FUNCTIONAL MORPHOLOGY OF THE POSTCRANIUM OF *THEROPITHECUS BRUMPTI* (PRIMATES: CERCOPITHECIDAE)

by

EMILY HENDERSON GUTHRIE

A DISSERTATION

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Student: Emily H. Guthrie

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Stephen Frost	Chairperson
Frances White	Member
John Lukacs	Member
Samantha Hopkins	Outside Member

and

Kimberly Andrews Espy	Vice President for Research & Innovation/Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

Degree awarded December 2011

DISSERTATION ABSTRACT

Emily Henderson Guthrie

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This dissertation describes the postcranial functional morphology of *Theropithecus brumpti*, a fossil cercopithecoid primate from the Plio-Pleistocene of East Africa. *Theropithecus* is often used as an analogue for human evolution, but much of our understanding of its paleobiology is based on the grassland adapted *Theropithecus oswaldi*, masking potential morphological and ecological breadth within the genus and limiting its use as an ecological comparator. To better understand the evolutionary history and ecological breadth of the genus, an analysis of the woodland associated *T. brumpti* is presented.

All available *T. brumpti* postcranial material is included, along with comparative data on *T. oswaldi* and a large extant sample. Skeletal elements were metrically described using 125 postcranial measurements believed to have functional relevance. Measurements were transformed into 46 ratios to reflect shape and the functional lengths over which muscles act and to reduce the effects of differences in scale among individuals and species.

Contrary to previous findings, there is no evidence *T. brumpti* was arboreal; rather it is clearly a terrestrial papionin. While *T. brumpti* retains a degree of flexibility (at the shoulder, elbow, hip, knee and ankle), this is not exceptional when compared to other members of the genus, notably *T. oswaldi*. Not only are traits similar in both species, but there is a wide range of variation and overlap in both. Features historically used to reconstruct *T. brumpti* as more arboreal are interpreted here as part of a suite of traits that characterize early *Theropithecus.* This suite of traits may instead be adaptations to manual terrestrial foraging, in particular adaptations related to forest floor locomotion and gleaning, which may be primitive for *Theropithecus* and possibly for papionins. This interpretation of the paleobiology of *T. burmpti* compared to that of *T. oswaldi* offers a parallel with hominins. New fossil evidence suggests use of terrestrial substrates in more woodland habitats for late Miocene to early Pliocene hominins, in contrast to more open habitats associated with later hominins. Therefore, this dissertation develops a framework for understanding the woodland to grassland transition among large bodied primates including hominins.

CURRICULUM VITAE

NAME OF AUTHOR: Emily Henderson Guthrie

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
University of Massachusetts, Amherst

DEGREES AWARDED:

Doctor of Philosophy, Anthropology, 2011, University of Oregon
Master of Science, Anthropology, 2006, University of Oregon
Bachelor of Arts, Anthropology, 2001, University of Massachusetts

AREAS OF SPECIAL INTEREST:

Biological anthropology, evolution of human morphology and behavior, human and non-human primate fossil record; human biological variation, vertebrate paleontology

PROFESSIONAL EXPERIENCE:

Graduate Research Assistant, Department of Anthropology, University of Oregon, 2008-2011

Graduate Teaching Assistant, Department of Anthropology, University of Oregon, 2004-2008

GRANTS, AWARDS, AND HONORS:

Graduate Research Fellowship, Department of Anthropology, University of Oregon, 2008-20011

Doctoral Dissertation Improvement Grant, National Science Foundation 2010

Leakey Foundation Doctoral Research Grant, Leakey Foundation, 2009

Research Grant, Geological Society of America, 2009

Student Research Grant, Paleontological Society, 2009

Graduate Teaching Fellowship, Department of Anthropology, University of Oregon, 2004-2008

Graduate School Research Award, University of Oregon, 2008

Cressman Prize, Department of Anthropology, University of Oregon, 2008

Graduate School Research Award, University of Oregon, 2006

Dissertation Research Scholarship, University of Oregon, 2006

Student Travel Grant, Department of Anthropology, University of Oregon, 2006

Honorable Mention, National Science Foundation Graduate Research Fellowship, 2006

Research Grant, Department of Anthropology, University of Oregon, 2005

Phi Beta Kappa, University of Massachusetts, 2001

Golden Key International Honor Society University of Massachusetts, 1999

National Honor Society, Bromfield School, Harvard, MA, 1997

PUBLICATIONS:

Guthrie, E.H., Frost, S.R., 2011. Pattern and pace of dental eruption in *Tarsius*. Am. J. Phys. Anthropol.145, 446-451.

Turley, K., **Guthrie, E.H.,** Frost, S.R., 2011. Geometric morphometric analysis of tibial shape and presentation among Catarrhine taxa. Anat. Rec. 294, 217-230.

Singleton, M.S., McNulty, K.P., Frost, S.R., Soderberg, J., **Guthrie, E.H**., 2010. Bringing up baby: developmental simulation of the adult cranial morphology of *Rungwecebus kipunji*. Anat. Rec. 293, 388-401.

Henderson, E., 2007. Platyrrhine dental eruption sequences. Am. J. Phys. Anthropol. 134, 226-239.

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To Brandon

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CHAPTER I

INTRODUCTION

Fossil primates have long been the purview of biological anthropologists and paleoanthropologists. In a field that concentrates on the ecology, morphology and evolutionary history of humans, fossil primates are primarily used as ecological informants, helping to reconstruct the environments in which humans evolved. Although the fossil record of primates is diverse and interesting in its own right, there is one primate genus, the fossil baboon *Theropithecus*, that has been one of the most intensely studied in anthropology.

Theropithecus has been used as an analogue for human evolution beginning with Jolly's 1970 seed eating hypothesis. Noting similar adaptations between australopiths and the extant species *Theropithecus gelada* (including preference for open country habitat, opposability of thumb and index finger, features of the jaw and teeth), Jolly suggested that these features were evidence of an ancestral diet of small, hard-object feeding in hominins that may even have precipitated upright stance and bipedal locomotion (Jolly, 1970b). This analogy is often critiqued (Jolly, 2001) but an important point stands – hominins were subject to at least some of the selection pressures causing evolutionary change in other large bodied Plio-Pleistocene primates.

Further, *Theropithecus* appears to have occupied biogeographic ranges similar to those of early hominins (Strait and Wood, 1999). With some specimens of *Theropithecus* attaining body masses above 60 kg (Delson et al., 2000), these organisms are easily within range of Plio-Pleistocene hominins (Wood and Collard, 1999). Therefore, it is expected that *Theropithecus* and hominins would have to solve similar ecological problems with similar biological constraints (Wrangham, 1980; Dunbar, 1983; Foley, 1993; Pickford, 1993; Frost, 2007).

In addition to its role as an analogue, *Theropithecus* has also been important to paleoanthropologists and paleontologists as a habitat indicator. As such, reconstructing the behavior of *Theropithecus* species is of particular interest to anthropologists and these data are often used as a case study to determine how climatic forces shaped the evolution of large bodied terrestrial mammals including hominins (Delson, 1983; Behrensmeyer et al., 1997; Reed, 1997; Potts, 1998; Bobe, 2002; Alemseged, 2003; Bobe and Behrensmeyer, 2004; Bobe, 2006; Fernandez and Vrba, 2006; Elton, 2007; Frost, 2007).

Theropithecus is relatively rare in the modern African fauna, where the extant gelada baboon, *T. gelada*, is restricted to the highlands of Ethiopia (Fleagle, 1999). In contrast, fossil *Theropithecus* was the predominant primate in Plio-Pleistocene faunas where it is represented by two distinct and abundant lineages (referred to here as the *T. brumpti* and *T. oswaldi* lineages), which are frequently associated with the hominid bearing deposits (Delson, 1984).

Having been intensely studied since the 1970's, understanding of the *T. oswaldi* lineage is much greater (Jolly, 1972; Dechow and Singer, 1984; Eck, 1987; Delson, 1993; Delson and Dean, 1993; Delson et al., 1993; Dunbar, 1993b; Macho et al., 1996; Elton, 2002; Frost, 2007). This is, primarily, a product of the relative abundance of *T. oswaldi* in the fossil record, both within individual sites and across the continent generally. However, this bias may mask potential morphological and ecological breadth within the genus, limiting its use as an ecological comparator (e.g. Foley, 1993). *Theropithecus* *oswaldi* was a large-bodied, terrestrial, grass-consuming inhabitant of open woodland/grassland environments (El-Zaatari et al., 2005; Elton, 2002; Lee- Thorpe et al., 1989(Jolly, 1972; Teaford, 1993; Van der Merwe et al., 2003; Teaford et al., 2008). Therefore, *T. oswaldi* appears to be an excellent species to use as an indicator of expanding grasslands in the African Pleistocene (Bobe, 2002; Bobe and Behrensmeyer, 2004; Frost, 2007).

The importance of savannah (used here to imply grassland or C4-dominated) habitats in the origin of hominin adaptations has been pervasive in the anthropological literature, linking the expansion of grassland ecosystems in Africa with such events as the divergence of apes and hominins, evolution of bipedalism and specific dietary adaptations (Darwin, 1871; Smith, 1924; Dart, 1925; Bartholomew and Birdsell, 1953; Robinson, 1954; Jolly, 1970b; Laporte and Zihlman, 1983). Paleosol data demonstrate an expansion of C4 tropical grasses beginning in the late Miocene (Cerling, 1991; Wynn, 2000; Wynn, 2003; Levin et al., 2004; Wynn, 2004; Levin et al., 2008; Cerling et al., 2011). However, this expansion was not absolute. Mosaic C3 / C4 grassland habitats were present in the region for some time (Bonnefille, 1994) and have remained a component of the landscape (Segalen et al., 2007). Many studies have inferred a mosaic, heterogeneous landscape in hominin habitats (Kingston et al., 1994; Kappelman, 1997; Reed, 1997; Foley, 1999; Kingston, 2007). Additionally, new fossil evidence suggests a forest or woodland habitat for early hominins such as *Sahelanthropus, Ardipithecus* and *Orrorin* (White et al., 1994; WoldeGabriel et al., 1994; Pickford and Senut, 2001; Vingnaud et al., 2002; White et al., 2009; Cerling et al., 2011). Therefore, savannahs cannot be the exclusive driving force of novel hominin adaptations. As such, understanding the biology of non-grassland-adapted large-bodied primates is becoming increasingly important.

Although the genus *Theropithecus* is best known for the grassland adaptations of *T. oswaldi* and *T. gelada*, the less well known *T. brumpti* was associated with fossil faunas, pollen, and paleosols that indicate it was restricted to more woodland environments (Eck, 1976; Boaz and Howell, 1977; de Heinzelin, 1983; Wesselman, 1995). Our understanding of *T. brumpti* has been hampered by the lack of postcranial material directly associated with diagnostic cranial fossils. Since *T. brumpti* always co-occurs with other large papionins, the lack of associated postcranial remains has limited the study of its functional morphology, an essential component for making robust reconstructions of its paleobiology. In the past 10 years there have been some key finds of associated partial skeletons that facilitate an functional morphological analysis of the postcranium of *T. brumpti* to understand its positional behavior, locomotor mode and substrate preference, better estimate the phylogenetic position this species within *Theropithecus* and to develop a framework for understanding the woodland to grassland transition among large bodied primates (Jablonski, 2002b; Gilbert et al., 2011).

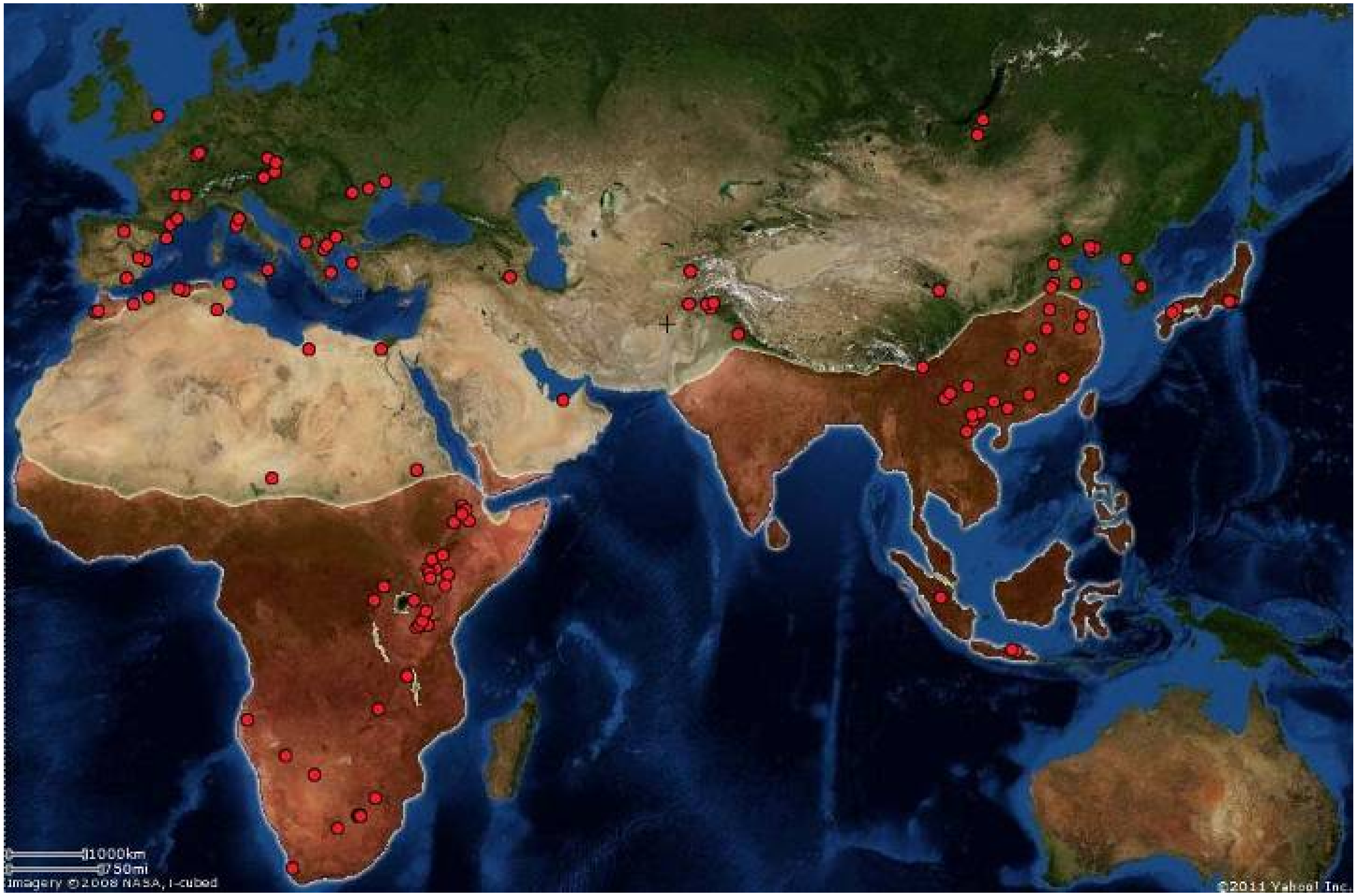
This dissertation is a detailed description of the postcranium of *Theropithecus brumpti* using only postcranial material directly associated with taxonomically identifiable cranio-dental remains. The chapters are as follows: Chapter II provides a background to the group of monkeys discussed in this dissertation (papionins) as well as detailed information about extant and extinct *Theropithecus* species including current understanding of their paleobiology. It also includes a geological overview of the sites where *T. brumpti* occurs; in order provide the reader with context on the material analyzed in this dissertation. Chapter III presents the materials and methods used in this dissertation. The details of the *T. brumpti* material included in this dissertation are provided, as is description of the comparative samples used, specifically that of the close fossil relative *T. oswaldi* as well as the extant sample. The exact measurements and functional indices used are described, as are the analytical and statistical methods. The next three chapters discuss regions of the postcrania in *T. brumpti*. Chapter IV is a description and analysis of the elements of the forelimb. The forelimb has played a disproportionately large role in previous analyses of cercopithecid functional morphology in general, and in that of *Theropithecus* in particular. Chapter V is a detailed description of the wrist and hand, which is one of the most distinctive regions of the postcranium in *Theropithecus*. Further, discussion of the hand has played a significant role in the debate about locomotor mode and substrate preference in *T. brumpti.* While the metacarpals and phalanges of *T. brumpti* have been described before, Chapter V importantly includes the first detailed description of the individual elements of the carpus in any fossil *Theropithecus* species. Chapter VI is an analysis of the hindlimb and foot, which have not been previously subjected to a broad metric comparative analysis. Thus, each region was specifically chosen and included based on previous studies of papionin functional morphology that suggested distinctiveness and functional implications of the regions discussed. Further, the areas highlighted in this dissertation include areas that are autapomorphic in the extant *Theropithecus* and may help us understand the locomotion of *Theropithecus brumpti* as well as the evolution and origin of the genus *Theropithecus*.

CHAPTER II

BACKGROUND

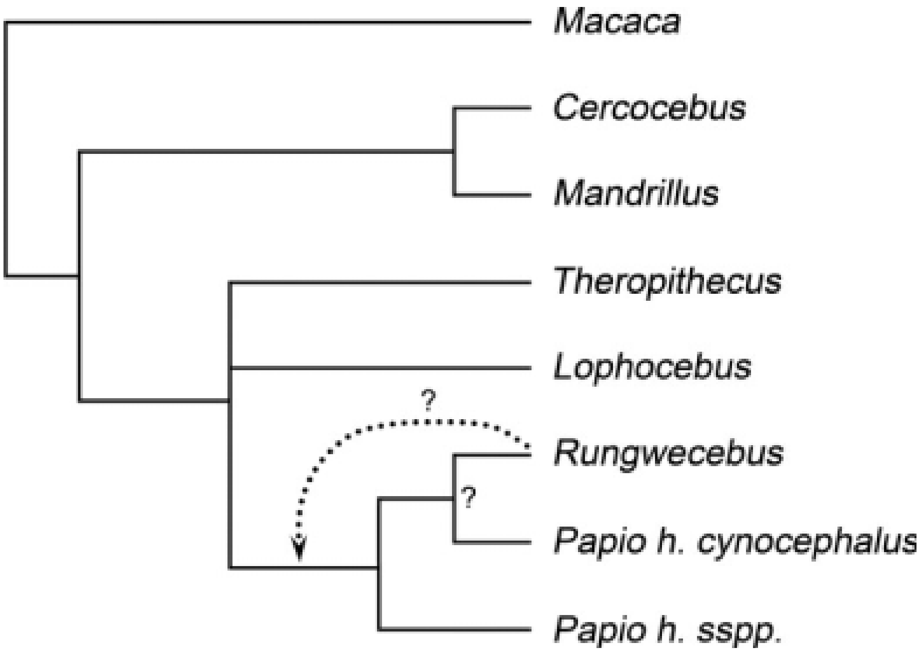
This dissertation focuses on the extinct baboon *Theropithecus brumpti,* a large Old World monkey (Family Cercopithecidae) from the African Pliocene. It is a member of the Subfamily Cercopithecinae and Tribe Papionini which is a successful group of monkeys including the extant macaques (*Macaca*), mangabeys (*Lophocebus*, *Cercocebus*), baboons (*Papio*), mandrills and drills (*Mandrillus*), the kipunji (*Rungwecebus*) and geladas (*Theropithecus*) (Fleagle, 1999). In addition it includes the extinct genera *Procynocephalus, Paradolichopithecus*, *Dinopithecus, Parapapio*, *Pliopapio*, *Gorgopithecus*, and *Procercocebus* (Szalay and Delson, 1979; Fleagle, 1999; Frost, 2001b; Gilbert, 2008). Extant papionins are spread throughout the Old World from southern Africa, to the mountains of Japan and the island rainforests of Southeast Asia. As further evidence of their adaptability and evolutionary success, papionin monkeys are widely present and abundant components of the Plio-Pleistocene fossil record (Figure 2.1.). For many years, molecular and morphological studies concerning the phylogenetic relationships among the extant Papionini were incongruent. Most morphological studies concluded that the mangabeys, *Cercocebus* and *Lophocebus*, were a monophyletic group and that the mandrills and drills (*Mandrillus*) were more closely related to the savannah baboons (*Papio*) (Jolly, 1972; Szalay and Delson, 1979; Strasser and Delson, 1987; Delson and Dean, 1993). Molecular data, however, consistently determined that mangabeys, as defined above, were a diphyletic group (Disotell, 1994, 2000; Harris, 2000) and reconfigured the phylogeny traditionally used for the tribe as defined by morphology.

Figure 2.1. Map of extinct (red dots) and extant (red shaded area) cercopithecine ranges. Courtesy of Frost (in press).



Given the power, and repeatability, of the molecular data sets, most researchers now accept the molecular phylogeny and place macaques as the basal extant papionin. *Cercocebus* and *Mandrillus* are a monophyletic group and *Papio, Theropithecus* and *Lophocebus*are placed in a separate clade (Figure 2.2.). As a result, morphologists are now revisiting the papionin anatomy in light of the molecular data (Fleagle and McGraw, 1999, 2002; Gilbert et al., 2009); an exercise to which this dissertation will eventually contribute. *Rungwecebus* is a recently discovered new extant papionin species known only from southern Tanzania (Rovero et al., 2009). Its phylogenetic relationship to other papionins remains unresolved (Figure 2.2) (Davenport et al., 2006; Burrell et al., 2009).

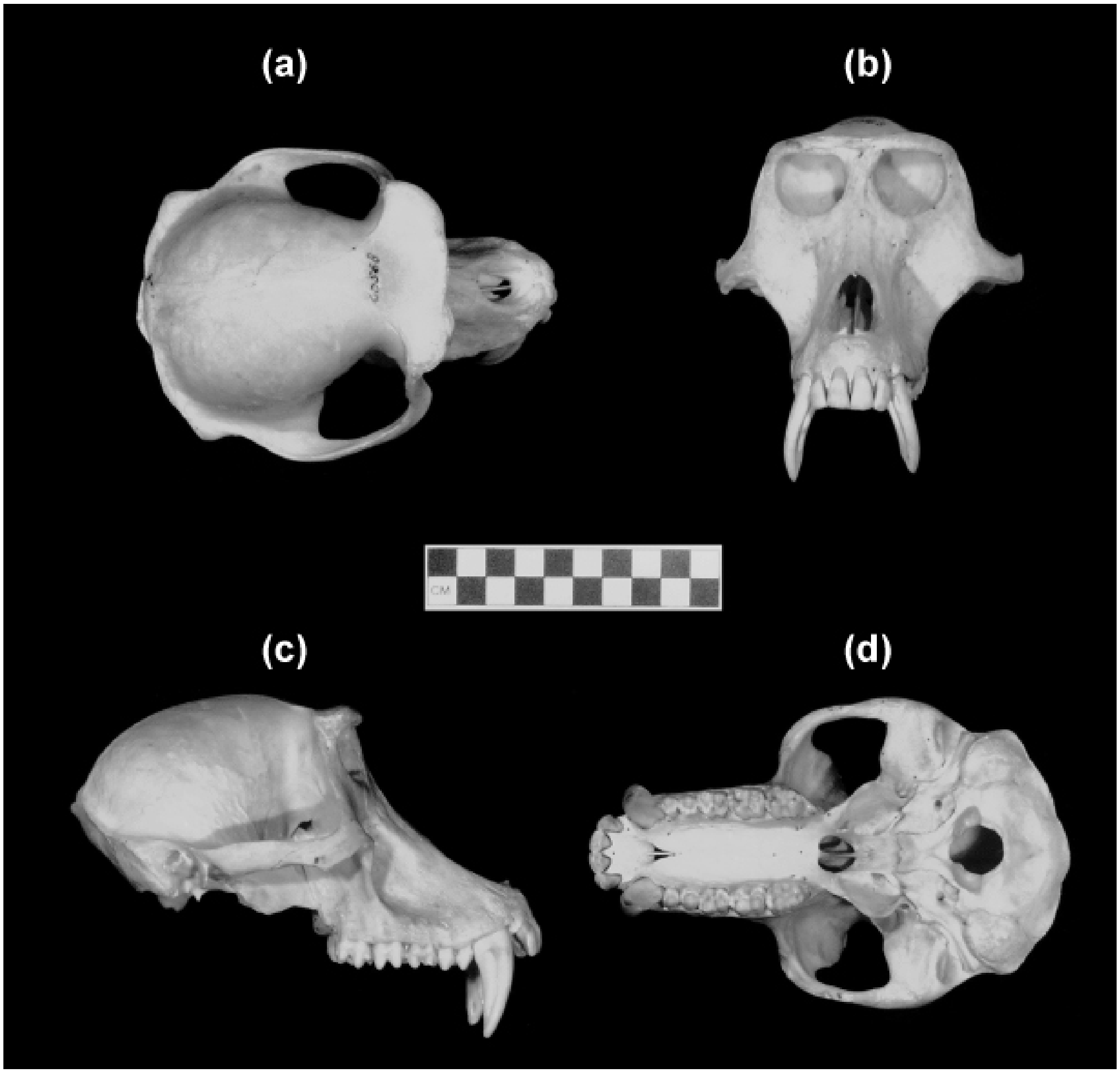
Figure 2.2. Phylogenetic tree of extant Papionini (figure from (Singleton et al., 2010)



Extant *Theropithecus*

Although papionins are widespread, extant *Theropithecus gelada* is very geographically restrained, occupying only the montane, highlands of Ethiopia (Dunbar, 1993a). Although geographically constrained, they can be found in very large herds (sometimes up to 400 individuals). Generally, however, geladas live in one-male herds of three to twenty individuals (Fleagle, 1999). While highly sexually dimorphic, both sexes do have distinctive red hourglass patches of skin on their chests and males have long shaggy mane-like pelage. The molar teeth of *Theropithecus* are very unusual and distinctive and are characterized by complex enamel folding and an hyposodont appearance (Szalay and Delson, 1979)(Figure 2.3.) Geladas are primarily terrestrial, foraging all day on the ground. However, they do retreat to the trees at night (Fleagle, 1999). Dietarily unique among primates, *T. gelada*, has a diet that is almost 90% grasses (Iwamoto, 1993) and its foraging style is notable as it harvests grasses primarily using the thumb and first finger while sitting and then 'shuffling' along the ground (Wrangham, 1980). Consequently, the postcranial morphology of *Theropithecus* has some unique features, thought to be adaptations for harvesting and feeding on grasses. These are: a relative elongation of the first metacarpal, a relatively short proximal phalanx of the second digit and a femur displaying a reversed carrying angle which may be related to the habitual sitting and bottom shuffling form of locomotion (Jolly, 1972; Etter, 1973; Krentz, 1993b). Additionally, *Theropithecus* has postcranial traits associated with a high degree of terrestriality including an ulnar olecranon process that is highly retroflexed and extending dorsally, and relatively short and robust manual and pedal phalanges (Jolly, 1972; Szalay and Delson, 1979; Frost and Delson, 2002; Guthrie and Frost, 2010)

Figure 2.3. An a. dorsal b. frontal c. lateral and d. occlusal view of a male *Theropithecus gelada* skull (AMNH 60568)

