus</i>	m	5	24.7	27.6	10.6	9.5
			1.46	1.52	1.07	0.95
			22.7-26.5	25.3-30.1	9.1-12.4	8.4-11.1
	f	4	19.6	22.4	8.32	6.8
			1.03	0.83	0.36	0.53
			18.0-20.9	21.1-23.3	7.7-8.6	6.0-7.5
<i>Cercopithecus mitis</i>	m	14	22.6	24.9	9.2	8.0
			1.38	1.26	0.70	0.57
			20.3-24.8	22.8-27.3	8.0-10.6	7.0-9.1
	f	9	18.4	20.7	7.1	6.2
			0.98	1.02	0.45	0.39
			16.7-19.6	18.9-22.2	6.5-7.7	5.6-6.9
<i>Cercopithecus mona</i>	m	12	21.3	22.2	8.4	7.4
			1.17	1.16	0.46	0.42
			19.5-23.9	20.2-24.3	7.7-9.3	6.8-8.1
	f	4	15.8	17.1	6.0	5.2
			0.48	0.23	0.32	0.19
			15.3-16.5	16.7-17.3	5.5-6.3	5.0-5.5
<i>Cercopithecus aethiops</i>	m	10	20.4	22.0	8.1	6.9
			1.79	1.83	0.91	0.59
			17.5-22.6	19.0-24.4	6.8-9.3	6.1-7.6
	f	16	16.6	18.2	6.4	5.5
			1.31	1.36	0.84	0.60
			14.6-19.7	15.6-20.6	5.2-8.1	4.6-6.6
<i>Papio</i> spp.	m	5	30.6	35.1	14.8	11.6
			27.9-32.3	32.4-37.9	13.1-17.8	9.7-15.6
	f	3	25.4	28.3	11.0	8.2
			24.3-26.5	27.4-29.2	10.8-11.2	8.0-8.4
<i>Colobus guereza</i>	m	15	24.5	29.4	10.9	9.9
			21.4-27.3	26.6-31.7	9.3-11.80	8.5-11.0
	f	15	23.0	27.3	9.9	8.8
			21.7-24.4	25.3-29.3	9.2-10.6	7.9-10.2
<i>Presbytis melalophos</i>	m	15	22.2	26.1	9.7	8.7
			20.0-25.0	24.0-28.8	8.8-11.3	7.6-9.7
	f	18	22.0	25.2	9.6	8.4
			21.2-22.9	23.9-27.0	8.8-11.8	7.8-9.5
<i>Nasalis larvatus</i>	m	1	23.7	28.1	10.2	9.3
			-	-	-	-
<i>Pan troglodytes</i>	f	3	38.6	53.2	21.0	15.8
			34.0-41.9	50.2-56.0	19.5-22.0	14.2-17.3
<i>Hylobates lar</i>	m	2	17.9	23.8	9.3	6.5
			17.3-18.5	22.9-24.6	9.1-9.5	6.4-6.5
<i>Alouatta seniculus</i>	m	2	18.1	22.3	7.5	6.3
			17.8-18.3	21.9-22.7	7.3-7.8	6.0-6.7
<i>Cebus</i> spp.	m	4	15.8	19.2	7.1	6.3
			14.3-17.4	17.8-20.5	6.0-8.0	5.8-6.7
	f	4	14.5	18.9	7.0	5.9
			13.4-15.1	17.9-19.5	6.5-7.5	5.3-6.2
<i>Ateles paniscus</i>	m	3	20.7	29.1	10.6	9.5
			20.0-21.6	28.4-30.6	10.3-10.9	9.2-10.0
	f	3	20.1	27.7	10.5	8.3
			17.8-22.5	25.2-29.4	9.5-11.3	7.8-9.0

Note

- measurement 1: humeral length
- measurement 2: humeral head diameter
- measurement 3: greater tuberosity diameter
- measurement 4: lesser tuberosity diameter
- measurement 7: circumference of the mid-humeral shaft
- measurement 8: width of the distal articular surface
- measurement 9: capitulum width
- measurement 11: femoral length
- measurement 12: greater trochanter height
- measurement 13: femoral neck length
- measurement 14: femoral neck diameter
- measurement 16: femoral head diameter
- measurement 17: circumference at the mid-femoral shaft
- measurement 18: depth of the distal epiphysis of the femur
- measurement 19: patellar surface rim height
- measurement 20: bicondylar width
- measurement 21: width of the medial condyle
- measurement 22: width of the lateral condyle

**Appendix 2.** Specimen location in museums and institutes.

species	museum and institute		
<i>Cercocebus albigena</i>	BMNH	PCM	MCA
<i>Cercocebus torquatus</i>	BMNH	PCM	
<i>Cercocebus galeritus</i>	PCM	MCA	
<i>Cercopithecus mitis</i>	BMNH		
<i>Cercopithecus mona</i>	BMNH	PCM	MCA
<i>Cercopithecus aethiops</i>	BMNH	JMC	PRI
<i>Papio</i> spp.	PRI		
<i>Colobus guereza</i>	PCM	KNM	
<i>Presbytis melalophos</i>	BMNH	UNAND	
<i>Nasalis larvatus</i>	JMC		
<i>Pan troglodytes</i>	DUSM		
<i>Hylobates lar</i>	DUSM		
<i>Alouatta</i> spp.	JMC		
<i>Cebus</i> spp.	JMC	DUSM	
<i>Ateles</i> spp.	DUSM		

Abbreviations; BMNH: British Museum of Natural History (London), DUSM: Department of Anatomy, Dokkyo University School of Medicine (Mibu), JMC: Japan Monkey Centre (Inuyama), KNM: Department of Osteology, National Museums of Kenya (Nairobi), PCM: Powell-Cotton Museum (Birchington), PRI: Primate Research Institute, Kyoto University (Inuyama), MCA: Royal Museum of Central Africa (Tervuren), UNAND: Sumatra Nature Study Center, University of Andalas (Padang).