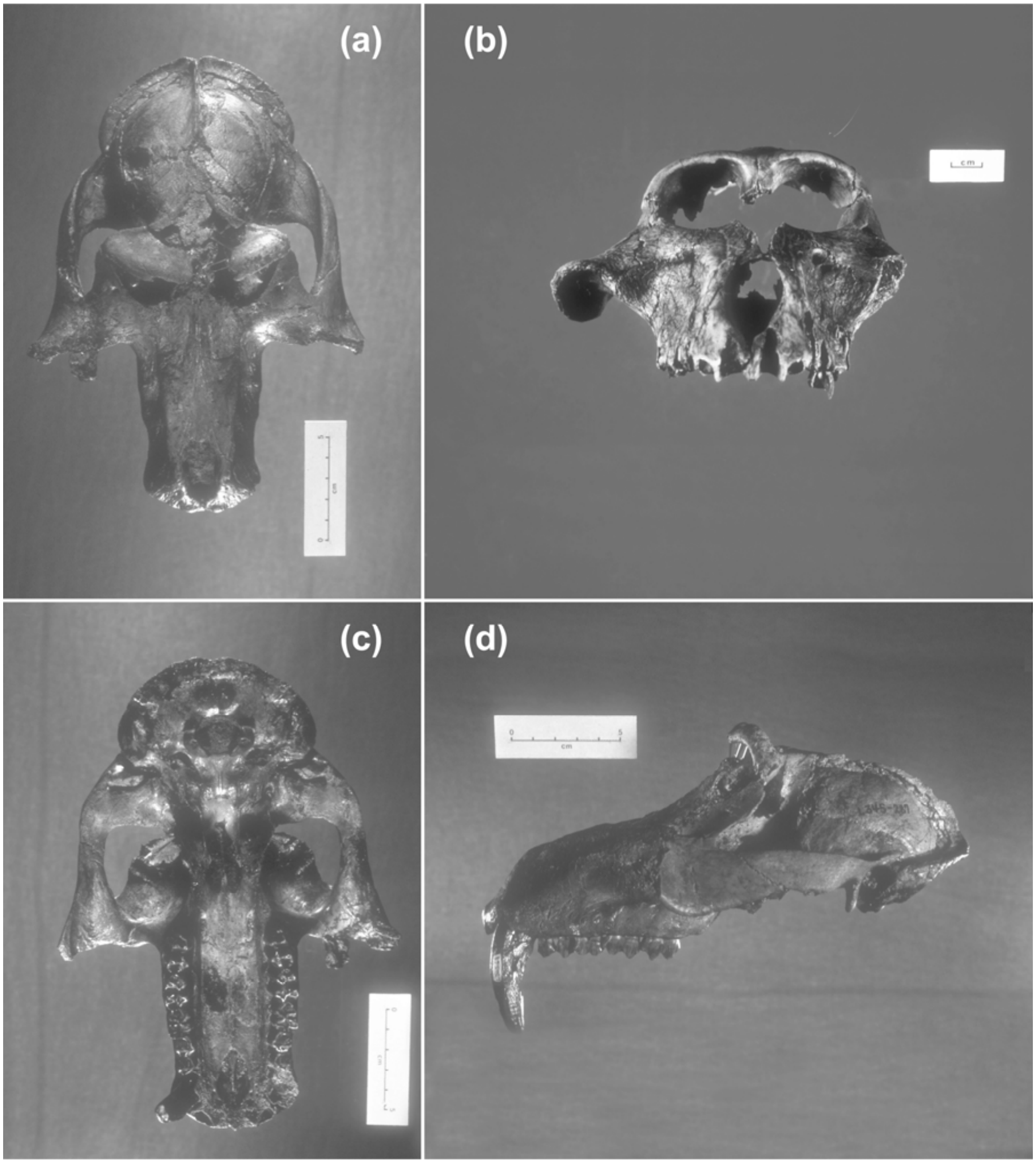


Fossil *Theropithecus*

In spite of the restricted range today, *Theropithecus* has the best fossil record of any papionin (Jablonski and Frost, 2010). It is found at virtually all Plio-Pleistocene African sites and is often the most abundant primate at those sites (Delson, 1984). As a consequence it is the focus of a myriad of anthropological research e.g. (Cronin and Meikle, 1972; Eck and Jablonksi, 1987; Eck, 1987; Delson, 1993; Eck, 1993; Foley, 1993; Jablonski, 1993c; Leakey, 1993; Pickford, 1993; Elton, 2002; Hughes et al., 2008). Two distinct lineages are known in the fossil record: *T. oswaldi* (Figure 2.4.) and *T. brumpti*. (Figure 2.5.). Delson (Delson, 1993) has separated these two lineages taxonomically in the subgenera *T. (Theropithecus)* and *T. (Omopithecus)* respectively. Notably, the relationship of extant *T. gelada* to either of these lineages is unclear in the absence of any fossil evidence. *T. gelada* appears to be a long isolated sublineage within *Theropithecus* (Delson, 1993; Jablonski, 1993b)

Figure 2.4. An a. dorsal b. frontal c. lateral and d. occlusal view of male *Theropithecus oswaldi* skull from Kanjera (M32102).

Figure 2.5. An a. superior b. frontal c. occlusal and d. lateral view of a *Theropithecus brumpti* skull (a)(b) and (d): male L345-287; (b): female L32-155). Images by Gerald Eck and used by permission from Eric Delson.



Currently, the earliest *Theropithecus* material (*Theropithecus sp*. indet.) are collections of isolated teeth from the Lokochot and Lonyumun Members (Early Pliocene) that can be assigned, with some certainty, to *Theropithecus* as the molar teeth have diagnostic *Theropithecus* anatomy including pinched and columnar cusps with thick molar enamel (Jablonski and Leakey, 2008). It has been suggested that these teeth may bear the most affinity to the *brumpti* lineage (Jablonski and Leakey, 2008).

After this, the two lineages appear in the Turkana Basin fossil record at roughly the same time, although relative frequencies differ greatly (Behrensmeyer et al., 1997). At older sites in the Turkana Basin *T. brumpti* dominates and the *T. oswaldi* lineage is rare. This situation steadily reverses over approximately 1 million years, so that the *T. oswaldi* lineage is the only one present in basin by 1.9 Ma (Frost, 2007; Jablonski and Leakey, 2008). It was thought that, outside of the Turkana Basin, during this entire timeframe, only the *T. oswaldi* lineage is present (Jablonski, 2002a). However, a new *T. brumpti* partial skeleton from the Tugen Hills was found during the writing of this dissertation, which, for the first time, places *T. brumpti* outside of the basin (Gilbert et al., 2011).

Of the two lineages, *T. oswaldi* is the far better known and is one of the best known fossil mammals in Africa. *T. oswaldi* is found throughout Africa (Freedman, 1957; Jolly, 1972; Eck and Jablonksi, 1987; Delson, 1993; Leakey, 1993) as well as India, Israel, Spain and possibly Italy (Gupta and Shani, 1981; Gibert et al., 1995; Belmaker, 2002; Rook et al., 2004). This lineage appears to be represented by three subspecies (or perhaps chronospecies) of *T. oswaldi*: *T. o. darti* for the early stage, *T. o.*

oswaldi for the intermediate stage and *T. o. leakeyi* for the latest stage (Leakey, 1993; Frost and Delson, 2002).

The taxonomy of the *T. brumpti* lineage is more complicated as many isolated and early fossils have variously been attributed to this lineage. Eck and Jablonski (Eck and Jablonksi, 1984) argue that two Pliocene species *Papio baringensis* and *Papio quadratirostris* should both be included in *Theropithecus brumpti* lineage. However, these two species are not very well represented. *P. baringensis* (3.2 Ma) is known, primarily, from a partial cranium from the Chemeron Formation in western Kenya (Leakey, 1969; Deino and Hill, 2002). Additional material, including a collection of fossils from the Angolan site of Leba, has been attributed to this species (Jablonski, 1994). *P. quadratirostris* (3.4-3.6 Ma)is represented by one nearly complete cranium from the Usno Formation of the Omo Valley in Ethiopia (Iwamoto, 1982; de Heinzelin, 1983). Delson and Dean (1993) have argued that *P. baringensis* may be a theropith, but that *P. quadratirostris* is better accommodated as a species of *Papio* (*Dinopithecus*) . Gilbert also found that *P. quadratirostris* showed affinities to *Papio* (*Dinopithecus*) (Gilbert, 2008). No postcranial material has been allocated to either of these species. Regardless, this dissertation only includes material unambiguously allocated to *T. brumpti* proper by all authors.

Current understanding of these two *Theropithecus* lineages characterizes their paleobiology as different. The genus *Theropithecus* is characterized by a unique suite of adaptations for harvesting and feeding on grasses. *Theropithecus gelada* has a diet of almost 90% grasses, at least in some seasons (Iwamoto, 1993). Data from dental microwear, jaw biomechanics, and stable isotopic analysis of enamel carbonates suggest that *T. oswaldi* was also a grazer (Lee-Thorpe et al., 1989; Jablonski, 1993a; Van der Merwe et al., 2003; Codron et al., 2005; El-Zaatari et al., 2005; Fourie et al., 2008; Teaford et al., 2008). Studies of the masticatory apparatus have hypothesized that the emergence and early diversification of *Theropithecus* was linked to the evolution of a feeding apparatus specialized for grazing (Jablonski, 1993a). Many of these adaptations are present in *T. gelada*, and in *T. oswaldi* lineage they become more extreme over time, including increase in body size, molar tooth complexity, development of the muscles of mastication and committed terrestriality (Jolly, 1972; Leakey, 1993; Frost and Delson, 2002). All studies of the postcrania of *T. oswaldi* have determined that is was terrestrial. Key evidence for the interpretation includes: a stable shoulder joint (as seen in the relative height of the humeral head, which is much lower that the greater tuberosity), a highly retroflexed medial epicondyle, a short and retroflexed olecranon process, and relatively short manual and pedal phalanges (Jolly, 1972; Krentz 1993b). Further, the *T. oswaldi* lineage also shows a distinct increase in body size over time. It is estimated that males ranged from 25-34 kg in *T. o. darti* (the oldest subspecies), 42-50 kg in *T. o. oswaldi* and 50-85 kg in *T. o. leakeyi* (Delson et al., 2000).

While *Theropithecus brumpti* exhibits some traits consistent with the grazing diet of *T. oswaldi*, other evidence indicates that its diet and locomotor patterns may have been tailored to its more wooded habitat. *T. brumpti* is not associated with grassland habitats, but it shares the distinctive molar morphology of the genus *Theropithecus* which is usually associated with a grazing diet (Eck and Jablonksi, 1987). However, microwear studies suggest that *T. brumpti* may have eaten more soft fruit than is typical for the genus (Teaford, 1993). Jablonski has noted unusual traits in the jaw mechanics of the species including distinct large, anterolaterally expanded zygomatic arches which allow for attachment of extremely large masseter muscles (Jablonski, 1993a)(Figure 2.5.). Jablonski specifically argues that this allows *T. brumpti* to maintain high occlusal forces over the molar row while allowing for a wide gape and emphasizing large-object feeding (Jablonski, 1993a). The body mass for male *T. brumpti* has been estimated to be approximately 44 kg (Delson et al., 2000; Jablonski et al., 2002), which is much larger than the average male baboon (32 kg) (Delson et al., 2000).

There have been relatively few studies of the postcrania of *T. brumpti*. In an analysis of a relatively complete *T. brumpti* hand (L865-1) from the Shungura Formation, dated to 2.36 – 2.4 Ma, Jablonski (Jablonski, 1986) noted arboreal adaptations including relatively curved middle phalanges. Krentz (Krentz, 1993b), attempted to assign cercopithecid postcrania from the Shungura Formation to different species of *Theropithecus*. None of the material studied by Krentz (other than L865-1) was directly associated with diagnostic cranial remains, however, and given the presence of both *T. brumpti* and *T. oswaldi* as well as multiple other similarly sized cercopithecids, renders it impossible to be certain of his allocations. Regardless, based on this unassociated material, he noted a suite of traits in the elbow and shoulder that indicate arboreal adaptations. These include increased flexibility in the shoulder joint and large rotator cuff musculature. As a result, *T. brumpti* is often described as the ‘arboreal’ theropith (Ciochon, 1993; Elton et al., 2003).

However, relatively recent new *T. brumpti* postcranial material makes the picture more complex. A description of a 3.3 Ma *T. brumpti* skeleton from West Turkana (KNM-WT 39368) presents a mixture of features some of which are generally associated with terrestrial locomotion such as a highly stable elbow joint (Jablonski, 2002b). Hindlimb elements, associated with a very well preserved skull, were found in the Chemeron Formation of the Tugen Hills (2.63 Ma) and were described in 2010. Interestingly, aspects of the femur and tibia seemed to differ markedly from the morphology described for the species, which was based on unassociated remains (Gilbert et al., 2011). Therefore, there is a growing divide between previous descriptions of the locomotor morphology of *T. brumpti* and new implications based on associated materials.

Finally, *T. brumpti* also has adaptations for manual grasping and fine manipulation shown by a large but retroflexed medial humeral epicondyle (for attachments of the *m. pronator teres* as well as the long carpal and digital flexor muscles). Proportions of the digital rays may denote capabilities for precise opposition. This seems to suggest that the food harvesting and processing anatomy that distinguishes the genus is present in this early representative. With the suite of material that is now available, it is possible to more fully analyze *T. brumpti* material to address these discrepancies.

Previous Cercopithecoid Locomotor Studies

"*several skeletal traits conventionally viewed as indicators of locomotor habits and/or substrate preferences in all cercopithecids, are not necessarily associated with the same behavioral adaptations in both subfamilies*" (Birchette 1982 pg. iii)

Researchers have long sought to understand how cercopithecoid postcrania may reflect behavior, from which they infer behavior in the fossil record (Jolly, 1972; O'Connor, 1975; Fleagle, 1977; Strasser, 1988; Ciochon, 1993). Schultz (1970) stated that there is little morphological variation in the postcrania of cercopithecoids as a result of their shared adaptation for quadrupedal locomotion. As such, cercopithecoids do not have specialized locomotion (i.e. vertical clinging and leaping) that would produce unique skeletal morphologies. Therefore, he concluded, differentiating and identifying postcrania of cercopithecoids would be very difficult (Schultz, 1970).

Most early studies were broad in taxonomic scope (Ashton and Oxnard, 1964), but recent research has shown there is considerable morphological diversity of particular skeletal traits among closely related taxa and that similar morphology is not necessarily indicative of similar behavior (Birchette, 1982). Birchette's work specifically documented this issue in colobines and spelled out the importance of interpreting behavior in extinct species within a carefully delineated subfamily-specific framework and outlined a set of colobine morphological patterns. No such framework currently exists for cercopithecines, although postcranial adaptations of specific taxa have been investigated (Gebo and Sargis, 1994; Fleagle and McGraw, 2002). Specific findings and diagnostic features of previous papionin research is discussed at length and in detail throughout this dissertation and will not be reviewed in detail here.

Geological Overview

Up until recently, *Theropithecus brumpti* had been known only from the Pliocene deposits in the Turkana Basin (Leakey, 1993). A partial skeleton of a female individual, however, was recently described from the Tugen Hills, in the northern Kenyan Rift Valley, but outside the Turkana Basin (Gilbert et al., 2011). The geology and paleoenvironment of the *T. brumpti* material from the Tugen Hills is still being analyzed and described. Therefore, this dissertation will only review the geology of the Turkana Basin. The geology and stratigraphy of the Turkana Basin have been extensively studied and described (de Heinzelin, 1983; Brown et al., 1985; Harris et al., 1988a; Harris et al., 1988b; Feibel et al., 1989; Brown and Feibel, 1991; Brown et al., 1992). They will only be summarized here as they relate to the *T. brumpti* material. In the Turkana Basin, *T. brumpti* postcranial material comes from all three main formations: Shungura (Ethiopia), Nachukui (West of Lake Turkana), Koobi Fora (East of Lake Turkana) (Figure 2.6.). Specifically, the *T. brumpti* material derives from the lower, middle and upper Lomekwi Members (3.36-2.5 Ma) of Nachukui Formation (Harris et al., 1988a; Feibel et al., 1989); the Lokochot and Tulu Bor Members (3.5-2.68) of the Koobi Fora Formation (Leakey, 1993); and Unit B-10 (2.95) to Unit G-13 (c. 2Ma) of the Shungura Formation (Eck and Jablonksi, 1987). To be complete, there is additional, older, material from Member A in the Shungura Formation, the Usno formation and from the Kenyan site of Lothagam (southwest Lake Turkana) that is published as *Theropithecus* cf. *brumpti* and is most likely *T. brumpti*. However, as there is no associated postcranial material, they are not included in this dissertation (Delson et al., 1993; Frost, 2001a; Leakey et al., 2003).

Sediments of the Turkana Basin have been extensively studied for over thirty years (de Heinzelin, 1983; Harris et al., 1988a; Feibel et al., 1989; Brown and Feibel, 1991; Feibel et al., 1991) and well documented stratigraphy and geochronology of these formations permits correlations between tuffs and formations across the basin and allows for relatively good chronological control of most material (Figure 2.7.).

Figure 2.6. Map of the Turkana Basin showing the relative positions of the formations of the Omo Group from (Harris et al., 2006)

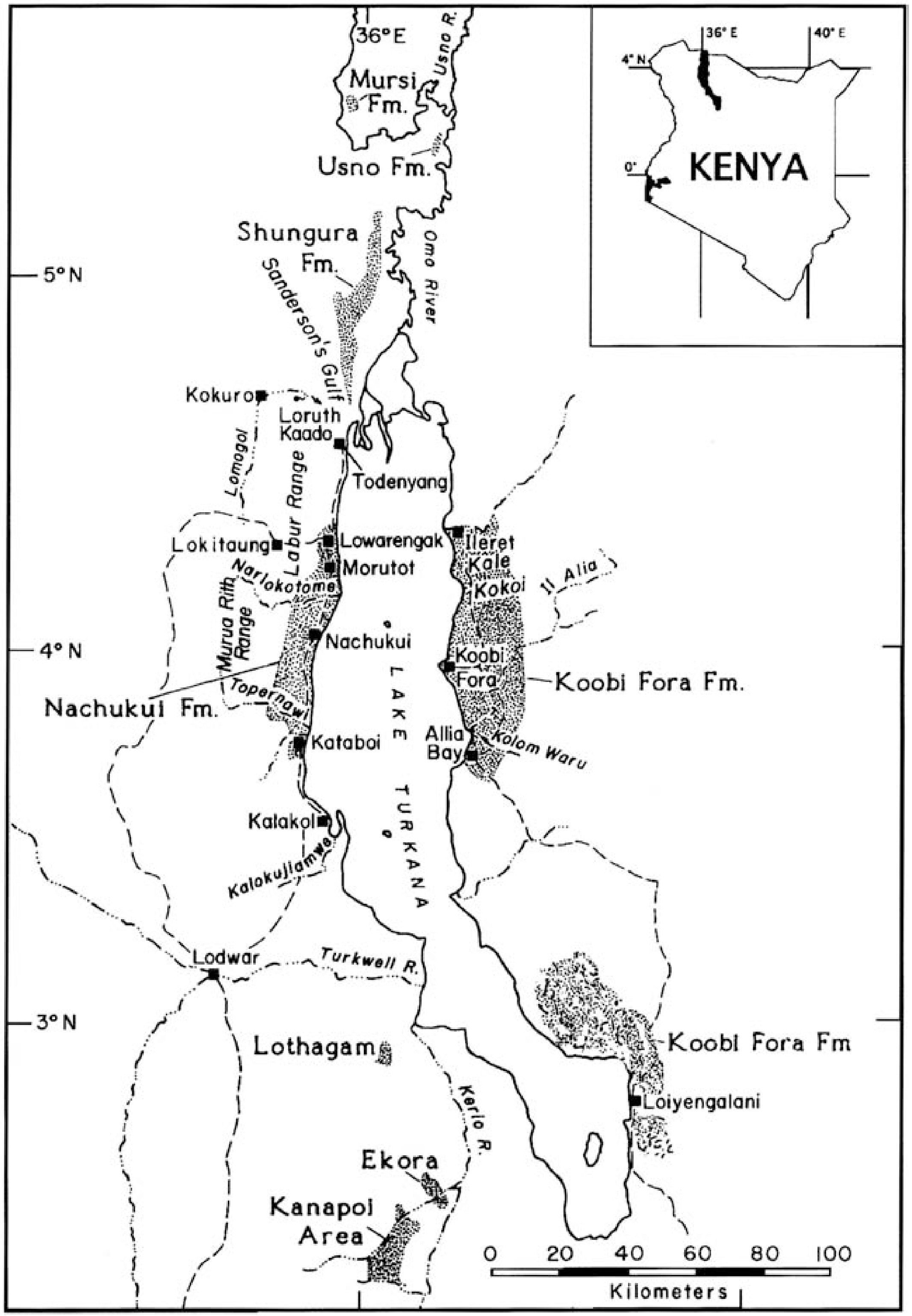
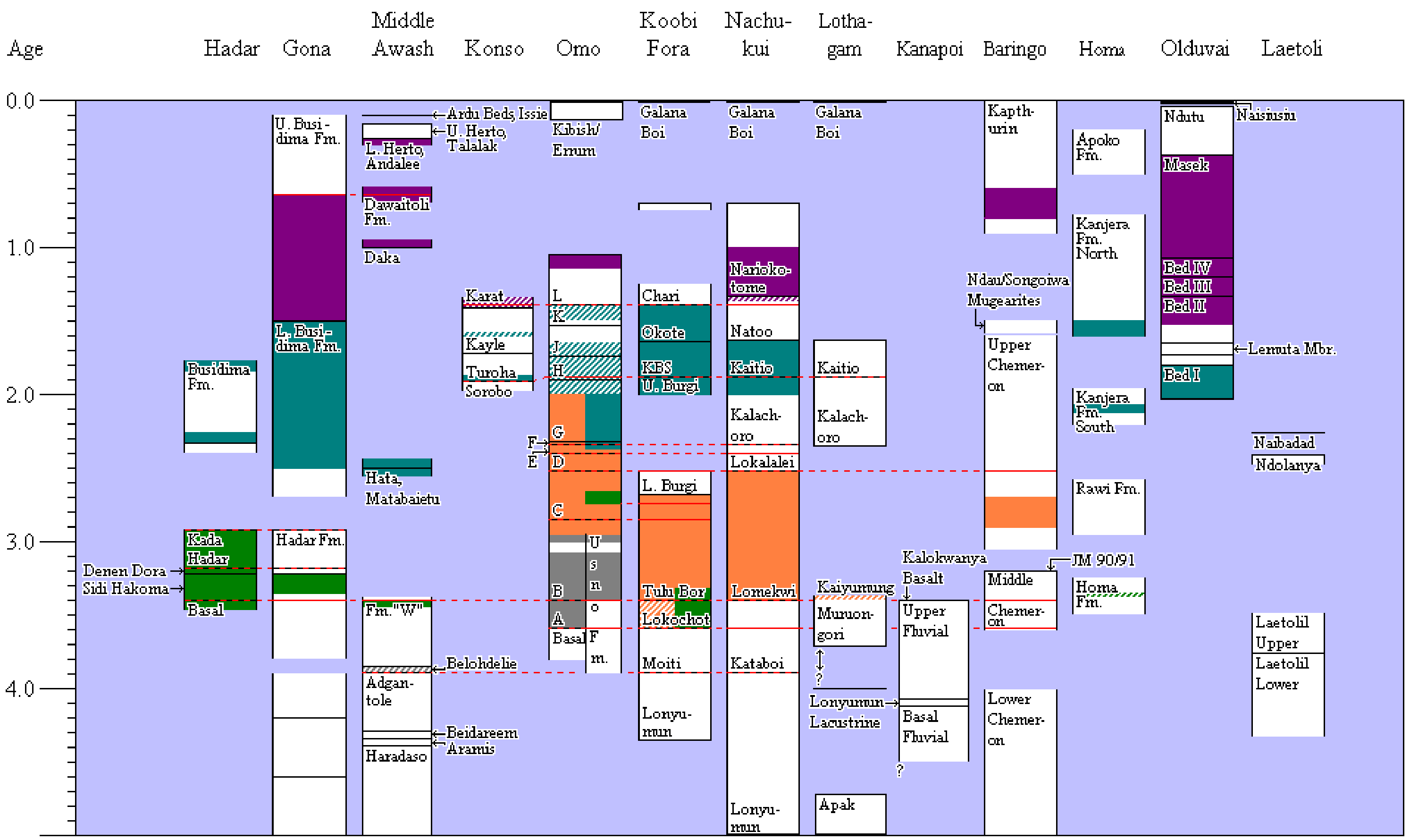


Figure 2.7. Correlations and tuffs in East Africa. Also shown are occurrences of *Theropithecus* within this system. *T. brumpti* is shown in orange, *T. oswaldi darti* in green, *T. oswaldi oswaldi* in blue and *T. oswaldi leakeyi* in purple. Area shaded in grey is Theropithecus material of unknown species. (Courtesy of S. Frost)



The associated faunas at specific *T. brumpti* localities have also been examined (Plummer and Bishop, 1994; Kappelman, 1997; Reed, 1997; Spencer, 1997; Bishop, 1999; Elton, 2000; Bobe and Eck, 2001; Bobe, 2002) as well as soil carbonates, paleosols and enamel isotopic ratios (Feibel et al., 1991; Schoeninger et al., 2003; Wynn, 2004; Lepre et al., 2007). These data consistently place *T. brumpti* in woodland habitats.

The *T. brumpti* partial skeleton from the Chemeron Formation of the Tugen Hills represents the first *T. brumpti* outside the Turkana Basin. The Chemeron Formation spans over 3.7 Ma from 5.3 Ma at the base to less than 1.6 Ma at the top. (Gilbert et al., 2011). This skeleton is known from BPRP # 152 and, based on both chronostratigraphy and detailed sedimentation rates calculated of the lake margin at this site, this skeleton is dated to 2.63 Ma. Paleoenvironmental reconstruction is ongoing at this site; however, early results suggest that this area was characterized by grassy woodlands (Gilbert et al., 2011).

CHAPTER III

MATERIALS AND METHODS

All available post-cranial material of *Theropithecus brumpti* that is directly associated with diagnostic cranial material was described and analyzed in this dissertation (Table 3.1.).

The majority of the associated *Theropithecus brumpti* material is from the formations in the Kenyan part of the Turkana Basin. Materials from Koobi Fora (East Turkana Basin, formerly East Rudolf), the Nachukui Formation (West Turkana), and the Chemeron Formation, Tugen Hills are all housed at the Nairobi National Museum a part of the National Museums of Kenya (KNM) system. All of these collections are assigned accession numbers beginning with the museum ID (KNM) followed by a two letter reference to the collecting area: ER for specimens from Koobi Fora; WT for those from the Nachukui Formation; and TH for those from the Tugen Hills. Additionally, there is one partial skeleton from the Shungura Formation, in the lower Omo Valley, in the Ethiopian portion of the Turkana Basin. It is housed at the National Museum of Ethiopia, and was collected by the American contingent of the International Omo Expedition. This collection uses a numbering system where collecting localities are given a number beginning with the letter L, followed by a dash and the individual specimen number. The *T. brumpti* partial skeleton included here is numbered L865-1 and L865-2 for the first and second fossil specimens from locality 865.

Table 3.1. Associated *Theropithecus brumpti* material used in this dissertation.

Catalogue Number	Specimen Description	Member	Area	Geological Age	Sex
KNM-ER 3084	Fragment Left Scapula with Glenoid Fossa Fragment Proximal Right Humerus Fragment Distal Right Humerus Fragment Proximal Right Ulna	Lokochot	Area 117	3.44 Ma	UK
KNM-ER 30385	Fragment Left Scapula with Glenoid Fossa Fragment Left Calcaneus	Lokochot	Area ?206	~3.5 – 3.6 Ma	UK
KNM-ER 3119	Fragment Right Humerus Shaft Fragment Proximal Right Femur	Tulu Bor	Area 102	3.4 Ma	M
KNM-ER 3013	Distal Fragment Right Humerus Distal Fragment Left Humerus Proximal Fragment Left Ulna Proximal Fragment Right Femur	Tulu Bor	Area 204	3.4 Ma	UK

Catalogue Number	Specimen Description	Member	Area	Geological Age	Sex
KNM-WT 39368	Complete Left Scapula Right Glenoid Fossa Complete Right Humerus Right Proximal Ulna Complete Left Ulna Complete Right Radius (Distal End *in situ*) Left Radial Head Left Carpals (See Chapter X) Complete Right MC1-MC5 (*in situ*)	Lower Lomekwi	LO 5	3.3 Ma	M

	Complete Left MC1-MC5				
	Right Carpal Proxmal Phalanges Ray 1-5				
	Right Carpal Intermediate Phalanges Ray 1-5				
	Right Carpal Distal Phalanges Ray 1-5				
	Complete Right Tibia				
	Complete Right Fibula				
KNM-WT 17554	Partial Glenoid Fossa	Lower Lomekwi	LO 5	3.3 Ma	UK
	Lt. Radial Head				
	Right Talus				
KNM-WT 17560	Proximal Right Ulna	Middle Lomekwi	LO 9	2.6-3.24 Ma	UK

Catalogue Number	**Specimen Description**	**Member**	**Area**	**Geological Age**	**Sex**
KNM-TH 46700	Complete Right Femur	Chemeron	BPRP#152	2.63 Ma	F
	Complete Right Tibia				
	Fragment Proximal Left Tibia				
	Compete Left Cuboid				
	Proximal Fragment Left MT III				
	Proximal Fragment Left MT V				
	Left Os Cox				

Catalogue Number	**Specimen Description**	**Member**	**Area**	**Geological Age**	**Sex**
L 865-2	Complete Left MC1-MC5	E	Unit 4 Locality 865	2.2 Ma	M
	Left Carpal Proxmal Phalanges Ray 1-5				

Left Carpal Intermediate Phalanges Ray 2-4
Distal Fragment Right Humerus
Complete Right Astragalus
Complete Right Calcaneus

There are nine associated partial skeletons of *T. brumpti*; all are included in this dissertation (Table 3.1.). There are four from Koobi Fora: KNM-ER 3084 is preserves aspects of the forelimb and hindlimb and is associated with a mandible, KNM-ER 30385 is a partial skeleton associated with a diagnostic cranial fragment and a left M3, KNM-ER 3119 is a male partial skeleton with forelimb and hindlimb elements associated with a mandible and KNM-ER 3013 is associated with a maxilla and a mandible with diagnostic *T. brumpti* dentition. These have all been described in Jablonski and Leakey's Koobi Fora Volume (Jablonski and Leakey, 2008), but they have never been analyzed in full. This is also true of some of the West Turkana material (KNM-WT 17554 and 17560), but KNM-WT 39368 is a relatively complete skeleton of an old adult male, with an associated mandible, recovered *in situ* from LO 5 (~3.3 Ma) in West Turkana. This skeleton was described in detail by Jablonski *et al*. (2002). L865-1 is an older adult male partial skeleton associated with a mandible, found *in situ* and excavated. It is from near the top of member E and there just older than 2.36 Ma. The hand was described by Jablonski (1986) and the cranial material by Eck and Jablonski (1987). Most recently a complete skull and partial skeleton of an adult female was found in the Chemeron Formation of the Tugen Hills at BPRP Site #152 (2.63 Ma) and was described by Gilbert et al. (2011).

Comparative Sample: Extant

The extant comparative sample was restricted to the subfamily Cercopithecinae. This was a decision made deliberately and in reference to a previous postcranial study, which found that the postcrania of Cercopithecoidea is best understood when compared within subfamily (Birchette, 1982).

There are 11 extant genera (and approximately 71 species) of cercopithecines (Fleagle, 1999; Tosi, 2004). These are limited to sub-Saharan Africa except for macaques that range from far eastern Asia to north Africa and Gibraltar (Fleagle, 1999). There are two tribes: Cercopithecini (the guenons) which include: *Allenopithecus, Miopithecus, Chlorocebus, Cercopithecus* and the tribe Papionini: *Macaca, Lophocebus, Rungwecebus, Papio, Theropithecus, Cercocebus* and *Mandrillus*. Inadequate sample size and representation in museum collections made it impossible to include *Allenopithecus*, *Miopithecus* or *Rungwecebus* postcrania in this dissertation. All other cercopithecine genera are represented (Table 3.2.). All comparative specimens were from wild-shot adult individuals without obvious skeletal pathology. See Table 3.3. for species abbreviations used throughout this text and in boxplots. See Appendix C for a list of specimens included in the comparative sample.

Table 3.2. Cercopithecine Taxa (Extant and Extinct (ǂ)) Sample

	MALE	**FEMALE**	**UNKNOWN**	**TOTAL**
Macaca fascicularis	4	4	3	11
Macaca nemestrina	6	4	0	10
Macaca thibetana	7	2	1	10
Cercocebus agilis	7	1	0	8
Cercocebus torquatus	5	4	1	10
Lophocebus albigena	16	6	0	22
Papio hamadryas anubis	13	6	1	20
Theropithecus gelada	3	2	0	5
Mandrillus sphinx	4	3	1	8
Mandrillus leucophaeus	2	3	0	5
Cercopithecus mitis	5	5	0	10
Cercopithecus neglectus	5	5	0	10
Chlorocebus aethiops	8	7	0	15
Chlorocebus patas	4	1	1	6
Theropithecus oswaldi ǂ	1	0	14	15
TOTAL	90	53	22	165

Table 3.3. Taxon Abbreviations

Taxon	ABBREV	Taxon	ABBREV
Macaca fascicularis	Mf	*Theropithecus gelada*	Tg
Macaca nemestrina	Mn	*Mandrillus sphinx*	Ms
Macaca thibetana	Mt	*Mandrillus leucophaeus*	Ml
Cercocebus agilis	Ca	*Cercopithecus mitis*	Cm
Cercocebus torquatus	Ct	*Cercopithecus neglectus*	Cn
Lophocebus albigena	La	*Chlorocebus aethiops*	Cha
Papio hamadryas anubis	Pha	*Chlorocebus patas*	Chp

Comparative Sample: Extinct

The comparative sample also included all available East African (available at the KNM or NME) associated *T. oswaldi* material. Material from the Kenyan sites of Oloregsailie (0.99-0.74 Ma) and Kanjera (1.85-1.5 Ma) are included (Jolly, 1972; Delson et al., 1993). While this material is not strictly associated, it is very clear that this material is *Theropithecus oswaldi*, and, given the time range, there is no other possibility. The Olorgesailie *Theropithecus* material has all been recovered from one site DE/89B in Member 7 (~0.74 Ma). The Kanjera material is also all from one locality, but it is not as well-dated. However, based on similarity with *Theropithecus* material from Bed 1 in Olduvai Gorge, the age range for the Kanjera material is between 1.85-1.5 Ma.

Data Collection

All material (extant and extinct) was described with qualitative assessments including taphonomic and preservation states, non-metric assessment of functional features , and linear measurements. Linear measurements were taken with Mitutoyo digital calipers (573-725 Digital Extended Pointed Jaw) and these were entered directly into a Microsoft Access database.

For the extant specimens, all measurements were taken on the right element, unless pathological or missing in which case the left was used. For documentation and eventual publication, digital photographs were made of a large sample of the material. The photographs were taken using a Cannon Rebel mounted on a tripod using a 28-200mm lens. In the majority of photographs, a black cloth was used. All photographs were made with a centimeter scale in view. Different postcranial elements were photographed in different orientations including non-standard views to maximize anatomical and functional information,

Description of Measurements

One hundred and twenty five linear measurements of the postcrania were analyzed, including 6 measurements of the scapula, 21 of the humerus, 9 of the ulna, 8 of the radius, 8 each of metacarpals and carpal phalanges, 22 of the femur, 12 of the tibia, 7 of the talus, 6 of the calcaneus, 2 on the cuboid and 8 each of metatarsals and pedal phalanges Carpal elements were analyzed qualitatively. Table 3.4 gives a description of each measurement and illustrations are shown in Figure 3.1. All are either standard postcranial measurements or believed to have functional relevance to this study following the results of past authors: (Jolly, 1972; Birchette, 1982; Harrison, 1989; Strasser, 1989; Frost and Delson, 2002; Almecija et al., 2007).

Table 3.4. Postcranial Measurements Used In Study

	Scapula	
S1	Scapula Length	depth of glenoid fossa to vertebral border at spine
S2	Scapula Width	superior angle to inferior angle
S3	Glenoid Fossa Length	cranial edge to caudal edge
S4	Glenoid Fossa Width	medial edge to lateral edge on caudal part of fossa
S5	Supraspinatus Fossa Length	superior angle to superior surface of spine
S6	Infraspinatus Fossa Length	inferior angle to spine
	Humerus	
H1	Humerus Length 1	greater tuberosity to distal capitulum
H2	Humerus Length 2	humeral head to distal capitulum
H3	Maximum Humeral Length	proximal-most point to most distal point of trochlea
H4	Proximal ML	maximum medio-lateral dimension of the proximal humerus including the tuberosities
H5	Proximal AP	maximum anterio-posterior dimension of the proximal humerus including the tuberosities
H6	Humeral Head Length	anterior edge of articular surface of the head to posterior edge
H7	Humeral Head Width	medial edge of articular surface of the head to lateral edge
H8	Humerus Length 3	distal extension of deltoid tuberosity (V) to humeral head
H9	Humerus Deltoid Plane Width	medio-lateral width of deltoid plane at widest portion
H10	Humeral AP Diameter at V Deltoid Tuberosity	maximum anterio-posterior dimension of the midshaft
H11	Humeral ML Diameter at V Deltoid Tuberosity	maximum medio-lateral dimension of the midshaft
H12	Humeral AP Diameter at Proximal Bracioradialis Flange	maximum anterio-posterior dimension of the shaft at proximal extent of the bracioradialis flange
H13	Humeral ML Diameter at Proximal Bracioradialis Flange	maximum medio-lateral dimension of the shaft at proximal extent of the bracioradialis flange
H14	Humerus Length 4	proximal brachioradialis flange to distal capitulum

H15	Humeral Distal End Width	medial edge of medial epicondyle to lateral edge of lateral epicondyle
H16	Humeral Distal Articular Surface Width	medial edge of trochlea to lateral edge of capitulum
H17	Humeral Harrison's Breadth	lateral epicondyle to medial side of trochlea
H18	Humeral Trochlea Length	proximal edge of trochlea to distal edge
H19	Humeral Capitulum Depth	anteriormost point to posterior point of capitulum
H20	Humeral AP Height of Olecranon Fossa	maximum anterio-posterior length of the olecranon fossa
H21	Humeral ML Width of Olecranon Fossa	maximum medio-lateral width of the olecranon fossa
	Ulna	
U1	Ulna Length	proximal edge of olecranon process to distal edge of styloid process
U2	Ulna Length 2	length minus styloid process
U3	Ulnar Olecranon Process Height	deepest point of semilunar notch to the top (anterio-posterior length of the olecranon process)
U4	Ulnar Olecranon Process Depth	proximo-distal height of the olecranon process
U5	Ulnar Trochlear Notch Length	from beak to coroniod process
U6	Ulnar Distal Trochlear Notch Width	medio-lateral width of the trochlear notch
U7	Ulnar Proximal Articular Breadth	lateral tip of the radial facet to the most medial point of the humeral facet
U8	Ulnar Head AP Diameter	maximum anterio-posterior breadth of ulnar head
U9	Ulnar Head ML Diameter	maximum medio-lateral breadth of ulnar head
	Radius	
R1	Radius Length	maximum length without styloid process
R2	Radis Length with Styloid	maximum length
R3	Radial Neck Length 1	distal limit of radial head to proximal radial tuberosity (proximo-distal height of the radial neck)
R4	Radial Neck Length 2	mid radial tuberocity to top radial head (proximo-distal height of the radial neck and head)

R5	Radial Head Width AP	anterio-posterior dimension of the radial head
R6	Radial Head Width ML	medio-lateral dimension of the radial head
R7	Radial Distal End Maximum Diameter	medio-lateral dimension of the distal radius
R8	Radial Distal End AP	anterio-posterior dimension of the distal radius
	Metacarpal	
MC1	Metacarpal Length	maximum anterio-posterior length
MC2	Metacarpal Base ML Diameter	medio-lateral diameter at base
MC3	Metacarpal Base DP Diameter	dorso-palmar width at base
MC4	Metacarpal Midshaft ML Diameter	medio-lateral diameter at midshaft
MC5	Metacarpal Midshaft DP Diameter	dorso-palmar width at midshaft
MC6	Metacarpal Head ML Diameter	medio-lateral diameter at head
MC7	Metacarpal Head DP Diameter	dorso-palmar width at head
	Phalanges (proximal, intermediate, distal)	
P1	Phalanx Length	maximum anterio-posterior length
P2	Phalanx Base ML Diameter	medio-lateral diameter at base
P3	Phalanx Base DP Diameter	dorso-palmar width at base
P4	Phalanx Midshaft ML Diameter	medio-lateral diameter at midshaft
P5	Phalanx Midshaft DP Diameter	dorso-palmar width at midshaft
P6	Phalanx Head ML Diameter	medio-lateral diameter at head
P7	Phalanx Head DP Diameter	dorso-palmar width at head
	Femur	
F1	Femur Length 1	to the greater trochanter
F2	Femur Length 2	to the femoral head
F3	Femoral Maximum Proximal Breadth	maximum proximal breadth

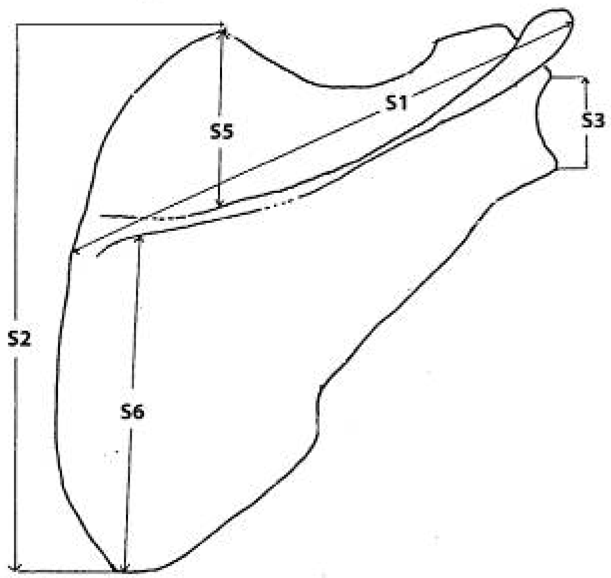
F4	Femur Length 3	distance from fovea (midpoint) to lesser trochanter (midpoint)
F5	Proximal Extension of Greater Trochanter	height of greater trochanter above the neck
F6	Medial Extension of Lesser Trochanter	measure medial extension of lesser
F7	Femoral Head Length	proximal edge of head to distal edge
F8	Femoral Head Width	medial edge of head to lateral edge
F9	Femoral Head Breadth	anterior edge of head to proximal edge
F10	Femoral Midshaft AP Breadth	anterior edge of shaft to posterior edge (midshaft located by measuring half the length of femur)
F11	Femoral Midshaft ML Breadth	medial edge of shaft to lateral edge (midshaft located by measuring half the length of femur)
F12	Femoral Patellar Groove Length	distal edge of groove (distal edge of condyle) to proximal extent of groove
F13	Femoral Patellar Groove Width	medial patellar ridge to lateral patellar ridge along distal edge (from anterior view)
F14	Femoral Biepicondylar Breadth	medial edge of medial condyle to lateral edge of lateral condyle (from anterior view)
F15	Femoral Distal AP Diameter	anterior edge of distal end to posterior
F16	Femoral Medial Condyle Depth	posterior edge of medial condyle to anterior edge of medial patellar ridge (from distal view)
F17	Femoral Lateral Condyle Depth	posterior edge of lateral condyle to anterior edge of lateral patellar ridge (from distal view)
F18	Femoral Medial Condyle Width	medial edge of lateral edge (from posterior view)
F19	Femoral Lateral Condyle Width	medial edge of lateral edge (from posterior view)
F20	Femoral Medial Condyle Length	proximal edge to distal edge (from posterior view)
F21	Femoral Lateral Condyle Length	proximal edge to distal edge (from posterior view)
F22	Femoral Groove Depth	depth of intercondylar groove to the depth of the patellar surface
	Tibia	
T1	Tibia Length 1	maximum length of tibia
T2	Tibia Length 2	maximum length of tibia without medial malleolus
T3	Tibial Proximal End ML	medio-lateral length of proximal end

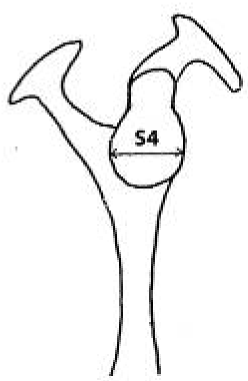
T4	Tibial Proximal End AP	anterio-posterior length of proximal end
T5	Tibial Lateral Condyle Length	anterio-posterior length of the lateral condyle
T6	Tibial Medial Condyle Length	anterio-posterior length of the medial condyle
T7	Tibial Lateral Condyle Width	medio-lateral width of the lateral condyle
T8	Tibial Medial Condyle Width	medio-lateral width of the medial condyle
T9	Tibial Distal End Width	medio-lateral width of the distal end
T10	Tibial Medial Malleolus Width	medio-lateral width of the medial malleolus (from distal view)
T11	Tibial Distal Articular Surface (Lateral Astragalar Facet) Width	lateral edge of medial malleolus to lateral edge of articular surface
T12	Tibial Distal Articular Surface (Lateral Astragalar Facet) Length	anterio-posterior length of the articular surface
	Talus	
TL1	Talus PD Length	maximum proximo-distal length
TL2	Talus PD Length Laterally	maximum proximo-distal length of lateral margin
TL3	Talus Breadth 1	maximum breadth
TL4	Talus Breadth 2	excluding lateral malleolar facet
TL5	Talus Height	maximum height of talar body measured on lateral view
TL6	Trochlear Surface Breadth Posteriorly	medio-lateral breadth trochlear surface at posterior extent
TL7	Trochlear Surface Breadth Anteriorly	medio-lateral breadth trochlear surface at anterior extent
	Calcaneus	
C1	Calcaneus PD Length	maximum proximo-distal length
C2	Calcaneus PD Length Anterior Segment	from anterior of posterior talar facet to cuboid facet
C3	Calcaneus PD Length Anterior Segment and Posterior Articulation	including posterior talar facet
C4	Calcaneus Posterior Facet Length	proximo-distal length of posterior facet

C5	Calcaneus Anterior Articular Facet Length	proximo-distal length of anterior facet
C6	Calcaneus ML Breadth	maximum medio-lateral breadth
	Cuboid	
CB1	Cuboid Length	anterio-posterior length
CB2	Cuboid Breadth	medio-lateral breadth
	Metatarsal	
MT1	Metatarsal Length	maximum anterio-posterior length
MT2	Metatarsal Base ML Diameter	medio-lateral diameter at base
MT3	Metatarsal Base DP Diameter	dorso-palmar width at base
MT4	Metatarsal Midshaft ML Diameter	medio-lateral diameter at midshaft
MT5	Metatarsal Midshaft DP Diameter	dorso-palmar width at midshaft
MT6	Metatarsal Head ML Diameter	medio-lateral diameter at head
MT7	Metatarsal Head DP Diameter	dorso-palmar width at head

Figure 3.1. Illustration of Postcranial Measurements Used In Study (adapted from Birchette, 1982)

A. SCAPULA





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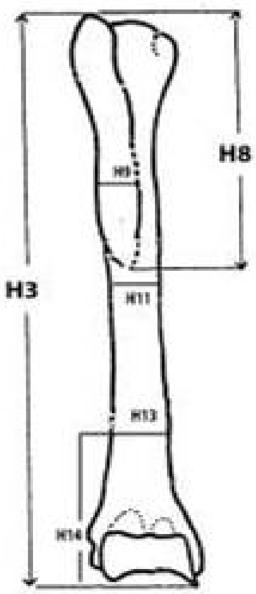
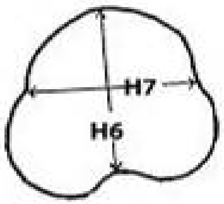
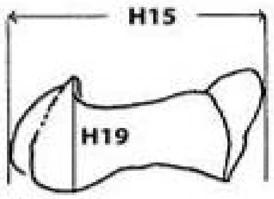
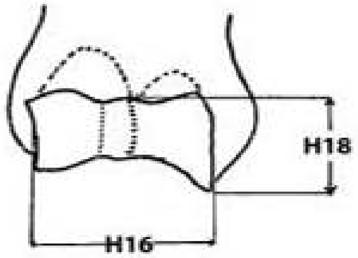
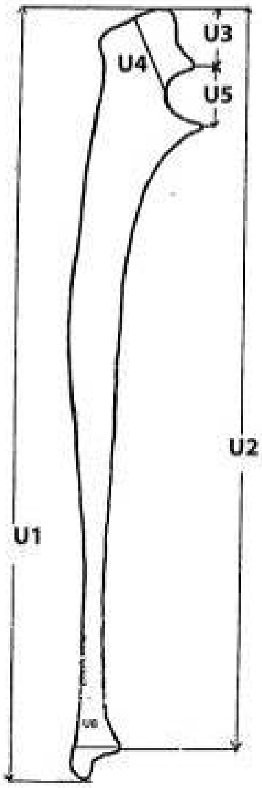


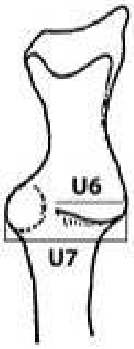




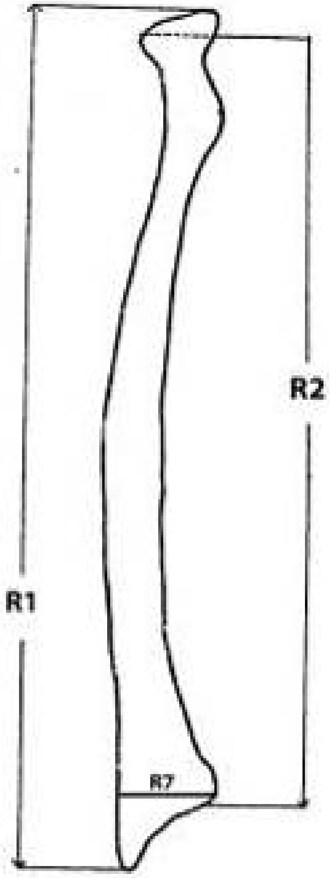


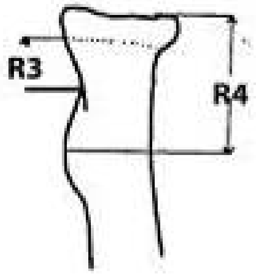
C. ULNA



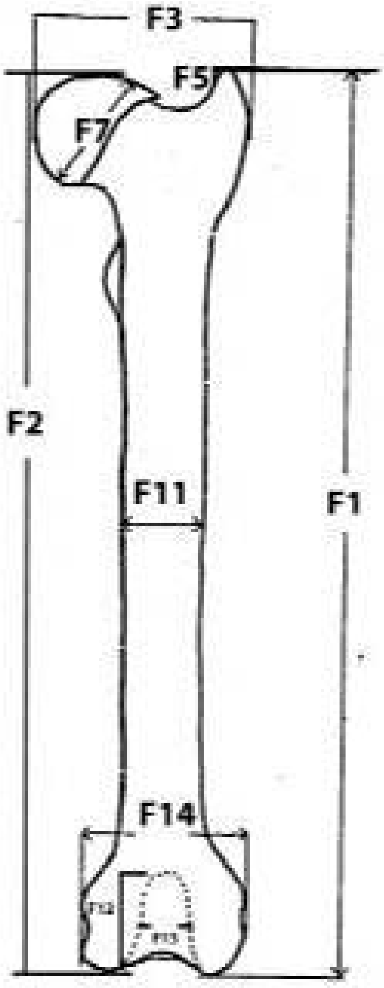


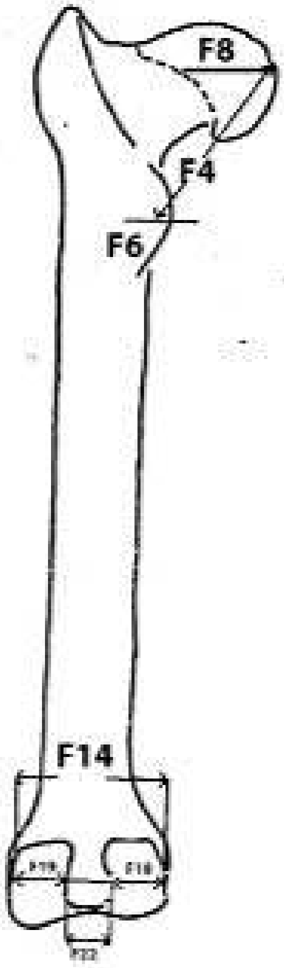
D. RADIUS

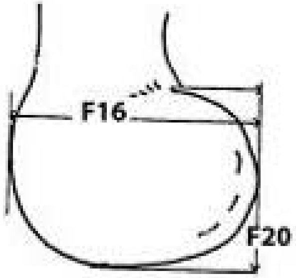




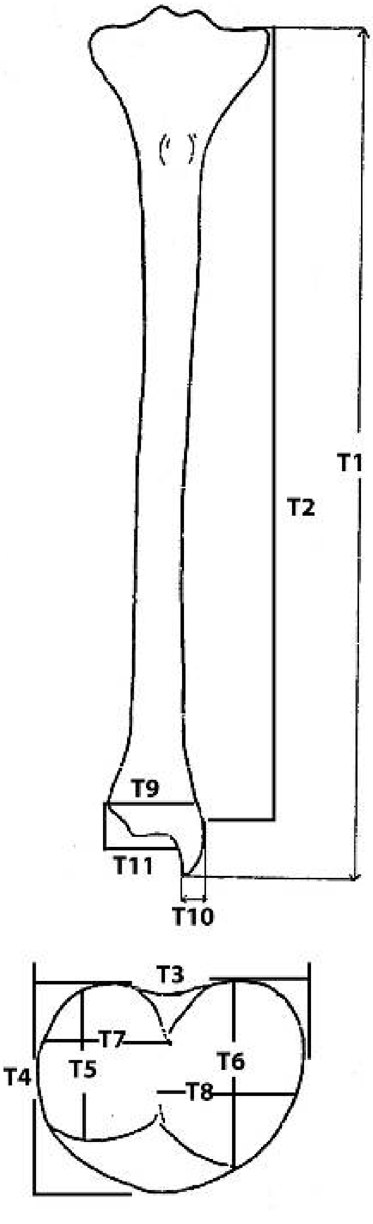
E. FEMUR



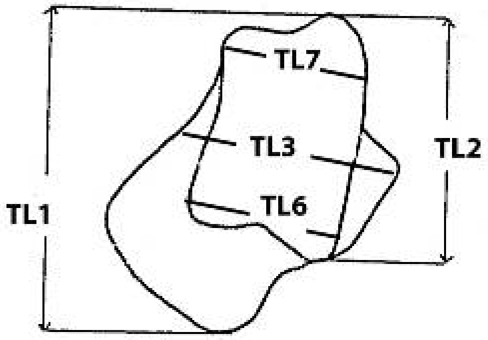


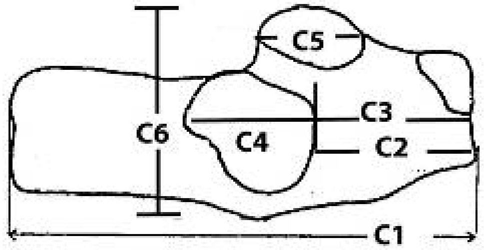


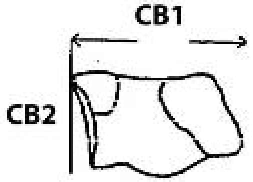
F. TIBIA

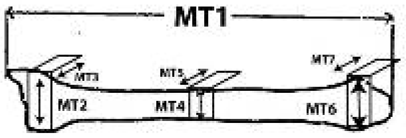


G. FOOT


TL7
TL3
TL2
TL1
TL6


C5
C6
C3
C4
C2
C1


CB1
CB2


MT1
MT3
MT5
MT7
MT2
MT4
MT6

Description of Indices

Standard osteological measurements were transformed into 46 simple ratios to reflect shape, the functional lengths over which muscles act, and to reduce the effects of differences in scale among individuals and species. These indices are either standard postcranial indices or believed to have functional relevance to this study (Jolly, 1972; Delson, 1973; Birchette, 1982; Harrison, 1989; Sargis, 2000; Frost and Delson, 2002). These indices, and references specific to each index are given in Table 3.5. These indices were plotted in box plots in which the bottom and the top of the box are the 25th and 75th percentile and the bar in the middle of the box is the 50th. The ends of the whiskers represent the 5th and 95th percentile and individual dots are outliers. In all plots, *T. brumpti* is shown in black boxes, other *Theropithecus* species are grey.

While ratios remove absolute scale from the included measurements, they do not account for the changes in shape correlated with size, i.e. allometry. To ensure that morphological differences observed among species or in relation to locomotor mode are in fact related to locomotor behaviors rather than body mass, each ratio was regressed against the relevant species-sex specific mean body mass taken from (Delson et al., 2000) except for *Cercocebus agilis* and *Mandrillus leucophaeus* (Smith and Jungers, 1997) and *Mandrillus sphinx* (Setchell et al., 2001). If the adjusted R^2 for the regression of body mass and the ratio exceed 0.3, that ratio was excluded from further analysis following previous researchers (Bishop, 1994; Elton, 2002). If the ratio exceeded 0.3 for just one sex, the ratio was also excluded. This analysis excluded 4 indices from further analysis (Index numbers 9, 25, 27 and 46), but are sometimes discussed in the text as some have been used in previous postcranial studies or specifically used in previous *T. brumpti* analyses. These are highlighted in red below (Table 3.6.)

Morphological similarities and dissimilarities of *T. brumpti* to other cercopithecines are noted in each section and are quantified whenever feasible. Functional explanations are posited based on extrapolations from locomotor studies of living animals, and/or on simple biomechanical models. All analyses were performed using Stata /IC 11.1.

Table 3.5. Postcranial Indices Used in Study

	Scapula	
1	Scapula Shape Index	Scapula Width/ Length * 100
2	Glenoid Fossa Shape Index	Glenoid Fossa Width/ Length * 100
3	Supraspinatus Fossa Index	Supraspinatus Fossa Length/ Scaplua Length*100
4	Infraspinatus Fossa Index	Infraspinatus Length/Scapula Length *100
	Humerus	
5	Humeral Head Height Index	Humerus Length 1/ Humerus Length 2 * 100
6	Humeral Head Shape Index 1	Humeral Head Diameter ML/ Humeral Head Diameter AP
7	Humeral Head Shape Index 2	Humeral Head Width/ Length *100
8	Delto-Pectoral Crest Length Index	Humeral Length 3/ Maximum Humerus Length * 100
9	Trochlea Length Index	Trochlea Length/ Humeral Distal End Width * 100
10	Capitulum Depth Index	Capitulum Depth/ Humeral Distal End Width * 100
11	Humeral Distal End Width Index	Humeral Distal End Width/ Humerus Length *100
12	Medial Epicondyle Projection Index	Biepicondylar Breadth (BEB) - Medial Distal Articular Limit to Lateral Epicondyle * 100/ BEB
13	Harrisons Breadth	Harrison's Breadth/ Humeral Distal End Width * 100
14	Olecranon Fossa Index	AP Height/ ML Width * 100
	Ulna	
15	Olecranon Process Length Index 1	Olecranon Process Length/ Ulna Length * 100
16	Olecranon Process Length Index 2	Olecranon Process Length/ Ulnar Trochlear Notch Length* 100
17	Olecranon Process Shape Index	Ulnar Olecranon Process Height/ Ulnar Olecranon Processs Length * 100
18	Ulnar Trochlear Notch Index 1	Ulnar Trochlear Notch Length/ Ulnar Distal Trochlear Notch Width * 100
19	Ulnar Trochlear Notch Index 2	Ulnar Trochlear Notch Length/ Ulnar Proximal Articular Breadth * 100
20	Ulnar Trochlear Notch Index 3	Ulnar Proximal Articular Breadth/ Ulnar Distal Trochlear Notch Width * 100
	Radius	

21	Radial Head Shape Index	Radial Head Length/Width * 100
22	Radial Neck Length Index	Radial Neck Length 1/ Radial Head Width ML * 100
	Metacarpals	
23	Robusticity Index	Midshaft Breadth * 100/ Maximum Length
24	Proportion Index	Length of MC 1/ Average Length MC2-MC5
	Phalanges	
25	Robusticity Index	Midshaft Breadth * 100/ Maximum Length
	Femur	
26	Femoral Head Shape Index	Femoral Head Width/ Length 1* 100
27	Femoral Breadth Index	Femoral Maximum Proximal Breadth/ Length 1 * 100
28	Greater Trochanter Length Index	Proximal Extension of Greater Trochanter/Femur Length 1* 100
29	Lesser Trochanter Length Index	Medial Extension of Lesser Trochanter/Femur Length 1 * 100
30	Femoral Distal Shape Index	Femoral Biepicondylar Breadth/ Femoral Distal AP Diameter * 100
31	Femoral Groove Index	Femoral Groove Depth/ Length 1 *100
32	Patellar Groove Shape Index	Patellar Groove Width/Length * 100
33	Femoral Condyle Depth Index	Femoral Lateral Condyle Depth/ Medial Condyle Depth *100
34	Femoral Condyle Length Index	Femoral Lateral Condyle Length/ Medial Condyle Length *100
35	Femoral Condyle Width Index	Femoral Lateral Condyle Width/ Medial Condyle Width *100
	Tibia	
36	Tibial Proximal End Shape Index	Tibial Proximal End Length/Width * 100
37	Tibial Condyle Width Index	Tibial Lateral Condyle Width/ Medial Condyle Width * 100
38	Tibial Condyle Length Index	Tibial Lateral Condyle Length/ Medial Condyle Length * 100
39	Tibial Medial Malleolus Length Index:	Tibial Length 1-Tibial Length 2/ Tibial Length 1 * 100
40	Tibial Medial Malleolus Width Index:	Tibial Medial Malleolus Width/ Tibial Length 1 * 100
41	Tibial Distal Articular Suface (Lateral Astragalar Facet) Shape Index	Tibial Distal Articular Surface Length/Width * 100
	Talus	

42	Trochlear Shape Index	Trochlear Surface Breadth Posteriorly/ Trochlear Surface Breadth Anteriorly * 100
	Calcaneus	
43	Anterior Index	Calcaneus PD Length Anterior Segment/Calcaneus PD Length * 100
44	Posterior Facet Index	Calcaneus Posterior Facet Length / Calcaneus PD Length * 100
45	Anterior Facet Index	Calcaneus Anterior Articular Facet Length / Calcaneus PD Length * 100
	Cuboid	
46	Cuboid Index	Cuboid Length/ Cuboid Breadth * 100

Table 3.6. R^2 scores by sex. Those indices with an R^2 score higher than 0.30 were excluded from analysis.

	M	F		M	F
Scapula			**Phalanges**		
1	-0.01	0.01	25	.	0.97
2	0	0.04	**Femur**		
3	0.01	-0.02	26	0.05	-0.01
4	0.04	0.04	27	0.4	0.23
Humerus			28	0.28	0.13
5	0.09	0.31	29	0.01	0.04
6	0.05	0.19	30	0.02	0.06
7	-0.01	-0.02	31	0.08	0.05
8	0.05	0.03	32	0.09	0.14
9	0.41	0.17	33	0.18	0.29
10	0.21	0.1	34	0	-0.01
11	0.05	-0.02	35	0.07	0.07
12	0.02	-0.01	**Tibia**		
13	0.04	0.08	36	0.18	-0.01
14	-0.01	0.18	37	0.03	0.05
Ulna			38	0.07	-0.02
15	0.09	0.02	39	0.22	0.35
16	0	-0.01	40	0	0.11
17	0.03	0.19	41	0.08	-0.02
18	-0.01	-0.01	**Talus**		
19	0.07	0.02	42	-0.02	-0.05
20	0	0.09	**Calcaneus**		
Radius			43	0.02	0.33
21	0.03	-0.02	44	-0.02	0.25
22	0.19	0.4	45	0	-0.05
Metacarpals			**Cuboid**		
23	0.02	0.09	46	0.34	0.08
24	0.09	0.24			

CHAPTER IV

FORELIMB

The forelimb morphology of extinct members of the genus *Theropithecus* have been relatively well described compared to that of other fossil cercopithecids (Ciochon, 1993; Krentz, 1993a). In spite of this, previous studies have focused primarily on one extinct species, *Theropithecus oswaldi,* masking potential morphological and ecological breadth within the genus. Previous attempts to study the morphology of *Theropithecus brumpti*, the other well known fossil theropith species, have been hampered by a lack of postcranial material directly associated with cranial remains (Krentz, 1992; 1993). Since that time, significant associated postcranial material has become available permitting detailed analysis.

Theropithecus brumpti is found throughout the Turkana Basin from prior to 3.4 million years ago (Ma), until it is replaced by *T. oswaldi* around 2 Ma; it is also known from the Tugen Hills at approximately 2.6 Ma (Jablonski et al., 2002; Gilbert et al., 2011). The extinction of *T. brumpti* and its replacement by *T. oswaldi*, though often discussed, are not well understood (Jablonski, 1993c; Jablonski and Leakey, 2008). It is often suggested that *T. brumpti* was woodland adapted and arboreal in its locomotor regime and/or perhaps frugivorous and therefore unable to cope with the increasing aridity of the early Pleistocene (Jablonski, 1986; Benefit and McCrossin, 1990; Krentz, 1993a). However, as more *T. brumpti* material is discovered the arboreality and dietary preferences of this species are being questioned (Jablonski, 2002b), forcing paleontologists to reevaluate the paleobiology of the species.

Although cranio-dental material has been studied (Eck and Jablonksi, 1987; Jablonski, 1993a; Leakey, 1993; Gilbert, 2008), a comprehensive functional analysis of *T. brumpti* postcrania has never been done using associated material. Postcranial studies are critical to understanding locomotor behaviors and foraging strategies and could help address questions such as 1) evolution of the genus, 2) evolution of the papionin tribe and 3) biotic responses to climatic change in the Turkana Basin during the past 5 million years of human evolution.

Previous studies of *Theropithecus brumpti* forelimb material have generally concluded that *T. brumpti* possessed numerous arboreal adaptations (Ciochon, 1993; Krentz, 1993a). Krentz (Krentz, 1993a), analyzing largely unassociated material from the Omo Shungura Formation estimated to represent *T. brumpti*, noted a suite of traits in the elbow and shoulder, which he described as relating to increased flexibility in the shoulder joint and increased elbow stability. Based on this, he concluded that *T. brumpti* was more arboreal than other species of *Theropithecus*. The features that he used to support this contention include: (1) greater tubercle inferior to the head of the humerus; (2) well-marked areas for the attachment of the rotator cuff musculature including a deep insertion for *m. infraspinatus*, distinct insertions for *m. teres minor* and *major*; (3) a relatively long olecranon process and (4) flatter radial tubercle, more circular radial head and slightly longer radial neck. However, Krentz also points out that these traits are variable. One major drawback to Krentz's analysis was that all of the material he studied, except for one specimen (L865), was unassociated with cranial remains. The fact that two species of *Theropithecus* are present in the Shungura Formation, along with the presence of other large cercopithecids, renders the taxonomic affiliation of the material he analyzed inconclusive.

Since the time of Krentz's analysis, several partial skeletons of *T. brumpti* have become available (Jablonski et al., 2002; 2008; Gilbert et al., 2011). Of particular importance is a partial skeleton of *T. brumpti* from West Turkana (KNM-WT 3968) that includes all of the forelimb elements. A recent reevaluation based on this specimen identified a mixture of features, but many are generally associated with terrestrial locomotion, including a relatively narrow scapula and a highly stable elbow joint (Jablonski, 2002b).

With the suite of associated material that is now available, it is possible to more fully analyze *T. brumpti* material to address discrepancies between previous analyses. Complete methods and materials are discussed in detail in Chapter III. The following table (4.1) shows the associated *T. brumpti* forelimb material used in this analysis.

Table 4.1: *Theropithecus brumpti* forelimb material used in this study

	SCAPULA	HUMERUS	ULNA	RADIUS
KNM-WT 39368	X	X	X	X
KNM-WT 17554	X			X
KNM-WT 17560			X	
KNM-ER 30385	X			
KNM-ER 3084	X	X	X	
L 865-2		X		

Forelimb Material Results

Scapula

Scapular elements are known from four specimens: a complete left scapula, a right glenoid fossa and right acromion from KNM-WT 39368, two left glenoid fossae (KNM-ER 3084 and 30385) and a partial glenoid KNM-WT 17554 (Figure 4.1.). However, WT-17554 was too damaged for any measurements, although qualitative variables were noted.

The scapula of *Theropithecus brumpti* is relatively narrow and well within the range of other papionins. When scapular width is compared to length (Figure 4.2., Index 1) *T. brumpti* groups with the terrestrial *Papio hamadryas anubis* and *Chlorocebus patas*, although not with *T. gelada. T. gelada* appears to be even narrower. In accordance with the overall narrowness of the *T. brumpti* scapula, both the infra and supraspinatus fossae are also relatively narrow (Figure 4.2., Index 3 and 4) and are similar in value to *T. gelada*, *Papio* and *M. fascicularis* suggesting dominance of terrestrial behaviors (Roberts, 1974). Notably, *Mandrillus*, although primarily terrestrial, does not group with other papionins on this index (Index 3), as the supraspinatus tends to be proximally expanded (Fleagle and McGraw, 2002).

The angle of the glenoid fossa to the scapular spine was discussed at length in Jablonski *et al*. (Jablonski, 2002b). The skeleton analyzed in their paper (KNM-WT 39368) is the only specimen to preserve this morphology, so the measurement was not reanalyzed here. They found that the glenoid fossa was oriented laterally and the angle to the spine (88°) was within the range of modern terrestrial baboons. While they also conclude that in general the scapula of KNM-WT 39368 appears to be that of a terrestrially adapted baboon, they point to an interesting exception. This specimen appears to have a large axillary gutter which they conclude means that KNM-WT 39368 "could engage in more humeral adduction and lateral rotation than is the case with most other baboons….*T. brumpti* possesses a forelimb that is more flexible at the shoulder joint than are those of other theropiths or large papionins" (Jablonski et al., 2002, pg. 914) although, as Birchette states, this feature is difficult to interpret functionally (Birchette, 1982).

The glenoid fossa of *T. brumpti* is piriform in outline as is typical for cercopithecoids (Birchette 1982). In all four *T. brumpti* specimens the supraglenoid tubercle is well developed and forms the base of the relatively robust corocoid process. The robusticity of the corocoid process is associated with strong supination of the forearm and elbow flexion as a result of a powerful short head of *m. biceps brachii* and a strong *m. coracobrachialis* (Jablonski and Leakey, 2008). In lateral/posterior profile the superior margin of the glenoid fossa protrudes beyond the greatest depth of the fossa. Notably, there is a distinct lack of a 'rim' around the glenoid, although the function of this feature as well as the meaning of its presence or absence is unclear. The glenoid fossa shape index groups the overall shape of *T. brumpti* with *T. gelada* and *Papio* (Figure 4.2., Index 2).

The depth of the glenoid fossa was assessed qualitatively. The glenoid fossa of *T. brumpti* is moderately indented with a relatively small area of contact between the glenoid fossa and the humeral head. The relative depth of the glenoid fossa appears to suggest the degree of flexibility of the shoulder joint "a small degree of indentation implies a relatively large glenoid surface area for articulation with the humeral head;

conversely, a markedly indented glenoid suggests a smaller total surface area for contact with the humerus" (Birchette 1982, pg. 120). This is an important point because it highlights an unusual feature of *T. brumpti* in which an essentially terrestrial shoulder is combined with a relatively high degree of flexibility. However, flexibility does not necessarily imply *arboreality*, although the skeletons of arboreal primates are characterized by a great deal of flexibility (Fleagle, 1977). This becomes increasingly clear as one looks at the comparative *Theropithecus* material. The Upper Burgi *Theropithecus oswaldi* also possesses a moderately indented glenoid fossa (KNM-ER 28 and 821) and, therefore, more flexible shoulder joint. This implies a flexible shoulder joint for early *Theropithecus* as a genus.

Figure 4. 1. Scapula. Posterior (a) and anterior (b) views of the left scapula of KNM-WT 39368. Inferior view of the left glenoid fossa of KNM-ER 3084 (c) and posterior view of the left glenoid fossa KNM-ER 30385 (d).

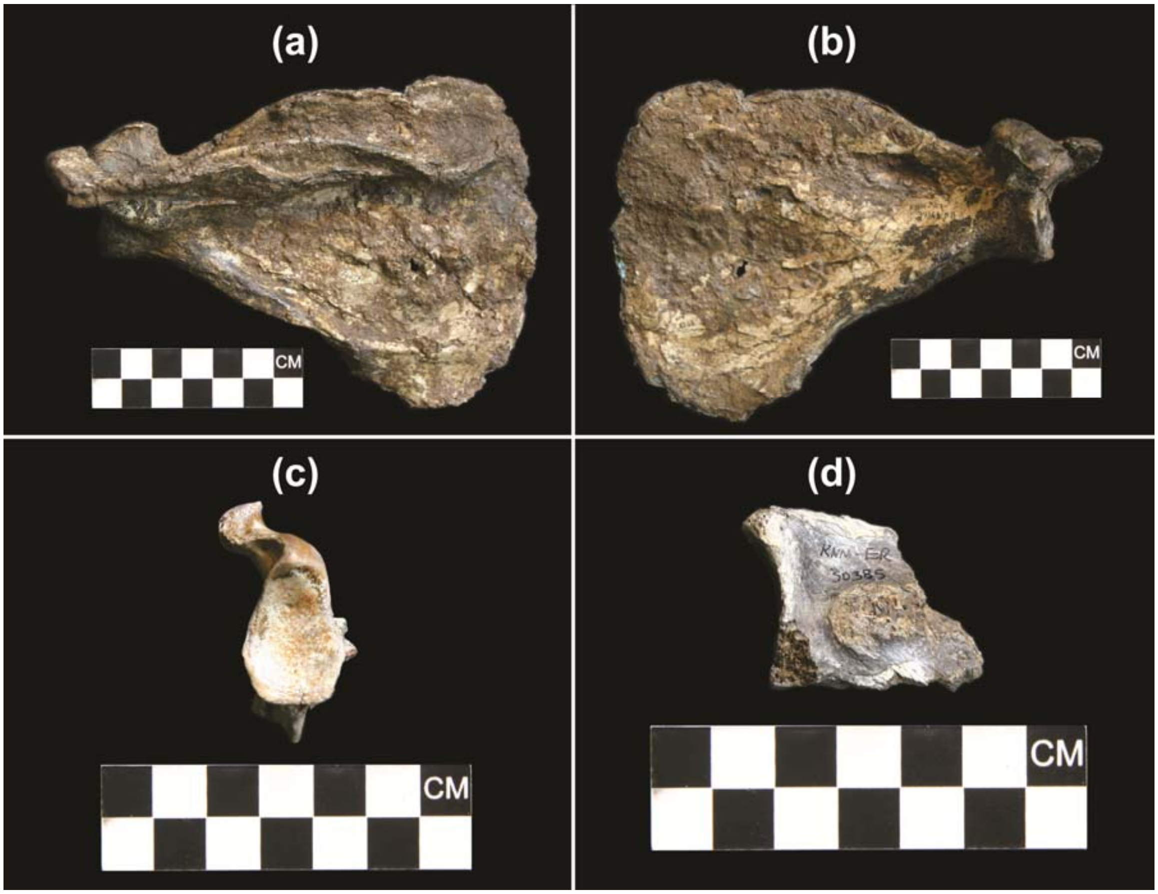
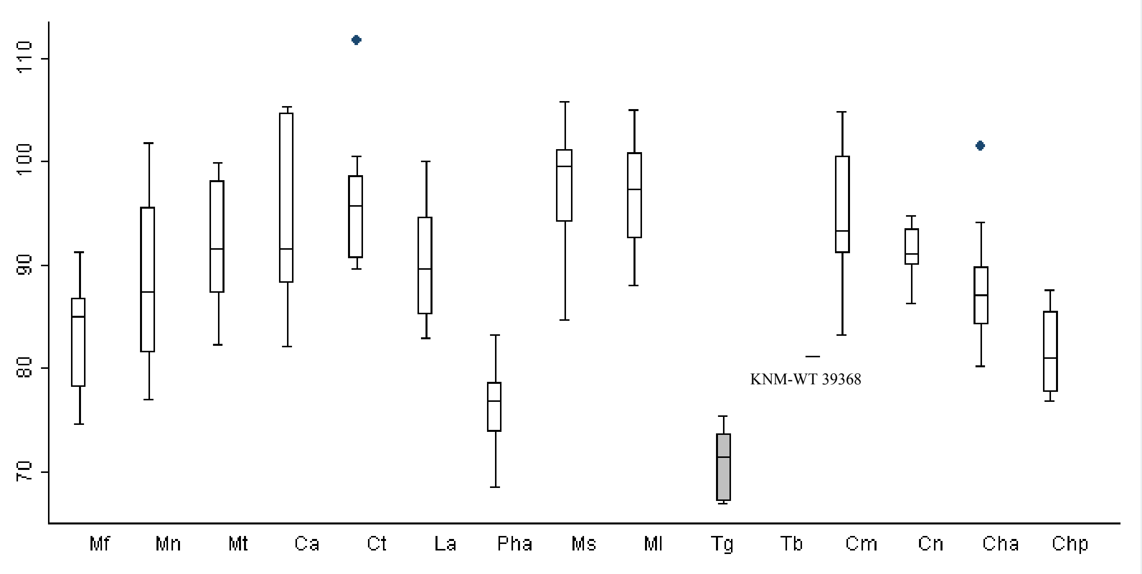
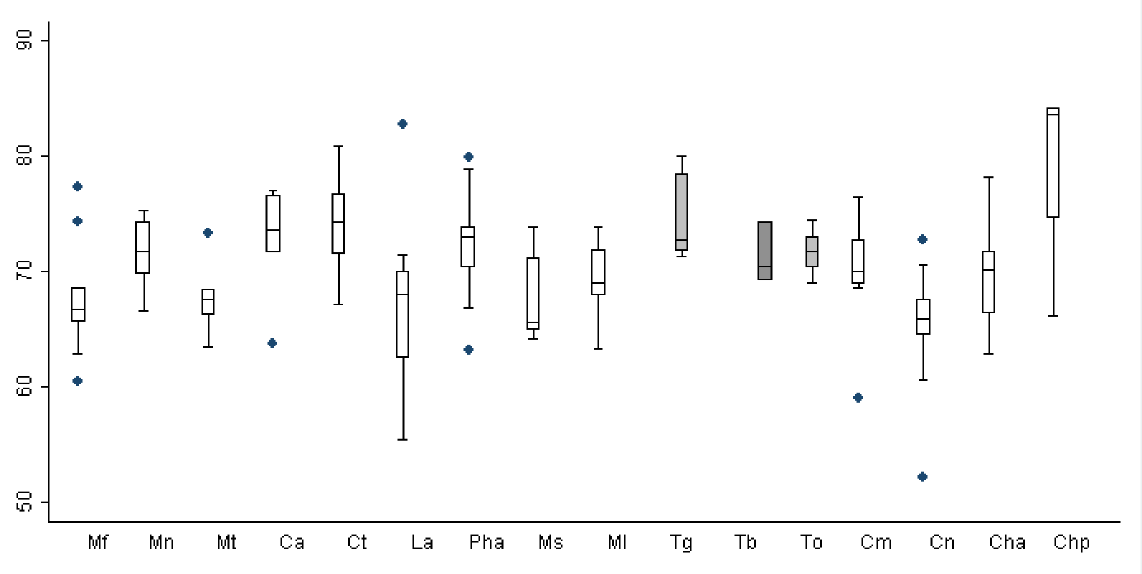


Figure 4.2. Scapula Indices. See Table 3.5 for definitions.

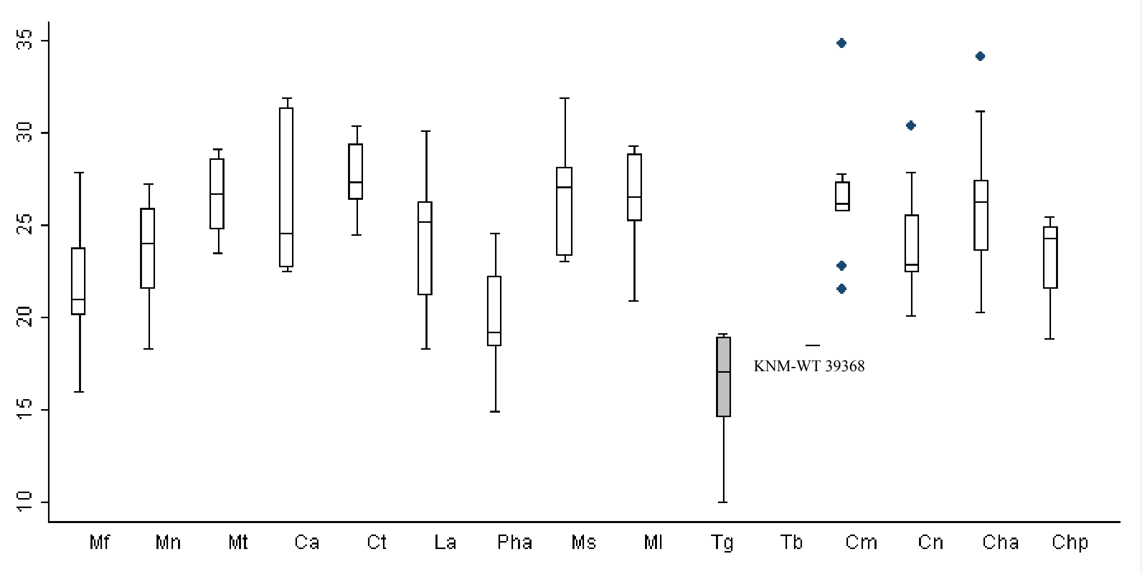
a. Scapular Index (Index 1)



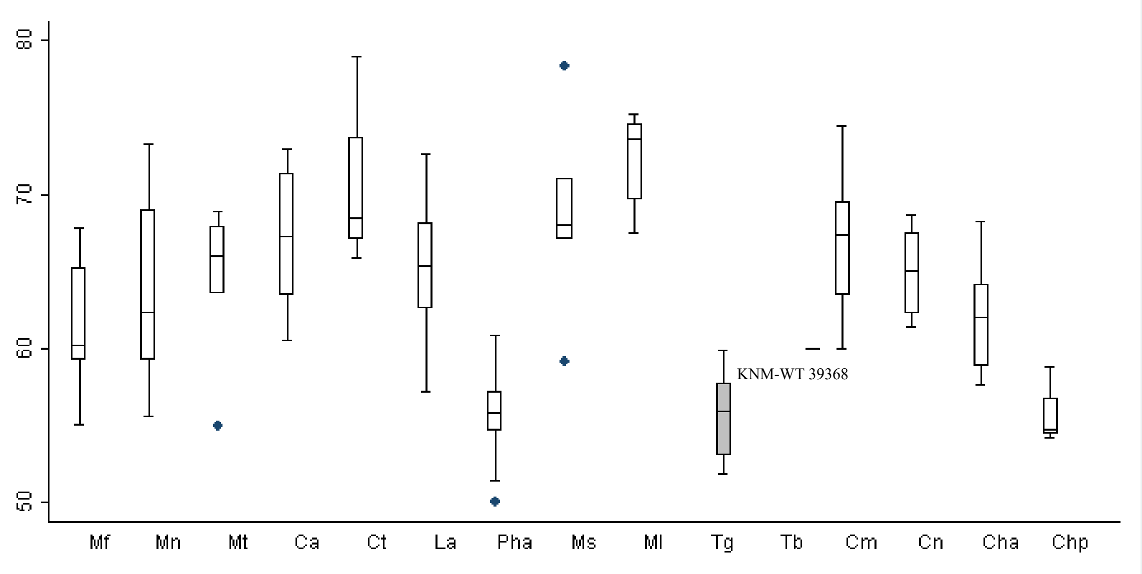
b. Glenoid Fossa Shape Index (Index 2)



c. Supraspinatus Index (Index 3)



d. Infraspinatus Index (Index 4)



Proximal Humerus

The proximal humerus of *Theropithecus brumpti* is known from 3 specimens: a complete right humerus (KNM-WT 39368), a left humeral head, a proximal right humerus (KNM-ER 3084) and a right humeral shaft (KNM-ER 3119) (Figure 4.3.). ER 3119 was too damaged for measurements, although qualitative variables were noted. KNM-ER 3013, which preserves distal fragments of the left and right humerus, is often identified as *Theropithecus brumpti* (Jablonski and Leakey, 2008) however, it is very small for *T. brumpti* and I agree with previous researchers who have reallocated this specimen to *Theropithecus sp.* (S. Frost, Personal Communication).

Both humeral heads in *T. brumpti* are slightly longer mediolaterally than anterioposteriorly, which differs slightly from other terrestrial papionins such as *Papio,* which appear to be more spherical (Figure 4.4., Index 6 and 7). Arboreal cercopithecines tend to have more elongated (longer in the AP direction) heads than terrestrial cercopithecines, aligning *T. brumpti* with the later.

The relative size, shape and proximal extension of the greater tuberosity has long been associated with the locomotor habits of papionins (Savage, 1957; Jolly, 1972; Larson and Stern, 1989). The tuberosities are the attachment sites for the rotator cuff musculature and some of the protractors and retractors of the humerus. In addition to motion at the shoulder, the rotator cuff muscles are important in maintaining the integrity of the glenohumerual joint throughout a range of postures (Potau et al., 2009). Therefore, variation in the morphology of the tuberosities reflects the importance of the rotator cuff musculature in both the action at the joint and the relative stability of the glenohumeral joint.

The greater tuberosity is relatively broad in *Theropithecus brumpti*, especially compared to *Papio hamadryas anubis* and the greater and lesser tuberosities are of more equal size than other *Theropithecus* species (Krentz, 1993a; Jablonski, 2002b). Terrestrial cercopithecines tend to have tuberosities more similar in size than arboreal monkeys, but there is considerable variation (Fleagle and Simons, 1982). However, the relatively large lesser tuberosity of *T. brumpti* compared to other *Theropithecus* species is notable and would ostensibly be related to the function of *m. subscapularis* which inserts on the anterior-medial aspect.

The positioning of the greater tuberosity relative to the humeral head relates to terrestrial or arboreal adaption (Jolly, 1967, 1972; Larson and Stern, 1989). In terrestrial primates the greater tubercle is higher than the humeral head. The greater tubercle lies well below the humeral head in primates that have greater flexibility at the shoulder joint such as arboreal quadrupeds (Fleagle and Simons, 1982; Gebo et al., 1988). Krentz (Krentz, 1993a) found that the difference in greater tuberosity height between *T. brumpti* and *T. oswaldi* clearly distinguish the two extinct species. Although previously reported that the greater tuberosity does not extend beyond the level of the humeral head in *T. brumpti* (Krentz, 1993b, a; Jablonski and Leakey, 2008) this is not actually the case. While the superior extension of the greater tuberosity in *T. brumpti* is less marked in than *T. oswaldi* and *T. gelada* (Figure 4.4., Index 5), *T. brumpti* does group with other terrestrial papionins including *Mandrillus sphinx*, *Mandrillus leucophaeus* and all the guenons including the terrestrial *Chlorocebus patas*. Further, there is variation in the greater tuberosity height in *T. brumpti* (especially when including unassociated material WT 38703 and 38738 both of which have greater tubercles higher than the humeral head). KNM-WT 39368 has a humeral head that is basically even with the greater tuberosity and KNM-ER 3084 the greater tuberosity does lie below the humeral head. While this trait is found in primates that have greater flexibility at the shoulder joint, it is not necessarily indicative of arboreal quadrupedalism. In the comparative primate sample other terrestrial papionins also expressed variability in this trait including *Mandrillus*, *Macaca thibetana*, *M. nemistrina*, and some *Chlorocebus patas*. In these taxa, many had humeral heads that were even with, or slightly above, the level of the greater tuberosity. Furthermore, some variability in this trait is also seen in *Theropithecus oswaldi*. KNM-ER 28 from the Upper Burgi Member is slightly damaged but it is clear that the greater tuberosity is not projecting proximally and in KNM-ER 866 from the Okote Member the humeral head is even with the greater tuberosity if not higher. Lastly, Frost and Delson (Frost and Delson, 2002) also found variability in this trait in *T. o. darti* specimens from Hadar. Therefore, it is most likely that this feature is simply representative of greater flexibility in the papionin shoulder rather than strict arboreal quadrupedalism. Given this variability in relative greater tuberosity height in the *T. brumpti* and *T. oswaldi* material, it does not seem possible to identify isolated *T. brumpti* proximal humeri based on this feature, contra Krentz (1993a, 1993b).

There is a large, well demarcated facet for the insertion of *m. infraspinatus* on the lateral surface of the greater tuberosity, which may reflect enhanced shoulder stability and increased lateral rotation of the humerus. The insertion site for *m. supraspinatus* on the superior greater tuberosity is not as clear in KNM-ER 39368 but is clearer in KNM-ER 3084. In this specimen the insertion site is not very pronounced, unlike the condition in arboreal primates, suggesting relatively infrequent abduction of the humerus. The relative prominence of the musculature of the rotator cuff is also thought to be a reflection of locomotion with more arboreal species exhibiting more robust musculature of the rotator cuff for increasing the range of motion at the shoulder while maximizing stability at the gleno-humeral joint during abducted limb postures (Harrison, 1989). The prominence of these insertions has been used to infer arboreality in *T. brumpti* (Krentz, 1993b) in contrast to more terrestrial species in which the muscles of the rotator cuff tend to be smaller. Again, this feature is most likely to indicate greater flexibility in the shoulder rather than strict arboreal quadrupedalism. Relatively prominent rotator cuff musculature is also seen in *T. oswaldi* material from the Upper Burgi (KNM-ER 13 and ER 601) and perhaps to some degree in later Okote Member material (Jablonski, 2002b).

The humeral shafts of all *Theropithecus* specimens are dominated by a long, relatively wide deltoid tuberosity including *T. brumpti* (KNM-WT 39368) (Figure 4.4., Index 8). As the insertion site for the deltoid muscle the distal extent of this tuberosity has been used to differentiate arboreal and terrestrial taxa with arboreal taxa exhibiting longer tuberosities relative to bone length (Maier, 1972). However, this is not a clear correlation and previous researchers have not found differences in deltoid tuberosity length in primates with differing locomotor strategies (Birchette, 1982; Ciochon, 1986). However, what is notable is that within cercopithecoids in general there is only modest variation in relative deltoid length, except for *Theropithecus*, in which in all species have a deltoid tuberosity that is relatively long. This dissertation confirms this interesting anomaly in *Theropithecus brumpti* contra Krentz (Krentz, 1993b). Ciochon suggested that perhaps this trait is not associated with locomotion but rather with the unique manual foraging behavior of *Theropithecus gelada* that may extend into the fossil record

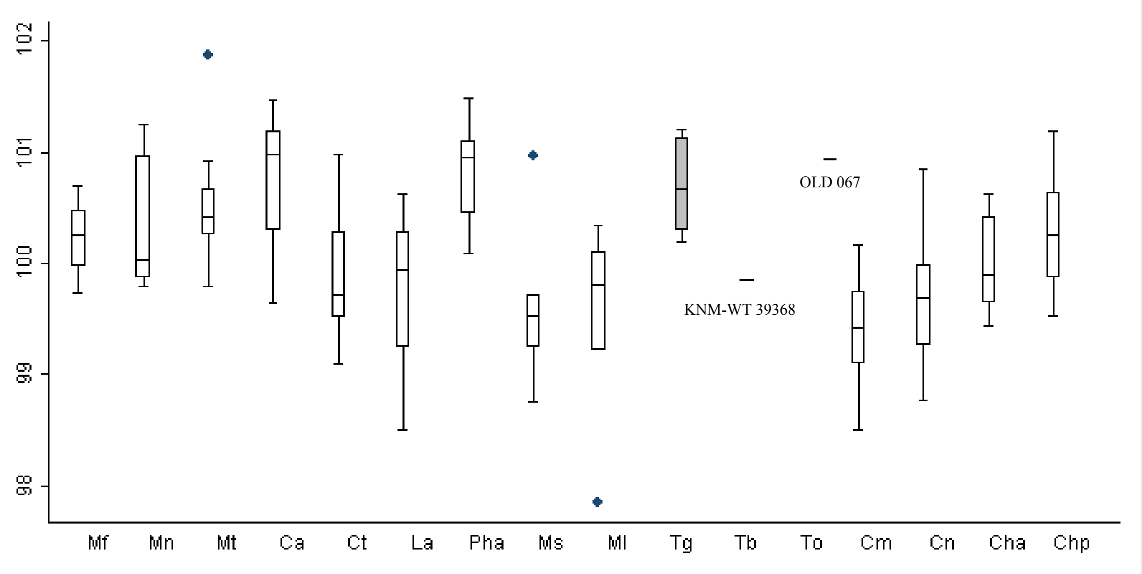
(Ciochon, 1993). Furthermore, there is a distinct impression on the distal surface of the deltoid tuberosity in *T. brumpti* which may be related to the use of the deltoid muscle (Ciochon, 1986; Krentz, 1993b).

Although the shaft of KNM-WT 39368 is damaged, it can be seen that the bracioradialis flange in *T. brumpti* is slightly more proximally extending than other *Theropithecus* species suggesting prominent wrist or digital flexor musculature aligning *T. brumpti* with *Mandrillus*. Mandrills seem to have much larger forelimb flexors then other papionins (Jolly 1972). Mandrills are forest floor animals which show greater adaptation to tree climbing than in typical baboons. However, *T. brumpti* does not share the scapular traits with *Mandrillus* that suggest tree climbing, but it does share traits in the elbow that have been associated with “aggressive manual foraging” (Fleagle and McGraw, 2002).

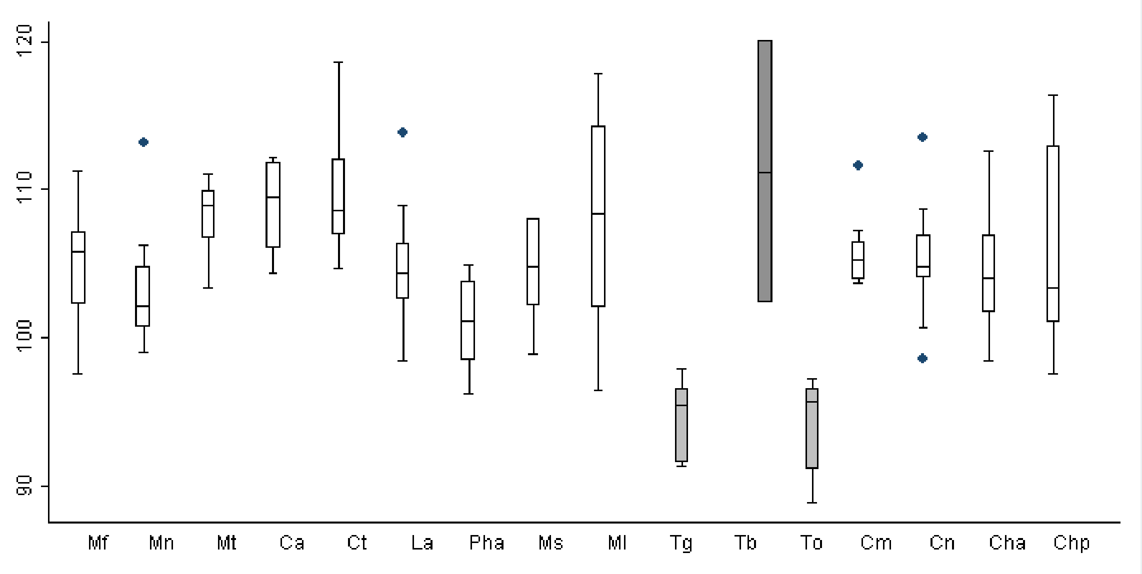
Figure 4.3. Proximal Humerus. Proximal right humerus of KNM-ER 3084 (a) and complete right humerus of KNM-WT 39368 (b)

Figure 4.4. Proximal Humerus Indices. See Table 3.5 for definitions.

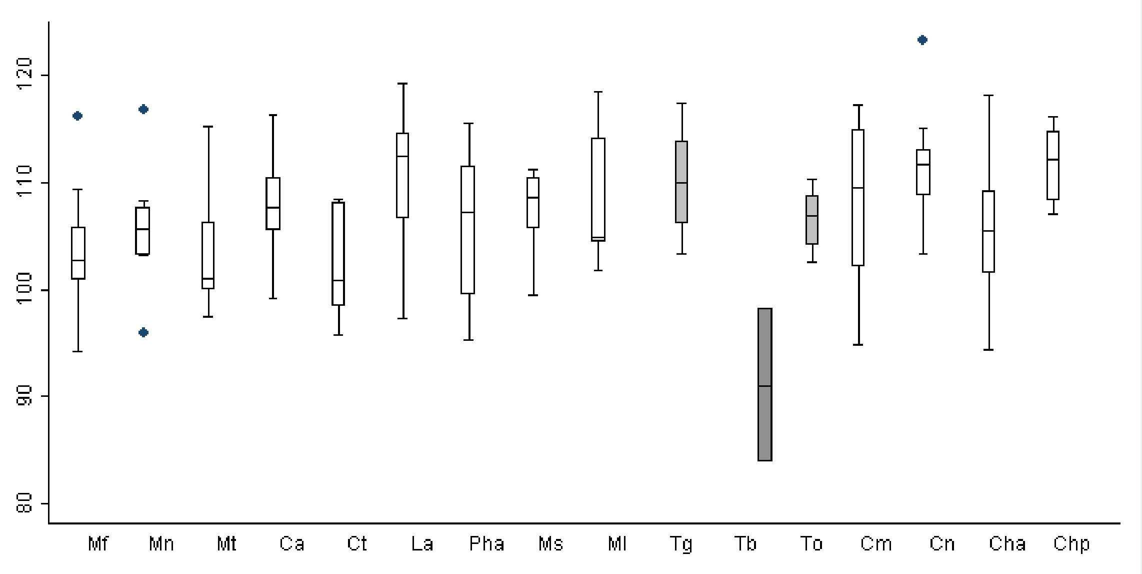
a. Humeral Head Height Index (Index 5)



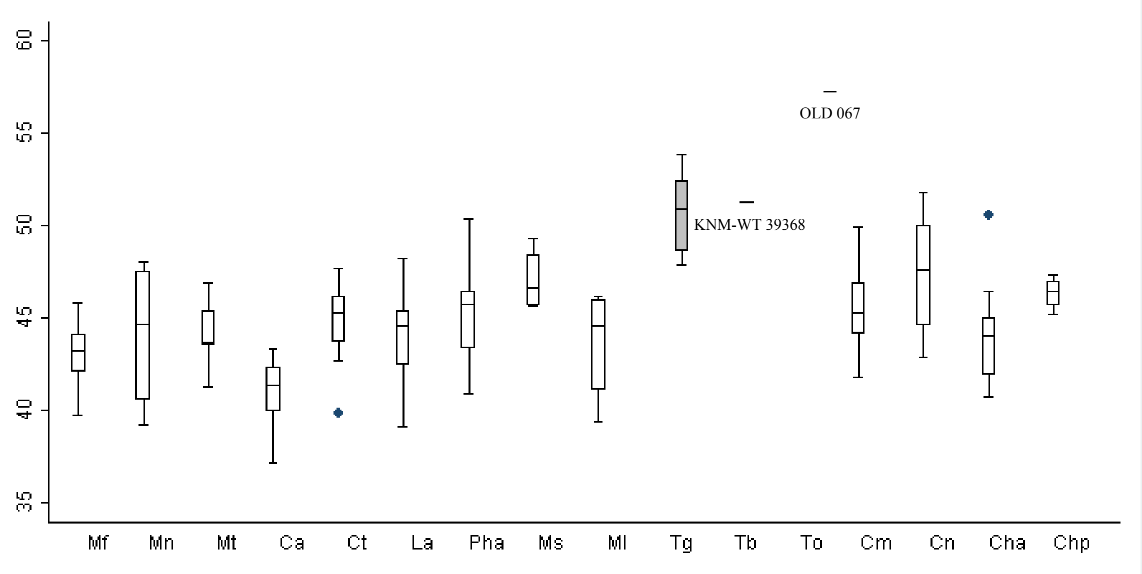
b. Humeral Head Shape 1 (Index 6)



c. Humeral Head Shape 2 (Index 7)



d. Delto-Pectoral Crest Length (Index 8)



Distal Humerus

The distal end of the humerus is known from two specimens KNM-WT 39368 and L865-1c (Figure 4.5.). In both the medial epicondyle is relatively large, highly retroflexed, and posteriorly projecting. It is slightly more posterior (or at least less medially projecting) than *T. oswaldi* and similar to *T. gelada* and *Papio* (Figure 4.6., Index 12). The lateral epicondyle is quite pronounced and slightly medially projecting, resulting in a distal end width in *Theropithecus brumpti*, and *T. oswaldi*, that is relatively wider than the extant papionins, with the exception of *M. thibetana* (Figure 4.6., Index 11; note this index could not be calculated for *T.brumpti*. Trochlear damage of KNM-WT 39368 did not allow for an accurate measurement of maximum humeral length. Visual comparison confirms similarity between *T. oswaldi* and *T. brumpti* in this feature).

Terrestrial primates tend to have a relatively short medial epicondyle. That is, a medial epicondyle that does not project medially but rather more posteriorly to enhance the action of the pronators and flexor muscles when the elbow is in an extended posture (Fleagle and Simons, 1982). A strongly medially projecting medial epicondyle is associated with relatively larger carpal and digital flexors that originate there (Jolly, 1972; Maier, 1972; Birchette, 1982). In *T. brumpti* the medial epicondyle is large and strongly retroflexed with little medial extension. This is actually unusual in *Theropithecus* species which typically have relatively large medial extension for a terrestrial primate and contra Krentz's findings for *T. brumpti* (Krentz, 1993b). Both *T. gelada* and *T. brumpti* have relatively posteriorly projecting medial epicondyles, more posterior than *T. oswaldi*. The relatively large size of the medial epicondyle has been noted by other researchers and Jablonski concluded that *T. brumpti* "appears to have possessed large carpal pronators and digital and carpal flexors, the origins of which were situated to enhance their mechanical advantage" (Jablonski et al., 2002, pg. 914-915). This appears to relate to greater strength of the digital and carpal flexors associated with manual dexterity and fine manipulation. This is also reflected in the relatively large lateral epicondyle.

Jolly (Jolly, 1972) used the relative breadth of the distal articular surface to distinguish arboreal from terrestrial species. In his study, animals with a ratio of articular breadth to biepicondylar breadth of 70 percent or higher indicated terrestrial locomotion. With a relative articular breadth index of 77 (as measured on KNM-ER WT 39368 and estimated in L865-1), *T. brumpti* is well into Jolly's terrestrial grouping. As Jablonski describes, there are marked areas of attachment on both the medial and lateral epicondyles for the tendons of the flexor and extensor muscles of the wrist and digits, respectively (Jablonski, 2002b). Index 13 shows the width of the distal humerus not including the medial epicondyle as a proportion of the total width of the distal end (Figure 4.6., Index 13). This is essentially a measure of the relative lateral projection of the lateral epicondyle in which *T. brumpti*, and *Theropithecus* in general, is not distinguishable from *Papio hamadryas anubis*.

The morphology of the capitulum is similar to other *Theropithecus* species. An index of capitulum depth (Figure 4.6., Index 10) shows that the capitulum is relatively deep in *T. gelada* and *T. brumpti* but less so in *T. oswaldi*.

A final feature of the distal humerus is the extent of distal projection of the trochlear flange. Specific aspects of the *T. brumpti* trochlea were difficult to interpret as the trochlea of KNM-WT 39368 is damaged, possibly as a result of osteroarthritis, and the majority of the articular surface is missing in L865-1c (Figure 4.5.). However, it appears that the trochlear flange extends somewhat distally, but not as far distally as in *Theropithecus gelada.* Distally projecting trochlear flange associated with terrestrial locomotion (Jolly, 1967), however, in this study, all *Theropithecus* species had a trochlear flange which was relatively short for a terrestrial papionin. This would allow for greater extension of the forearm than seen in other terrestrial monkeys or as Jablonski phrased it "a moderate, but not high, degree of stability of the elbow joint" (Jablonksi and Leakey 2008, pg. 166). This moderate, but not high, degree of stability seems to characterize both extinct and extant *Theropithecus* species (Krentz, 1993b), and appears to indicate more flexibility during most forelimb movements.

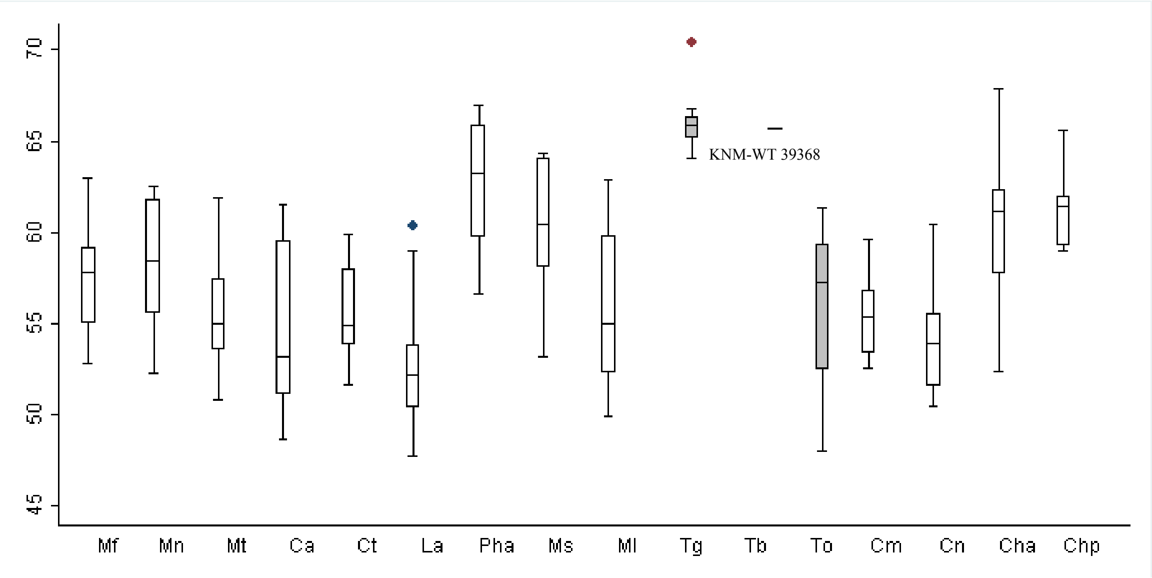
Lastly, Jablonski looked at the relative height and breadth of the olecranon fossa and found it to be relatively narrow (Jablonski, 2002b), which was also seen in this study and is related to stability in the elbow joint in terrestrial primates (Krentz, 1993a) (Figure 4.6., Index 14).

In summary, although it is reported that the distal humerus of *T. brumpti* is that of a terrestrial animal in juxtaposition with the flexible shoulder joint, evidence of flexibility was found at this joint as well. However, this flexibility is very much mapped onto an essentially terrestrial, highly stable, elbow. In the distal humerus the most informative locomotor features are the relative breadth of the distal articular surface, the retroflexion of the medial epicondyle, the projection of the trochlea and the narrowness of the olecranon fossa (Jolly, 1972; Harrison, 1989).

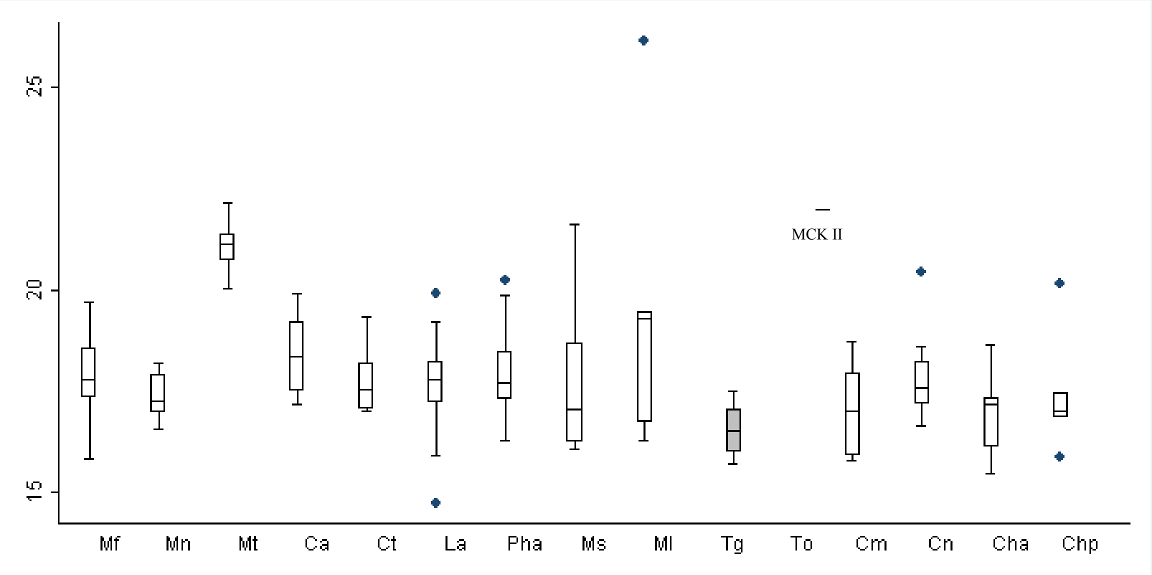
Figure 4.5. Distal Humerus. Anterior view of the distal portion of KNM-WT 39368 (a) and L865-1c (b).

Figure 4.6. Distal Humerus Indices. See Table 3.5 for definitions.

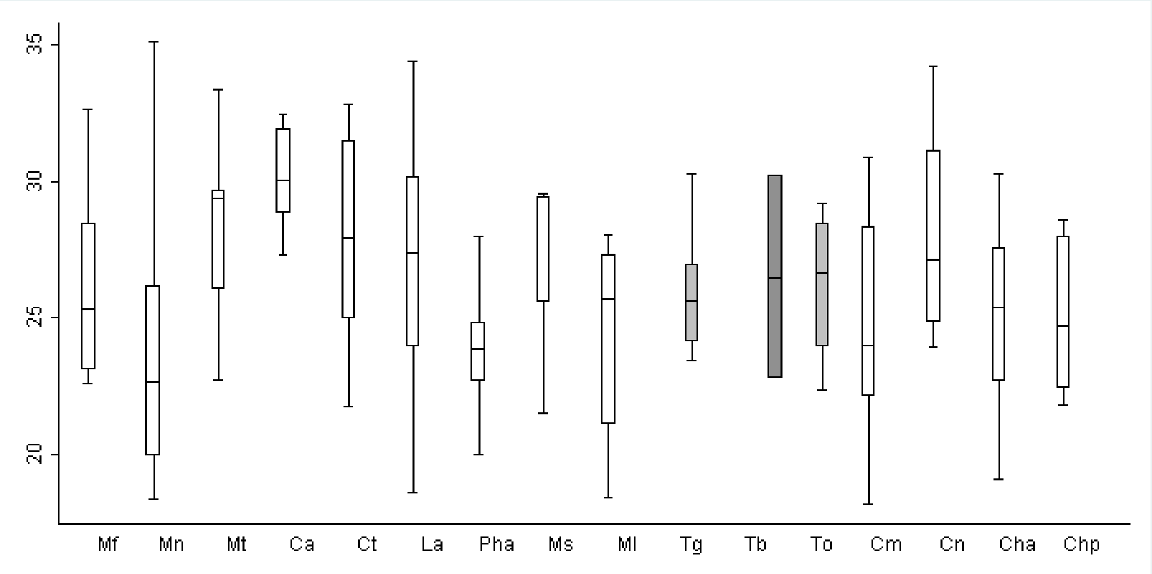
a. Capitulum Depth Index (Index 10)



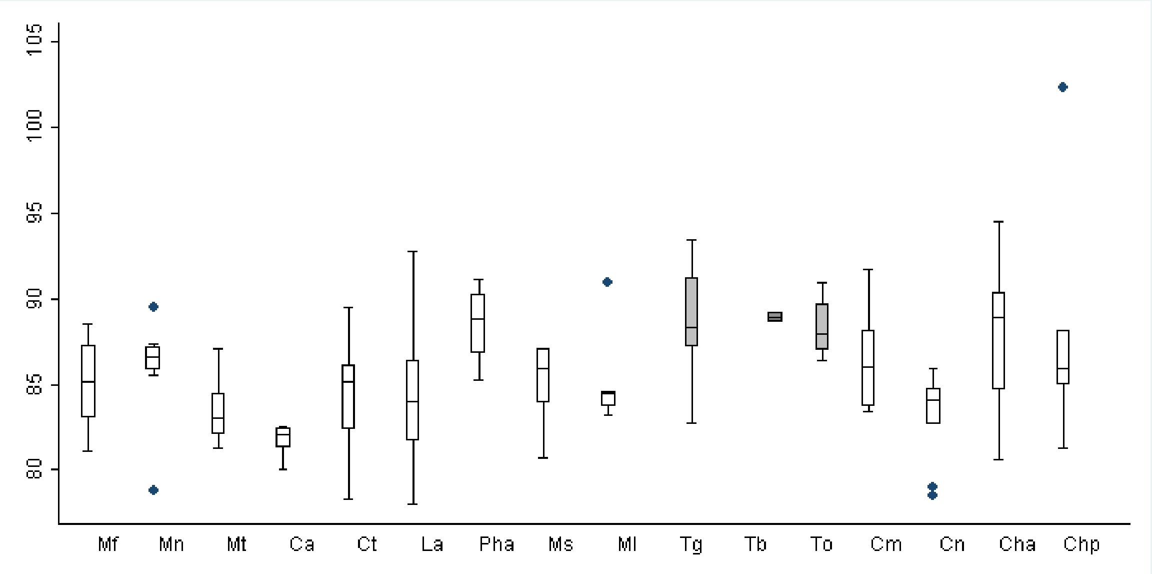
b. Humeral Distal End Width Index (Index 11)



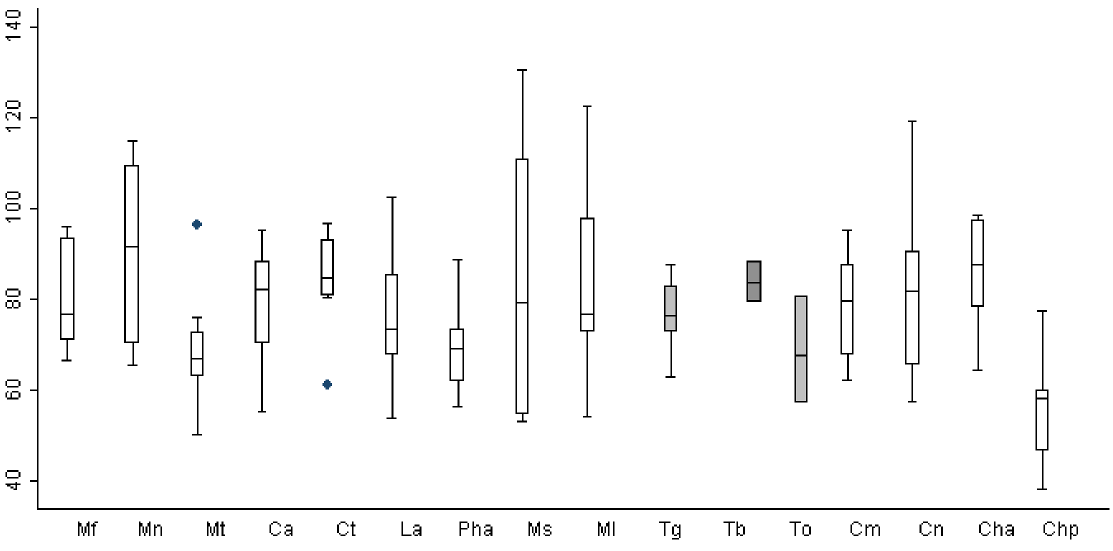
c. Medial Epicondyle Projection Index (Index 12)



d. Harrison’s Breadth Index (Index 13)



e. Olecranon Fossa Index (Index 14)



Ulna

Of the associated *Theropithecus brumpti* material there are 3 specimens which preserve ulnar elements. KNM-WT 39368 preserves a right proximal ulna (the distal part is preserved in situ along with right radius and right carpus) and a left ulna. The remaining material includes two proximal right ulnae (KNM-ER 17560 and KNM-ER 3084) (Figure 4.7.).

The ulna is considered to be highly informative as to locomotor habits (Jolly, 1972; Harrison, 1989). The proximal ulna is also related to elbow joint stability and habitual degree of extension, as it provides sites of attachment for the forelimb retractors, protractors, forearm and digital flexors and extensors. Specific areas of interest functionally are length, angulation and configuration of the medial surface of the olecranon process (Krentz, 1993a).

In *T. brumpti* the olecranon process is relatively short and retroflexed. The length of the olecranon process is related to the action of *m. triceps brachii* and therefore the length is a measure of the lever arm of the triceps muscle (Gray, 1968). Shorter, more retroflexed olecranon processes are associated with terrestrial locomotion and increase leverage of *m. triceps brachii* with the elbow in more extended postures. A longer olecranon process that is more in line with the unlar shaft characterizes more arboreal primates in which the longer process increases the leverage of the triceps and provides more power to the forearm when the forearm is in habitually flexed positions (Oxnard, 1963; Jolly, 1967; Gray, 1968; Conroy, 1974; Ashton et al., 1976).

Krentz (1993b) and Ciochon (1986) found that *T. brumpti* (and *T. oswaldi darti*) had much longer olecranon processes compared to other *Theropithecus* species and *Papio* thereby characterizing these groups as arboreal. Similar results were also reported by Jablonski *et al*. (Jablonski, 2002b). However, in this study, two different indices of relative olecranon length grouped *T. brumpti* with other *Theropithecus* species and other papionins in having a relatively short olecranon process characteristic of terrestrial primates (Figure 4.8., Index 15 and 16). The traditional index for relative olecranon process height requires the complete ulna. The only complete ulna, KNM-WT 39368, is damaged. Jablonski et al. (Jablonski, 2002b) estimated the length for this specimen. Using this measure, it is clear that *T. brumpti* has an olecranon process comparable in length to other *Theropithecus* species (Figure 4.8., Index 15). Using a different index of relative length of olecranon process that does not require the entire bone (Figure 4.8., Index 16), *T. brumpti,* again, groups with other *Theropithecus* species as well as other papionins.

The medial surface of the olecranon process in *T. brumpti* is marked by a distinct, large, rounded, superomedially directed flange, which develops into a rounded crest that extends distally down the posterior aspect of the shaft for over one-third its length (see Figure 4.7.). The proximal end of the olecranon, including its extensive flange and crest, is rugose and clearly accommodates the insertion of a large *m. triceps brachii* tendon. The medial aspect of the olecranon overshadowed by the flange is a deep fossa that accommodates the origins of *m. flexor carpi ulnaris* and *flexor digitorum profundus*, responsible for radial deviation of the wrist and flexion of the fingers, respectively (Jablonski, 2002b).

An index of olecranon process shape (OP length / OP depth, Figure 4.8., Index 17) *T. brumpti* separates from the other *Theropithecus* species, with an olecranon process that is slightly deeper for its height. This seems to be due to the extensive flange on the medial surface. In *T. brumpti* this crest continues as a ridge to the distal margin of the trochlear notch and even beyond. In *T. oswaldi* this crest is smaller and the corresponding fossa is less pronounced. The medial surface of the olecranon process is of functional significance because it is the site for the origin of *m. flexor carpi ulnaris* and *m. flexor digitorum profundus* which course down the forearm and insert at the wrist and digits. Because these are relatively well developed in all primates a concavity on the medial surface of the olecranon process is often present. However, the depth and proximal extent of this concavity is comparatively well marked in *T. brumpti* in relation to other papionins and other *Theropithecus* species. A deep medial cavity is associated, again, with arboreal monkeys, however others have noted how *Theropithecus* is an exception to this generalizion and that extant, highly terrestrial *T. gelada*, has a more pronounced concavity than *Papio* (Jolly, 1967, 1972). Perhaps this is related to the extreme manual dexterity exhibited by this species. As this trait is seen in the fossil material as well and is even more pronounced in *T. brumpti* than *T. oswaldi,* further confirms the presence of such traits in *Theropithecus* near the origin of the genus.

The trochlear notch in *T. brumpti* is relatively narrow, or at least narrower than other *Theropithecus* species (Figure 4.8., Index 18). Other indices of the notch show that the elbow joint in *T. brumpti* is different than committed terrestrial papionins *Papio*, *T. gelada*, *Macaca nemistrina* and *Macaca thibetana*. In *T. brumpti* the relative width of the total proximal ulnar articular surface is wider (Figure 4.8., Index 19) and the trochlear portion of that width is narrower (Figure 4.8., Index 20). The shape and configuration of the trochlear notch indicate a narrow but stable elbow joint. In *T. brumpti* the elbow joint is slightly narrower than other terrestrial papionins which appears to be associated with manual foraging as well (Fleagle and McGraw 2002).

Figure 4.7. Ulna. Medial view of the left ulna KNM-WT 39368 (a), proximal view of the right ulna KNM-WT 17560 (b) and medial view of the left ulna of KNM-ER 3084 (c)

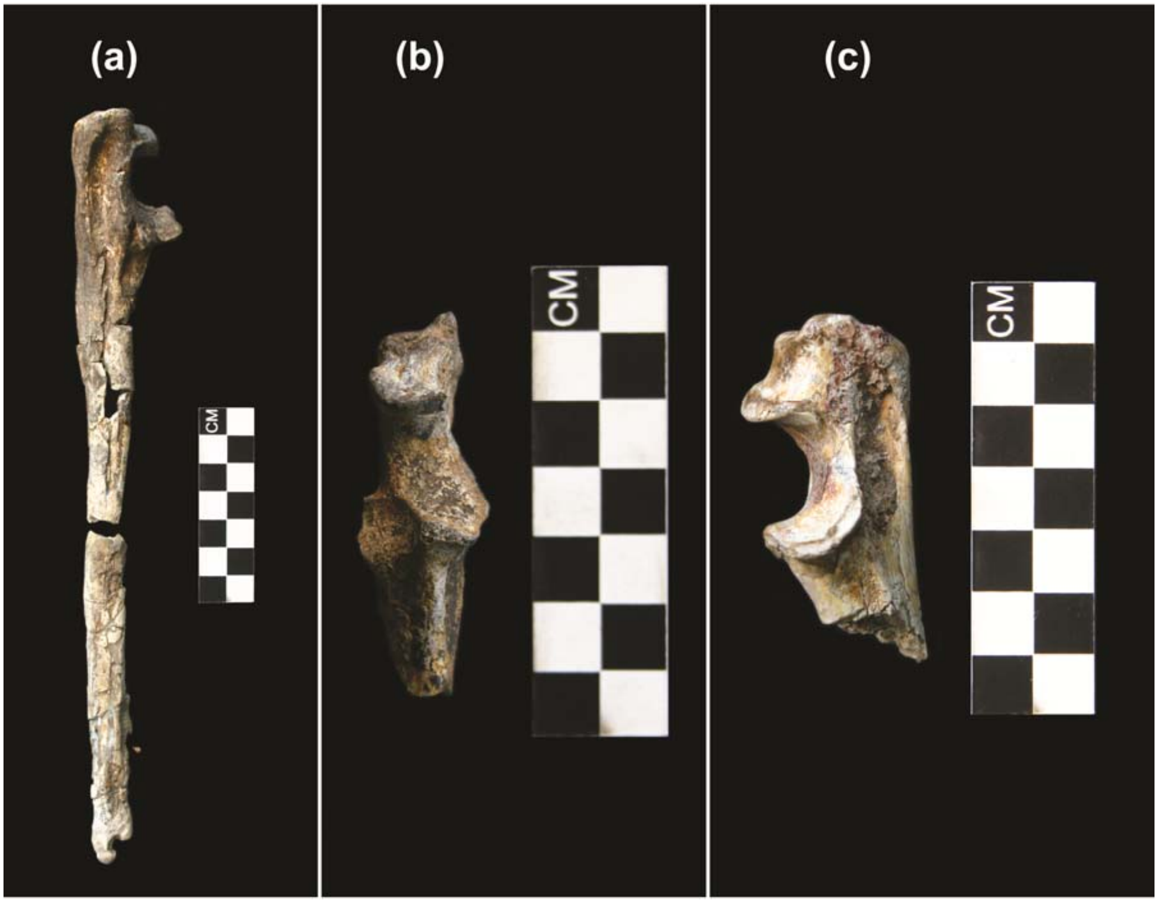
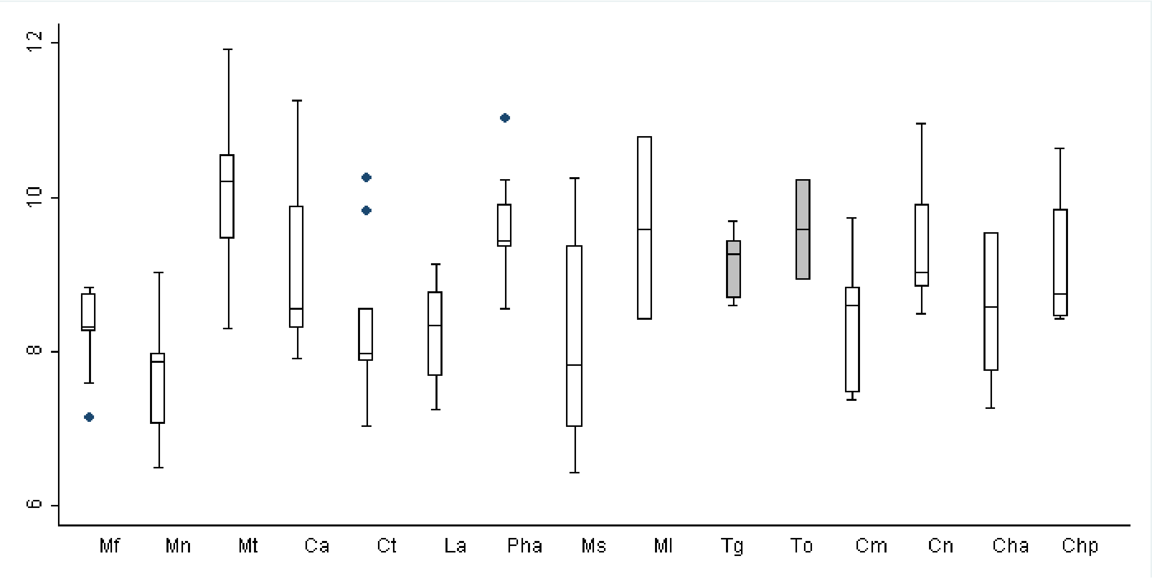
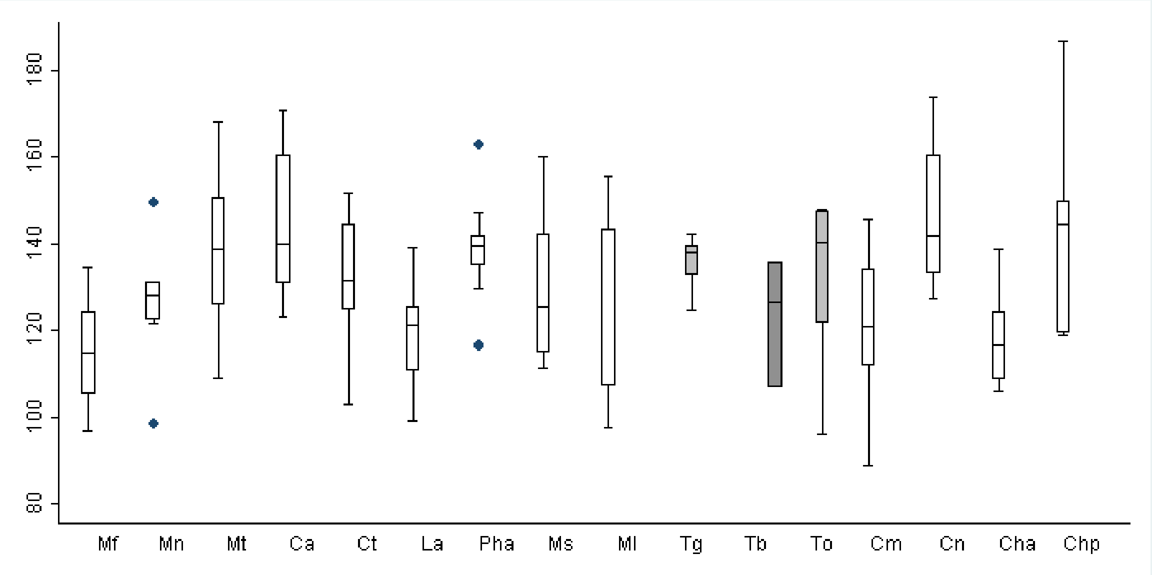


Figure 4.8. Ulna Indices. See Table 3.5 for definitions.

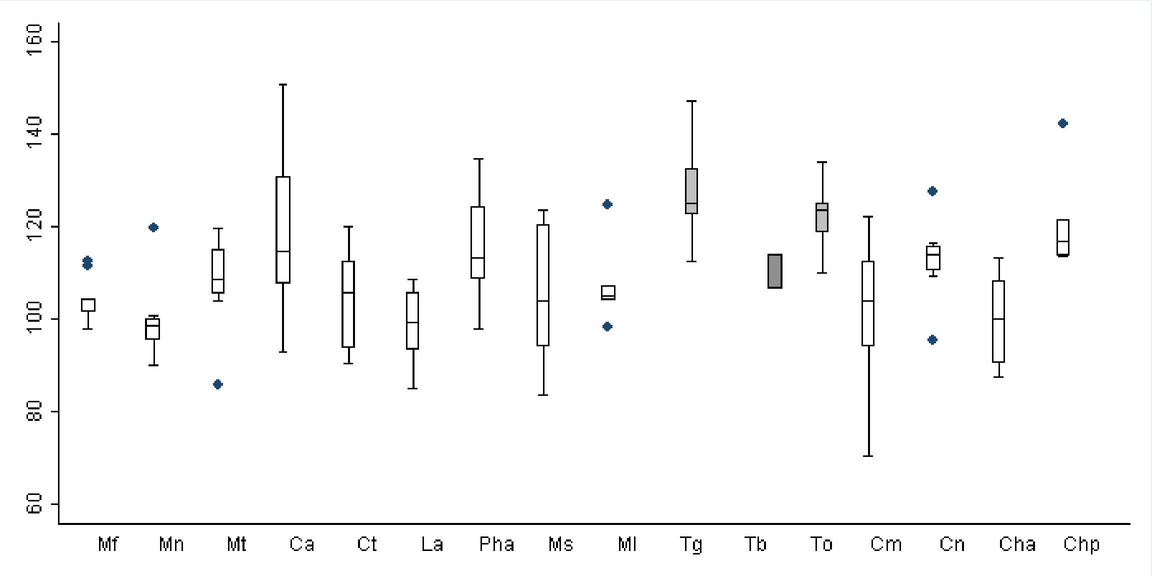
a. Olecranon Process Length Index (Index 15)



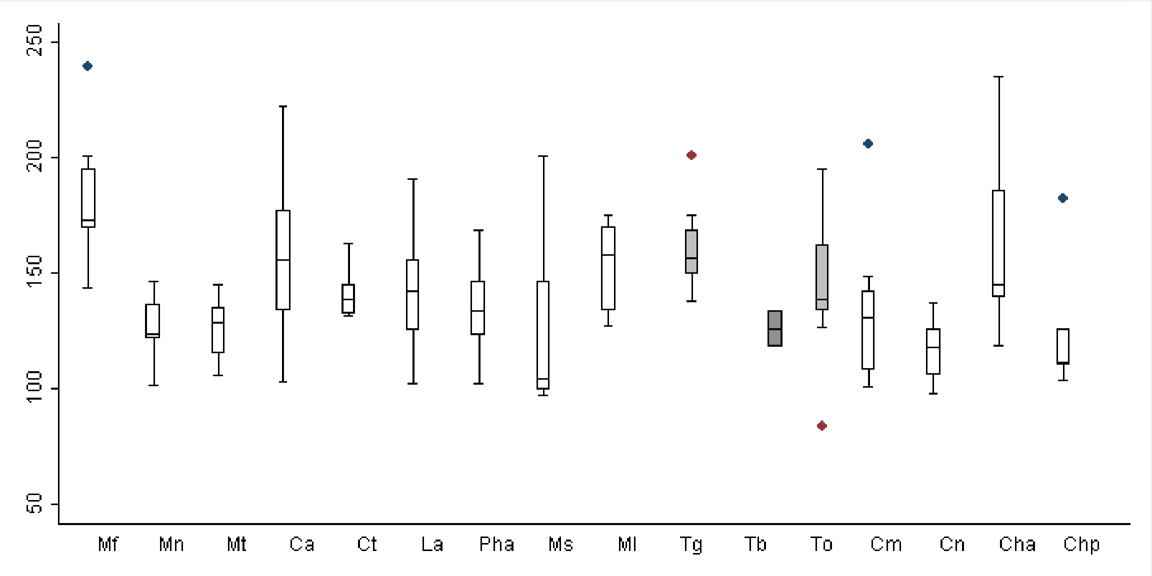
b. Olecranon Process Length Index (Index 16)



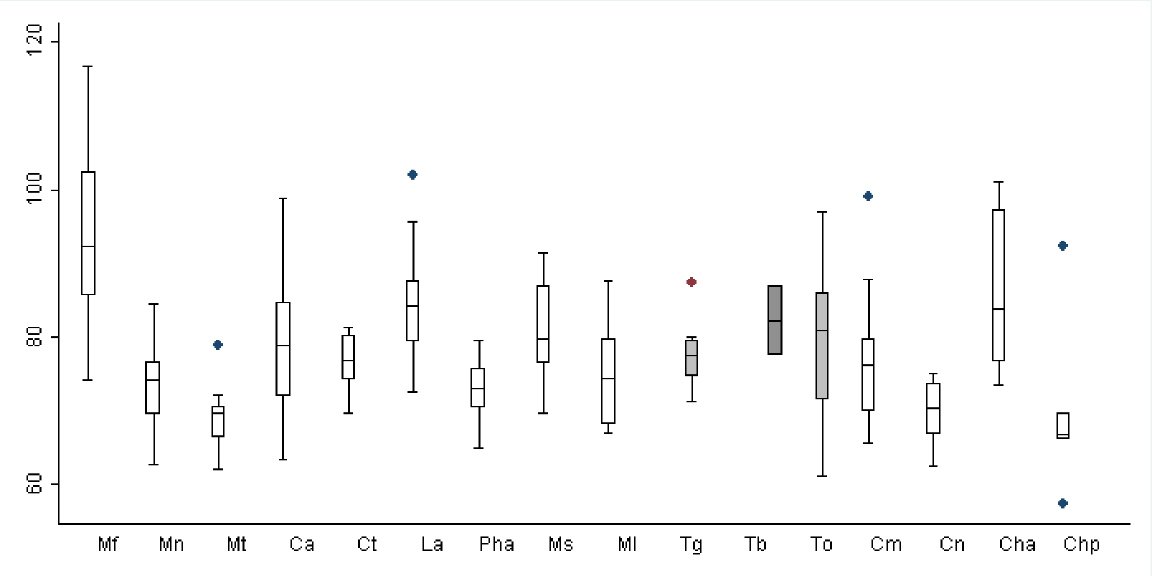
c. Olecranon Process Shape Index (Index 17)



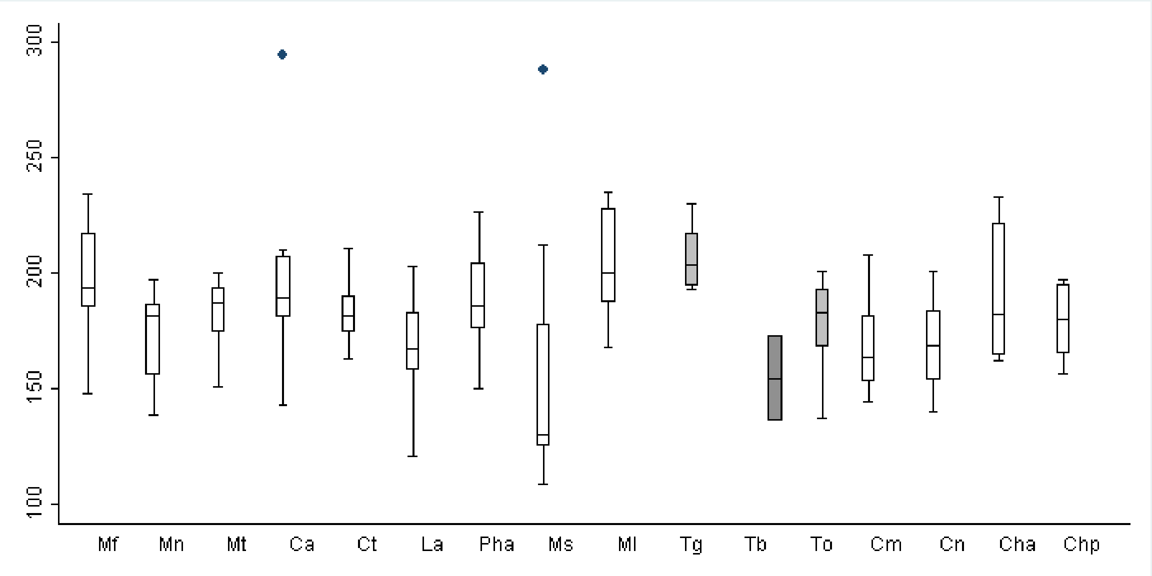
d. Ulnar Trochlear Notch 1 (Index 18)



e. Ulnar Trochlear Notch 2 (Index 19)



f. Ulnar Trochlear Notch 3 (Index 20)



Radius

Of the associated *Theropithecus brumpti* material there are 2 specimens which preserve radial elements. KNM-WT 39368 preserves a right proximal radius (distal part is preserved *in situ* along with distal right ulna and right carpus) and a left radial head. Also, from West Turkana, is a left radial head (KNM-WT 17554) (Figure 4.9.). The radii from KNM-WT 39368 were described in Jablonski *et al.* (Jablonski, 2002b).The radius has proved difficult to analyze in terms of morphology and locomotor behavior (Jolly, 1972; Birchette, 1982; Ciochon, 1986; Krentz, 1993b). However, Harrison (1989) and Jolly (Jolly, 1967) have described aspects of the radial head and neck that may be functionally informative.

The radial heads of *T. brumpti* are elliptical being slightly longer in the medio-lateral than the anterio-posterior diameter. The shape of the radial head may correlate with the range of movement of the forelimb at the radio-ulnar joint (Harrison, 1989). In this study, the radial head index (Figure 4.10., Index 21) grouped all *Theropithecus* species together, but not with *Papio*, which appear to have slightly rounder heads than *Theropithecus*. Elliptical radial head shape suggests stability at the radio-ulnar joint (O'Connor, 1975; Harrison, 1989). Animals that are more pronograde with limited supination tend to have more elliptical radial heads and, therefore, terrestrial cercopithecids would be expected to have more elliptical heads than arboreal cercopithecids. Jablonski found KNM-WT 39368 to have a radial head shape that is elliptical and within the range of those reported for other terrestrial cerocopithecines (Jablonski, 2002b). Krentz (Krentz, 1993b) found that radial head shape was variable and possibly quite round in *T. brumpti*. Jablonski (Jablonski, 2002b) states that rounder heads are found on smaller bones and therefore rounder head size may be more related to body size than the arboreality associated with them. Any true pattern between size and radial head shape was not found in this dissertation.

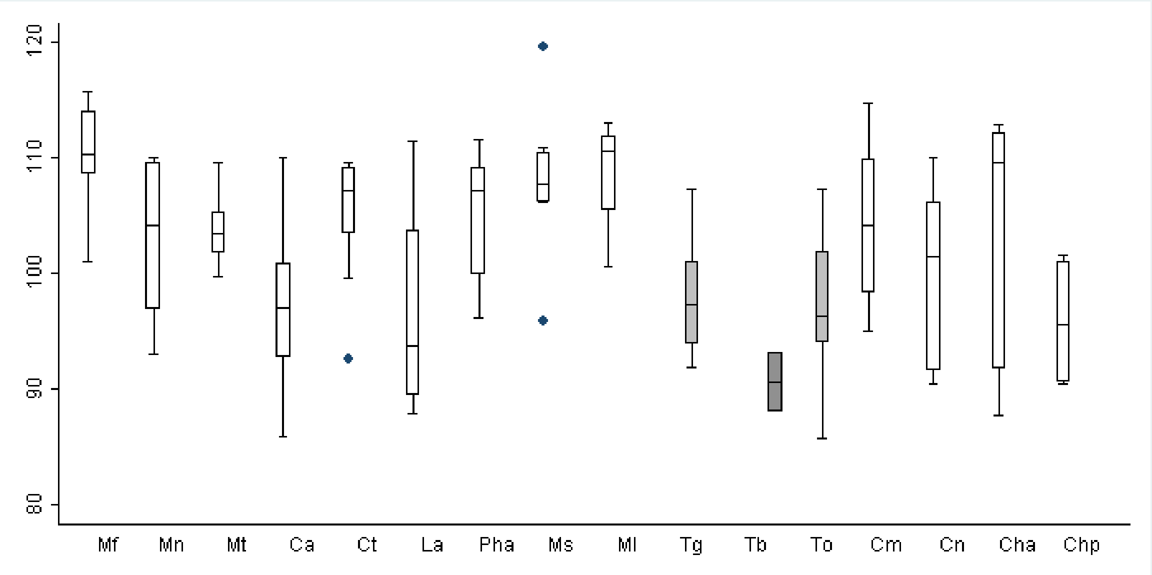
The radial neck in of WT 39368 appears to be rather robust and relatively short (Figure 4.10., Index 22). Relatively long necks are associated with arboreality as the long neck increases the moment arm of *m. biceps brachii* around the elbow and increased force during forearm flexion, both of which are important in an arboreal environment (Conroy, 1974; Harrison, 1989). A short neck would increase the velocity of action of *m. biceps brachii* and allows for rapid flexion of the forearm (Jolly, 1967). Therefore, the short neck of *T. brumpti* suggests both terrestriality and rapid locomotion on level surfaces and perhaps rapid flexion during manual feeding.

The radial tuberosity is large, oblong and divided by a deep proximo-distally aligned furrow. This tuberosity provides the site of attachment for the main tendinous insertion of *m. biceps brachii*. Jablonski and Leakey (Jablonski and Leakey, 2008) suggest that perhaps this furrow is the insertion site for slips or aponeuroses from the main tendon. The relatively large size of the insertion suggests that the *m. biceps brachii* was large and, as a flexor of the elbow, has been associated with arboreality (Ciochon, 1986), however other studies have been inconclusive about the functional signal for this trait (Birchette, 1982). Combined with the radial neck morphology described above, in *T. brumpti* this may, again, be a feature associated with forearm use and frequent supination associated with forearm flexibility. As this relatively prominent radial tuberosity is also seen in *T. oswaldi*, this combination seems to demonstrate an anatomical compromise between terrestriality and forearm flexibility in the genus. Finally, in the radial shaft there is a deep excavation on the ventral surface leading to a prominent interosseous crest and a sharp medial border. This morphology has been associated with prominent digital flexor musculature (Fleagle and McGraw, 2002).

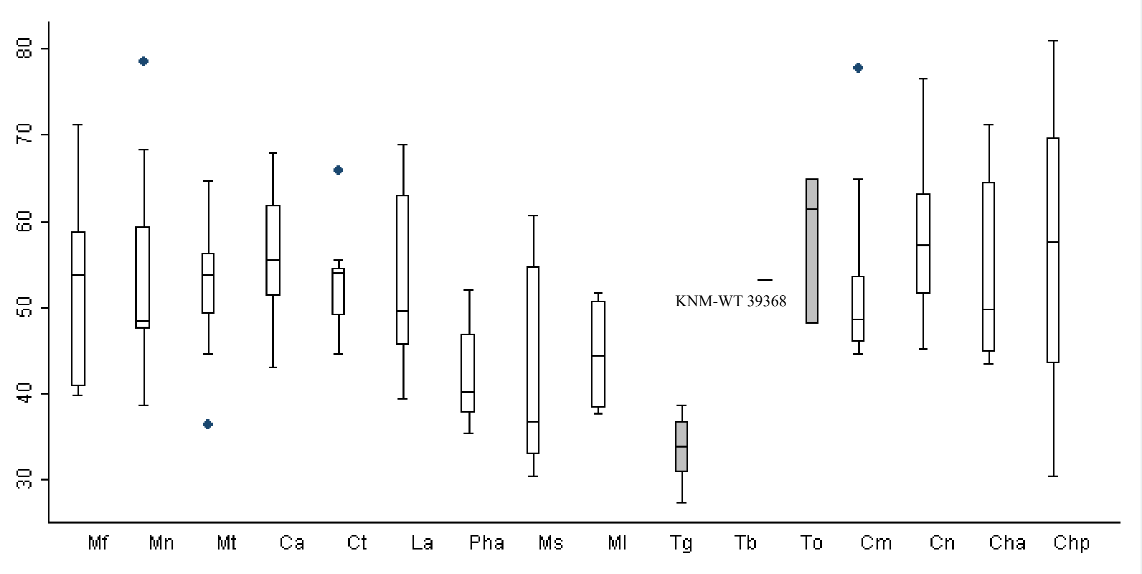
Figure 4.9. Radius. Inferior view of the left radial head of KNM-WT 17554 (a) and medial view of the right radius of KNM-WT 39368 (b).

Figure 4.10. Radius Indices. See Table 3.5 for definition.

a. Radial Head Index (Index 21)



b. Radial Neck Length (Index 22)



Conclusions

When the forelimb of all the associated *T. brumpti* material is analyzed and compared with the morphology of other papionins a more complete picture of the functional anatomy of this species emerges. *Theropithecus brumpti* is clearly a terrestrial papionin. While *T. brumpti* retains a degree of flexibility, this is not exceptional when compared to other members of the genus, notably *Theropithecus oswaldi*. Features historically used to reconstruct *T. brumpti* as more arboreal than other members of the genus are interpreted here as part of a suite of traits that characterize early *Theropithecus* including *T. oswaldi (T. o. oswaldi).* Further, not only are traits similar in both species, but there is a wide range of trait variation and overlap. It has been suggested that *T. oswaldi* was not exclusively terrestrial, based on many of the traits discussed here (Elton, 2002). Given the extreme size of later *T. oswaldi leakeyi* along with many features clearly consistent with terrestriality (Jolly, 1972; Krentz, 1993; Delson et al., 2000; Frost and Delson, 2002; Frost, 2007), it is more likely that *T. oswaldi* shared features associated with forearm flexibility with *T. brumpti* and *T. gelada*.

A narrow scapular blade, narrow supra- and infraspinatous fossa, a posteriorly projecting medial epicondyle, a relatively short and retroflexed olecranon process, an elliptical radial head and a short radial neck align *Theropithecus brumpti* with other terrestrial papionins. Greater flexibility, for a papionin, is seen in the moderately indented glenoid fossa, variation in relative humeral head height, relatively well developed rotator cuff musculature, relatively short trochlear flange and large radial tuberosity-traits which are also seen in the *Theropithecus oswaldi* comparative sample.

Theropithecus is characterized by a unique suite of adaptations for harvesting and feeding on grasses. The extant representative of the genus, *T. gelada,* has a diet that is almost 90% grasses (Iwamoto, 1993). Studies of the masticatory apparatus have hypothesized that the emergence and early diversification of *Theropithecus* was linked to the evolution of a feeding apparatus specialized for grazing (Jablonski, 1993a). While this may be the case, most lines of evidence do not support grazing in the woodland-adapted, perhaps frugivorous, *Theropithecus brumpti* (Teaford, 1993). *T. brumpti* is not associated with grassland habitats, but it shares the distinctive molar morphology of the genus typically associated with a grazing diet (Eck, 1987). *T. brumpti* also has forelimb features associated with the unique feeding behavior: relative long deltoid crest, large medial epicondyle and the large fossa on the medial surface of the olecranon process. Therefore, the suite of traits that defines the genus may likely be related to manual manipulation and/ or food processing. Gilbert and collegues (Gilbert et al., 2010) recently suggested that manual terrestrial foraging may have been primitive for papionin monkeys in general and so perhaps these traits are better interpreted as foraging adaptations related to forest floor locomotion and gleaning which may be primitive for *Theropithecus* and possibly for papionins. Further, if the common ancestor of *Theropithecus*, *Papio* and *Lophocebus* was arboreal, perhaps in the *Theropithecus* lineage the ability to manipulate arboreal environments was co-opted for fine manipulation of food objects on the ground. This idea will be expanded further in the next chapter. As a final note, this flexibility of the forelimb may, alternatively, be associated with actual arboreal behavior or climbing ability. The subsequent chapters will demonstrate that this unlikely.

> …it [*Theropithecus brumpti*] is not very ‘savanna baboon like in its forelimb anatomy. It is also not very ‘gelada’ baboon like in its forelimb. Both of these represent the most extreme terrestrial adaptations among cercopithecines. Of all the extant species it is most similar to *Papio* [*Mandrillus*] *sphinx*, a forest-dwelling terrestrial and ?arboreal species. *T. brumpti* was a very large species so it probably did not spend a (sic) much time in an arboreal habitat but whatever difference today separated the mandrill from the savanna baboon also separate *T. brumpti* from other wholly terrestrial and cursorial species

(Ciochon, 1986): based on no associated remains and only KNM-ER 2023 (a distal radius) from Kenya

CHAPTER V

WRIST AND HAND

Modern *Theropithecus gelada* has unusual hand morphology, thought to be related to its active grass harvesting behavior, (Maier, 1972; Etter, 1973; Jablonski, 1986, 2002b). First, *Theropithecus* has some of the relatively shortest and most robust digits among cercopithecoids (Jolly, 1972; Guthrie and Frost, 2010). This may be an adaptation for lightening the distal part of the limb enabling more efficient terrestrial locomotion, but at the expense of arboreal capability (Patel, 2010). Furthermore, and more strikingly, *T. gelada* has a hand structure that deviates from that of other terrestrial cercopithecines in the elongation of the first metacarpal (thumb) relative to the other digits and the relative abbreviation of the second digit. This abbreviation is created by the relative shortening of the second proximal phalanx (Napier and Napier, 1967). This arrangement indicates an adaptation for strong and precise pincer-like movements of digits I and II during foraging. This has been described as a high degree of opposability, the highest among non-human primates (Napier and Napier, 1967; Maier, 1972; Etter, 1973).

Because of this unique structure in the modern, the hand of the fossil *Theropithecus* species is relatively widely studied as similar unique structures in the fossil species would be especially interesting. A previous study of the hand of *Theropithecus brumpti* noted arboreal adaptations including relatively curved middle phalanges (Jablonski, 1986). This observation, plus the closed woodland habits that *T. brumpti* is associated with, has led to the characterization of *T. brumpti* as the ‘arboreal’ *Theropithecus* species (Eck and Jablonksi, 1987; Ciochon, 1993; Elton et al., 2003). However, later studies of the hand have revisited, and nullified, this hypothesis

(Jablonski, 2002b; Guthrie and Frost, 2010) demonstrating robusticity and stoutness of the metacarpals and phalanges associated with terrestriality.

Given the importance of manual morphology in the genus, this chapter focuses on the functional implications of the anatomy of the metacarpals, phalanges and carpal elements. Carpal elements are rare in the fossil record and have often been left undescribed and unidentified (Jolly, 1972; Krentz, 1993b; Jablonski, 2002b). However, the full suite of carpal bones is preserved in KNM-WT 39368. This chapter is the first description and identification of the carpal bones and functional analysis of the *T. brumpti* wrist.

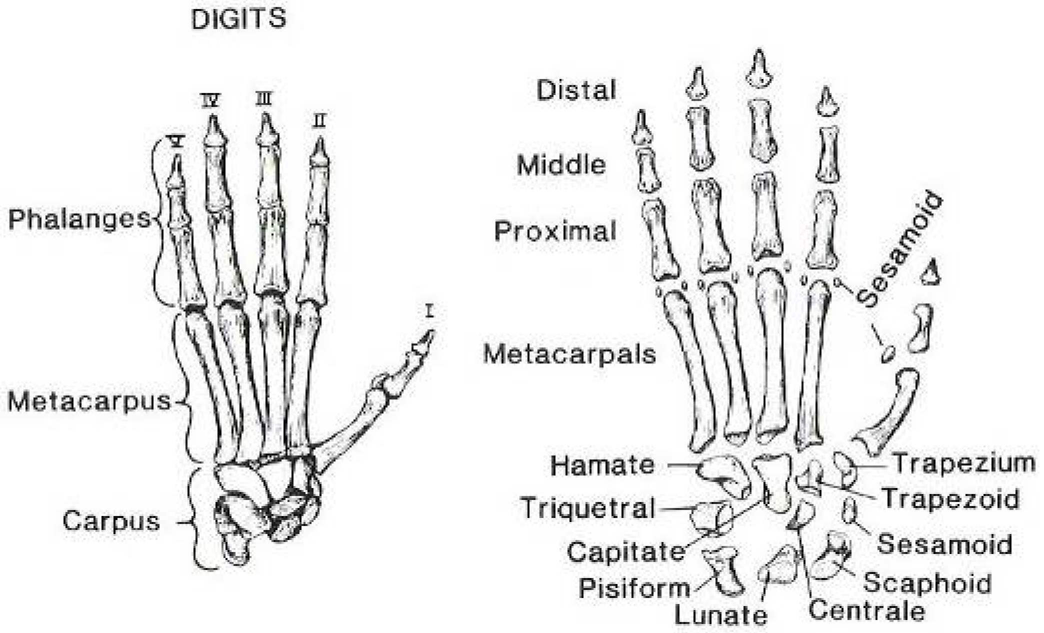
Materials and Methods

While the metacarpals and phalanges were studied in a manner similar to the other elements of this study (see Chapter III for full materials and methods), the carpals were analyzed slightly differently. The carpals were identified and then documented using gross anatomical descriptions and photographs, and measurements of features thought to be noteworthy or functionally relevant were taken. The *T. brumpti* carpals were visually compared with *Papio hamadryas anubis* and *Theropithecus gelada*. Differences, when found, were noted. Materials for this chapter are shown in Table 5.1. and an illustration of a baboon hand shown in Figure 5.1.

Table 5.1. *Theropithecus brumpti* wrist and hand material used in this study

	MC	Proximal Phalanges	Intermediate Phalanges	Distal Phalanges	CARPALS
KNM-WT 39368	**1-5**	**5**	**4**	**5**	**X**
L 865-2	**1-5**	**5**	**3**	**-**	

Figure 5.1. Dorsal view of a *Papio* hand. (From Fleagle, 1999)



Carpals

The only specimen to preserve any carpal bones is KNM-WT 39368. Fortunately, both wrists are completely preserved. The left has been fully prepared and the individual elements have been isolated, and can be fully identified and described. The right is still articulated and *in situ* preventing the morphology of some elements from being studied. Table 5.2 lists the carpal identifications for KNM-WT 39368, which differ slightly from the original publication of this material (Jablonski, 2002b). It was possible to identify a few right carpals (Table 5.2) and, specifically, it was determined that KNM-WT 39368 T, which was originally listed as right carpal is most likely a sesamoid based on the morphology of the sesamoids seen in the left hand. The following description and preliminary functional discussion of the wrist is based on the left hand. All of the carpals, with the exception of the os centrale, can be analyzed for *T. brumpti* from the KNM-WT 39368 skeleton.

Table 5.2 Carpal Bones of KNM-WT 39368

KNM-WT 39386 FS	Left Trapezium
KNM-WT 39386 FP	Left Lunate
KNM-WT 39386 FQ	Left Scaphoid
KNM-WT 39386 FR	Left Trapizoid
KNM-WT 39386 FT	Sesamoid
KNM-WT 39386 BQ	Sesamoid
KNM-WT 39386 BP	Left Capitate
KNM-WT 39386 AQ	Left Pisiform
KNM-WT 39386 AO	Left Triquetral
KNM-WT 39386 AN	Left Hamate
KNM-WT 39386 AR	Left Sesamoid
KNM-WT 39386 AB	Left Sesamoid

KNM-WT 39386 FV	Right Trapezium
KNM-WT 39386 U	Right Lunate
KNM-WT 39386 T	? Sesamoid ?
KNM-WT 39386 V	Right Scaphoid

KNM-WT 39386 FM	Two Right Sesamoid Bones
KNM-WT 39386 FM	Three Sesamoid Bones

In primates, the carpus is comprised of 8-9 individual carpal bones and the radioulnar articulation (Fleagle, 1999). The wrist has two rows of bones: the pisiform, triquetral, lunate, scaphoid in the proximal row and the hamate, capitate, trapezoid and trapezium in the distal row. However, some cercopithecoids, ceboids, and hylobatids possess a separate os centrale, In hominids (i.e. great apes) the os centrale generally fuses to the scaphoid bone, except in some *Pongo* (Schultz, 1936). Previous researchers have noted that the carpus is markedly stereotyped and homogenous across cercopithecids

(Schultz, 1970; Lewis, 1972, 1974; O'Connor, 1975). Unfortunately, few data exist on the ranges of wrist motion, and the skeletal morphology associated with variation in wrist motion, for nonhominoid taxa (Richmond, 2006). Some studies have shown suggestive functional indicators in specific carpal bones and these are cited when appropriate.

Pisiform

As in all cercopithecids, the pisiform of *T. brumpti* is relatively large and cylindrical with a long shaft that appears slightly twisted (Blue, 2002). Proximally the pisiform articulates with the triquetral and the styloid process of the ulna, creating a ‘cup’ for the ulnar styloid process (Lewis, 1972). In all cercopithecids, the pisiform is a non-weight bearing bone (Whitehead, 1993). *T. brumpti* has a very thick shaft, but this is variable in cercopithecids (Whitehead, 1993; Blue, 2002). The facet for the styloid process is medial facing in Cercopithecidae, but this is not clear in the *T. brumpti* specimen. The triquetral facet is distinct, flat and oriented distopalmarly (Figure 5.2.).

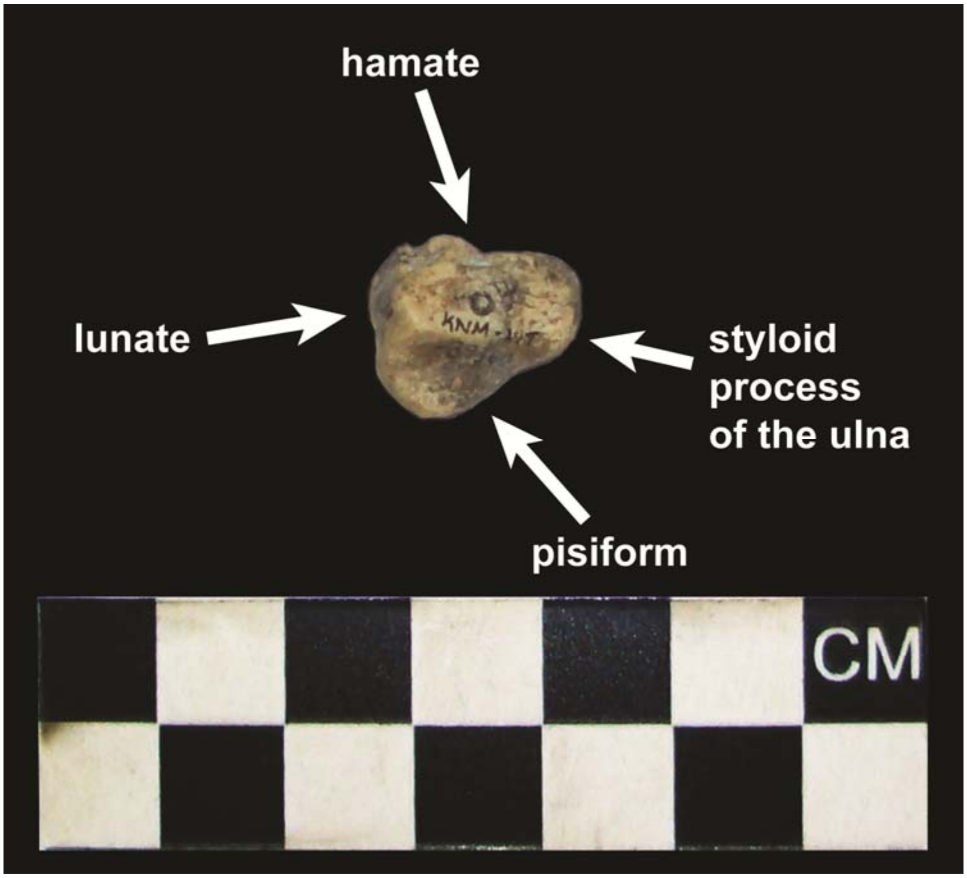
Figure 5.2. Left Pisiform. Arrow highlights triquetral facet.

Triquetral

The triquetral is a relatively large, cuboidal bone with a large medial tuberosity and four facets for the: pisiform, lunate, hamate and styloid process of the ulna (Figure 5.3.). Within cercopithecids the triquetral is uniform with similar length-to-width proportions (Blue, 2002).

The distal surface of the bone is dominated by the hamate facet which is relatively long compared to width as seen in more terrestrial species including *Papio* (Blue, 2002). A blocky nonarticular area exists between this hamate facet and the facet for the styloid process of the ulna. Dorsal to the facet for the styloid process there is a slightly concave, relatively long, facet for the pisiform bone. The lunate facet is proximolateral to the hamate facet.

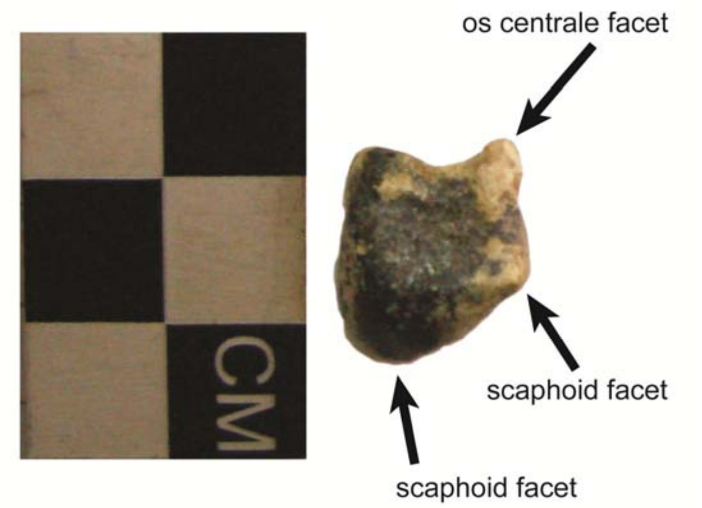
Figure 5.3. Left Triquetral.



Lunate

The lunate is a blocky bone with a large half moon crescent cut out distally. On the lateral surface of the lunate there are two articular surfaces for the scaphoid and the os centrale. The os centrale facet is located along the distal border of the lateral surface and extends as a smooth stripe dorsopalmarly. The scaphoid facet is a concave facet and located between the os centrale facet and the radial articulation (Figure 5.4.). On the proximal surface of the lunate is the radial facet, which is only slightly angled away from the facets for the os centrale and the scaphoid, which is common to all cercopithecoids, but distinct from African apes (Blue, 2002). The radial facet is rounded, convex and is longer dorsopalmarly (11.8 mm) than mediolaterally (9.5mm). This is typical in cercopithecids (Blue, 2002). The lunate articulates with the triquetrum on its medial side. This facet extends the dorsopalmarly the entire midsection of the bone. Distally, there is a deep curved facet with clear sharp edges for articulation with the capitate. On the dorsal edge of the capitate facet there is a small articular facet for the hamate bone.

Figure 5.4. Left Lunate

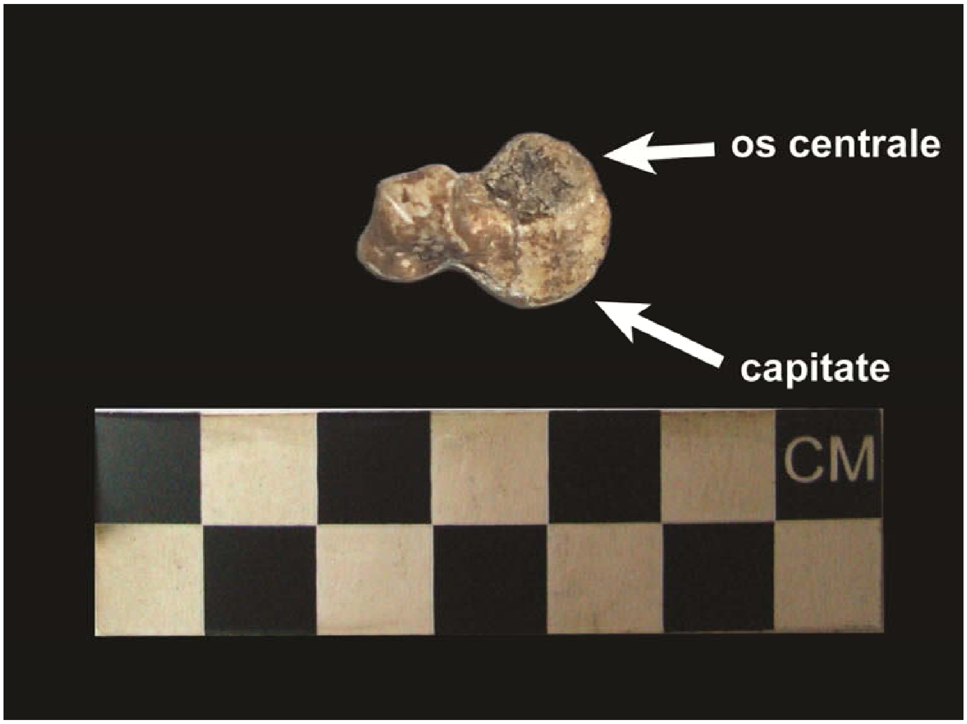


Scaphoid

The scaphoid is a sickle shaped bone, narrowed between the proximal and distal ends by a sulcus for the palmar radiocarpal ligament (Blue, 2002). Together with the lunate, the scaphoid creates a convex surface for articulation with the distal radius. The proximal surface is convex palmarly and concave dorsally, these surfaces are smooth with no separation or discernable grove as is usually present in hominoids. The presence of a dorsal ridge may have the effect of preventing further extension against the dorsal margins of the capitate and trapezoid, thereby limiting wrist extension. It is not clear if the absence of this trait implies more extended wrist postures in *T. brumpti*, however, *Papio* (which has similar morphology) uses more extended wrist postures while walking on branches (Schmitt, 1994). With the overall forearm flexibility described in the previous chapter, this ability would not be surprising.

The concave articular surface is relatively large and covers a large extent of the articular surface. The medial border of the scaphoid in *T. brumpti* is smooth and rounded. There is a relatively long, large tubercle that projects laterally from the radial articulation. The tubercle is sharp and perpendicular to the body of the scaphoid bone. There is a strong ridge running diagonally across the surface of the beak. On the dorsal surface is the facet for the articulation with the trapezium. Distally, there is a flat articular surface for the lunate bone palmarly and a concave articulation for the os centrale dorsally (Figure 5.5.)

Figure 5.5. Left Scaphoid



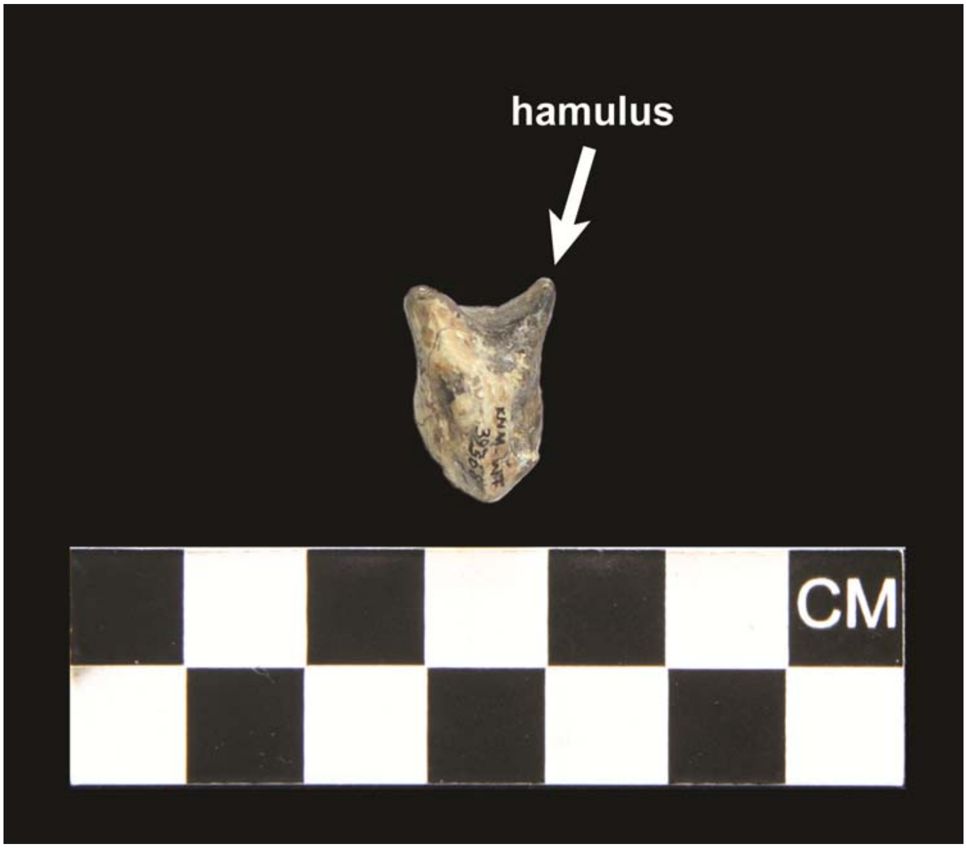
Hamate

The hamates of all cercopithecids are similar to one another, being stout wedge shaped bones, with a diagonal orientation when viewed dorsally (O'Connor, 1975) (Figure 5.6.). Distally, the hamate articulates with both the fourth and fifth metacarpals. In *T. brumpti*, both facets are concave dorsopamarly and the MCV facet extends further distally than MCIV. Both are typical traits in monkeys (Blue, 2002). It has been suggested that the morphology of the MCIV and MCV facets can be used to distinguish between digitigade (type of hand use in locomotion in which only the fingers and metacarpals touch the ground) and palmigrade monkeys (Whitehead, 1993). In palmigrade monkeys there should be distinct facets for the fourth and fifth metacarpals. In *T. brumpti* the two facets are not distinct. Rather there is a significant difference in dorso-palmar height between the two articular areas. There is also a small ridge partially separating these two areas, but it does not extend across the entire distal surface and it does not create two distinct facets. Blue saw height differences in the MCIV and MCV facet morphology in *Victoriapithecus* but was unsure if this would be considered distinct (Blue, 2002). The difference in height between the MCIV and MCV facets is interpreted here as not distinct, and is, therefore, considered evidence of digitigrady in *T. brumpti*.

In *T. brumpti* the facet for MCV is symmetrically curved, as is typical of cercopithecids (Blue, 2002). On the palmar surface of the MCV facet there is a distinct and pronounced mediolaterally flattened hooked hamulus that extends both palmarly and distally. Although the dorsal margin of the MCV facet is slightly worn, it does not appear that the hamulus extends any further distally that the facet for MCV. This large and hooked hamulus is suggested by Whitehead to indicate a digitigrade monkey (Whitehead, 1993). The hook of the hamulus in *T. brumpti* is quite vertical which is also seen in *Papio* (Blue, 2002). The significance of this feature is not well understood. It is generally thought that the function of the hamulus is related to actions of *m. flexor carpi ulnaris*, which attaches to the pisiform, but acts on the hamulus through the pisohamate ligament (Spoor et al., 1991).

The hamate also articulates with the triquetral and the facet is seen on the proximo-lateral surface of the bone. It is slightly helical in shape and flattened distally. This flattening on the distal portion of the triquetral facet is found in terrestrial species, such as *Papio*, in which the range of extension is limited (Spoor et al., 1991; Fleagle, 1999). The distal portion of the triquetral facet is also slightly 'foreshortened' in *T. brumpti*. This was previously described in *T. oswaldi*, and would result in reduced capacity for ulnar deviation (Whitehead, 1993). On the dorsal border of the triquetral facet there is a sharp ridge. On the medial surface of the hamate the facet for the capitate bone extends the entire length of the bone proximodistally. The facet is widest proximally and narrows distally. Mediopalmarly, there is a rough surface for attachment of the interosseous ligament between the hamate and capitate bones (Beard et al., 1986) and it is smooth rounded surface with no divisions as is seen in some apes (Spoor et al., 1991). Finally, proximo-medially, the hamate bone bears a facet for the lunate.

Figure 5.6. Left Hamate

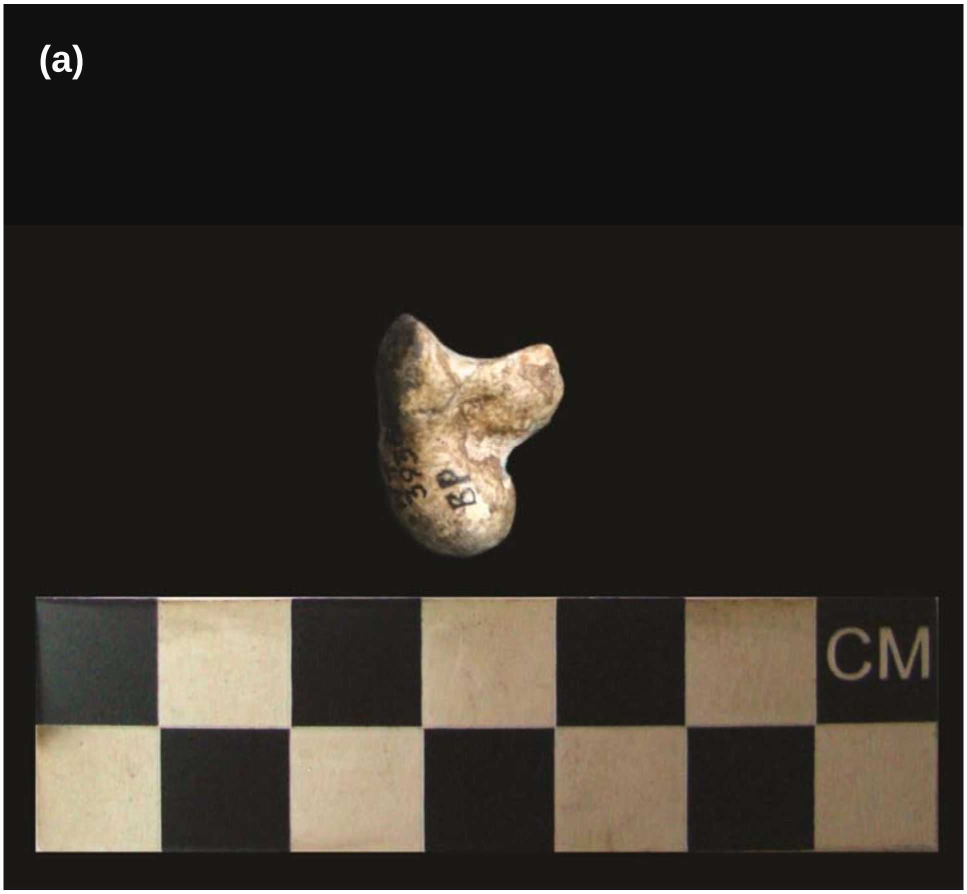


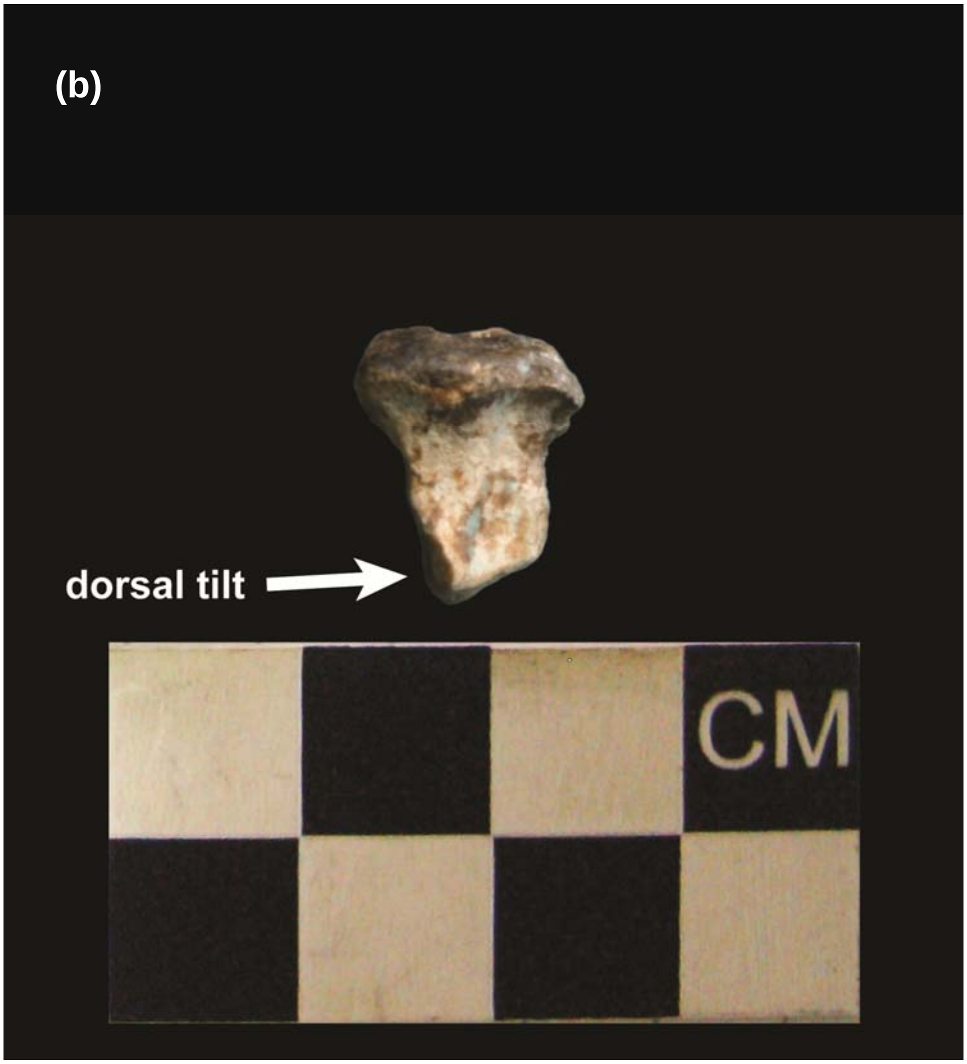
Capitate

The capitate is a distinctive bone with a large distal facet articulating with MCIII and a head, oriented proximally and articulating with the lunate, os centrale and the hamate (Figure 5.7.). The proportions of the capitate bone appear to be similar across all anthropoids, and its morphology is not known to vary greatly among taxa with different locomotor repertoires (Blue, 2002). The head of the capitate may be more medially expanded in cercopithecids, especially the more terrestrial species (Lewis, 1974). In the isolated *T. brumpti* capitate it is somewhat difficult to discern proper orientation of the capitate head, when placed within the carpus the head may be slightly medially oriented, but if so, it is not pronounced. On the lateral surface of the head of the capitate there is a small facet for articulation with the os centrale. Facets for the other two articulations on the head of the capitate are not as clear.

On the lateral surface of the capitate are two distinct and separate facets for articulation with the medial edge of the base of MCII (dorsally) and the trapezoid (palmarly). The distal surface of the capitate is mainly the articular facet for the third metacarpal, but there is slight articulation for the MCII and MC IV as well. There is, in *T. brumpti*, a strong ‘dorsal tilt’ of the MCII facet towards the MCIII facet. In the dorsomedial corner there is small sharp area of articulation with MC IV. On the palmar surface of the capitate proximal to the head there is a backward J shaped facet for the os centrale/scaphoid articulation. A long, proxiomodistally oriented facet for the hamate runs proximally into the head of the hamate bone on the dorsomedial side of the medial surface of the capitate. In *T. brumpti* this facet is significantly narrower than it is in *Papio hamadryas anubis*. Palmar to the hamate facet is a deeply excavated, concave, area for the interosseous ligament connecting the hamate and capitate.

Figure 5.7. Left Capitate (a) and (b)

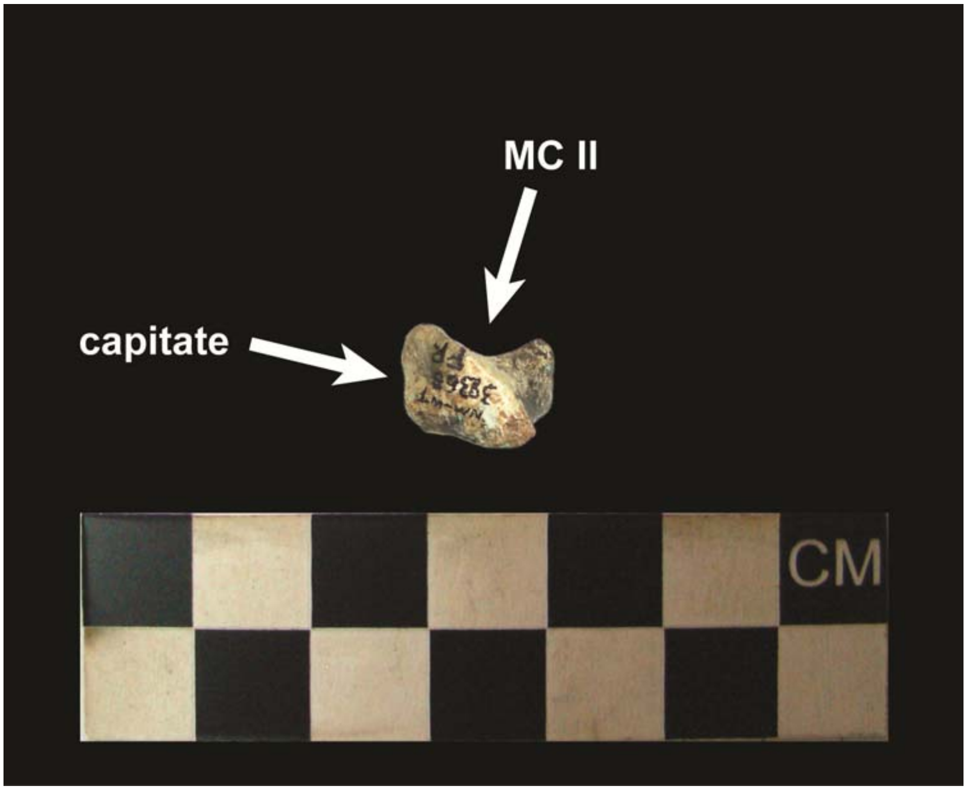




Trapezoid

The trapezoid is a parallelogram-shaped bone, when viewed dorsally, with an excavated curvature on its distal end for articulation with the second metacarpal. The trapezoid is oriented in the carpus obliquely along its long axis. The dorsal surface is rough and at the medial edge is a small incision is seen for articulation with the capitate (Figure 5.8). The distal surface is entirely devoted to articulation with the second metacarpal and is a large half moon shaped surface with a marked crest bisecting the articulation bilaterally. On the lateral surface there is a small smooth facet for articulation with the trapezium and a smooth and triangular facet on proximal surface for articulation with os centrale.

Figure 5.8. Left Trapezoid



Trapezium

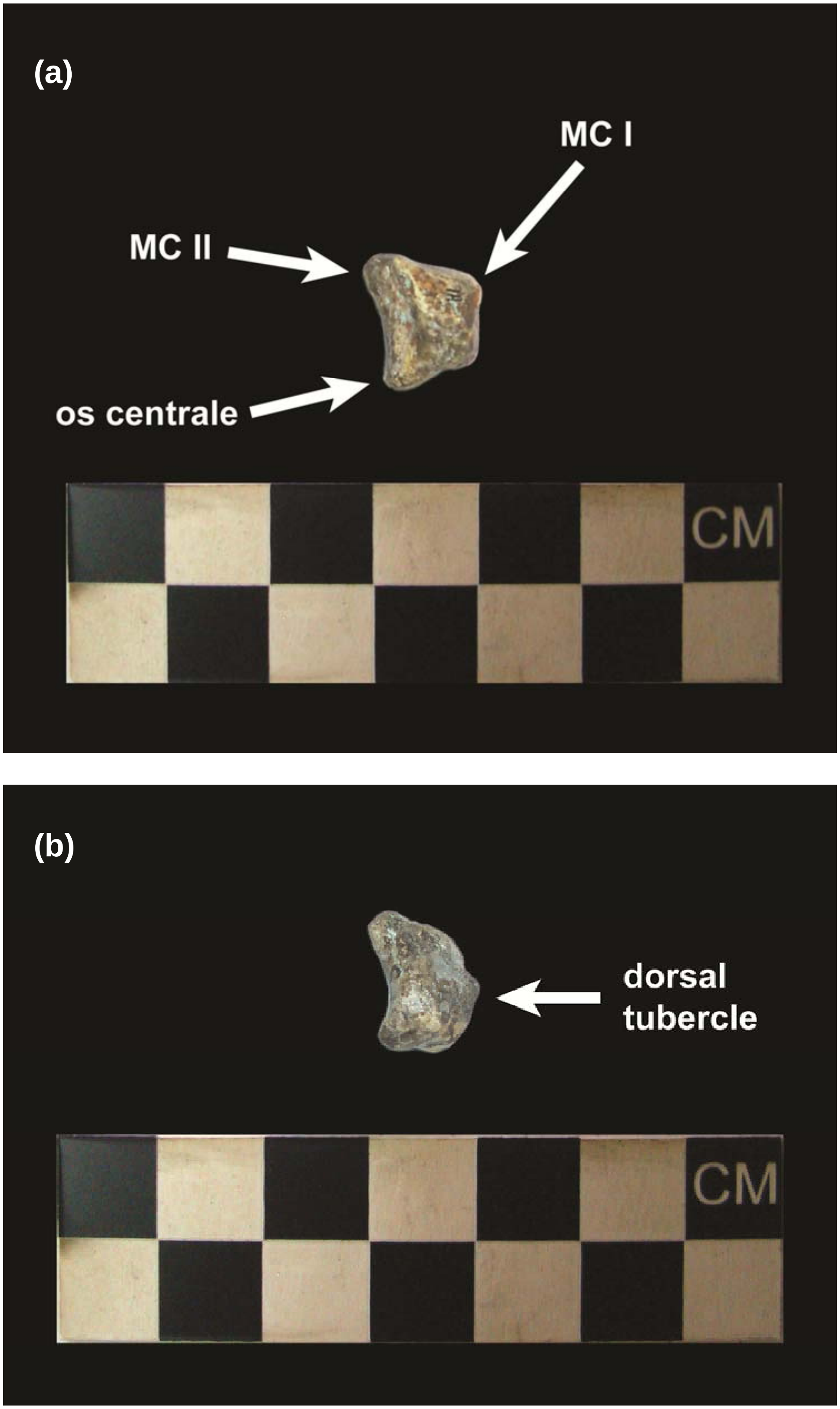
The trapezium is a stout bone with a sellar joint distally for articulation with the first metacarpal. It has a crescent shaped medial surface for articulation with the trapezoid and the second metacarpal. On the proximal surface of the trapezium is a medially placed facet for articulation with the os centrale, which is rectangular in shape. The os centrale facet extends dorsally as it reaches the medial border of the bone. On the lateral margin of the proximal surface is a smaller facet for articulation with the scaphoid tubercle. According to Beard et al. (1986) these proximal facets of the trapezium are separated by a low bony ridge, but this is not seen in KNM-WT 39368. The facet for the os centrale is expanded and accounts for over half of the proximal surface of the trapezium. The dorsal surface of the trapezium is non-articular but is marked with a large dorsal tubercle (Figure 5.9), whose presence is variable in cercopithecines, but as been documented in some *Papio* specimens (Blue, 2002).

The crescent shaped medial surface of the trapezium has three facets. Proximal most is the small facet for the articulation with the os centrale, distal to that is the facet for the trapezoid and distal-most is a small facet for articulation with the second metacarpal.

As the bone courses palmarly from the MCII facet to the MCI facet on the palmar surface a well defined groove, or notch is seen. This was noted by Lewis (Lewis, 1977) as possibly the origin of the anterior oblique carpometacarpal ligament. As in all primates the trapezium-MCI joint is sellar in morphology (Lewis, 1977, 1989). This facet is concave mediolaterally and convex dorsopalmarly (Beard et al., 1986). The facet for MCI extends across 80% of the palmar surface. As is typical of cercopithecids, the facet cannot be viewed dorsally (Beard et al., 1986).

In overall shape, the trapezium is longer proximodistally (13 mm) than mediolaterally (10.9 mm) and the base of the trapezium is slightly larger (10.48 mm) than the distal surface (9.52mm). This shape is most similar to *Chlorocebus patas* according to Blue (Blue, 2002) and in *Papio* is slightly different with the proximal and distal surfaces being more even.

Figure 5.9. Right Trapezium. a. Palmar View. Medial to the Left b. Dorsal View



Metacarpals

There are 15 associated *T. brumpti* metacarpals which are comprised by left MC I-V from L865-2 and complete left and right MC I-V from KNM-WT 39368. However, in the latter, the right hand remains *in situ.* Both specimens were described in detail by Jablonski (Jablonski, 1986, 2002b) and will only be summarized here as it relates to the functional morphology of the *T. brumpti* post cranium. In general morphology, the metacarpals of *T. brumpti* are similar in their relative proportions to *T. gelada* and *T.oswaldi* and in morphology to both *T. gelada* and *T.oswaldi* as well as other terrestrial papionins including *Papio*.

All the metacarpals are stout, straight, and robust as is typical of terrestrial species (Jolly, 1970b, a; Etter, 1973; Jablonski, 1986), and, in fact, they are among the stoutest of all cercopithecines except *M. thibetana* (Guthrie and Frost, 2010) (Figure 5.10, Index 24). The MCI is long in comparison to the other digits, an unusual trait, which characterizes all *Theropithecus* species, but is different from all other cercopithecids. Functionally, this arrangement indicates an adaptation for strong and precise pincer-like movements, which in the living species are related to foraging.

Figure 5.10. Left MC I and MC II of *Theropithecus brumpti* (KNM-WT 39368) compared to left MC I and MC II *Papio hamadryas anubis* (OM 5061). Note relatively long length of MC I in *T.brumpti*.

The remaining metacarpals are all relatively robust bones with rounded mediolaterally compressed heads which narrow slightly dorsally, although MCIII is slightly broader (Figure 5.11., Index 23). These are all traits typical of non-hominoid terrestrial primates (Harrison, 1989). Unfortunately, it does not appear that there are many features of the metacarpals, except for relative length, that are diagnostic of digitgrady or palmigrady (Patel, 2010). *T. brumpti*, with the exception of MCI, has metacarpals of similar length to other *Theropithecus* species and *Papio*, suggesting digitigrady.

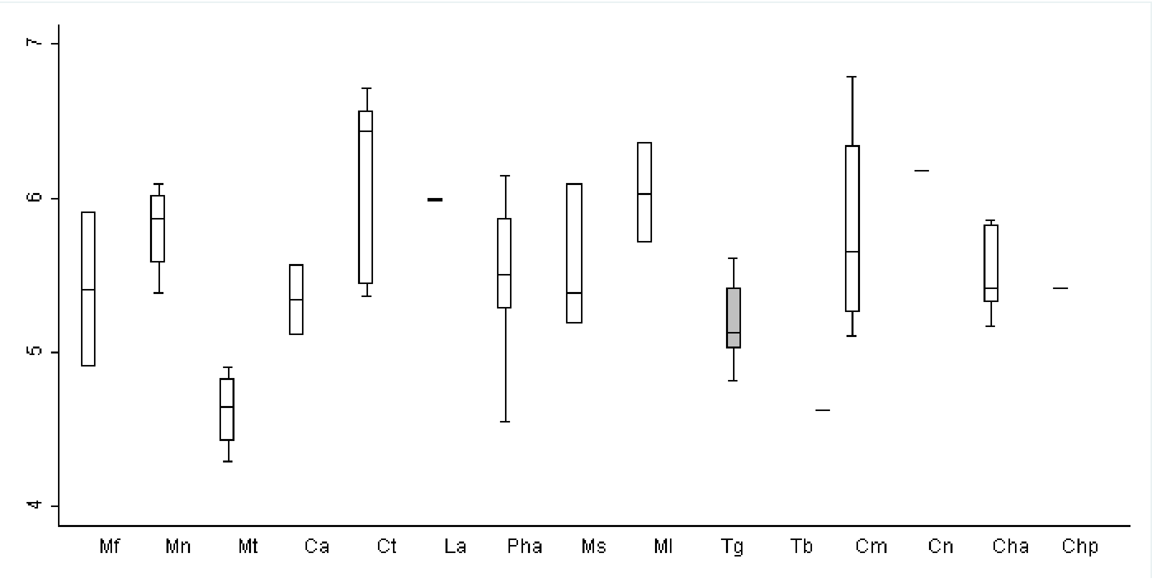
Phalanges

There are 23 associated *T. brumpti* phalanges. L 865-2 has all five proximal phalanges and three intermediate. KNM-WT 39368 (left hand only; right is still preserved *in situ*) has all five proximal, four intermediate and five distal forming a complete hand. As with the metacarpals each of these elements were described by

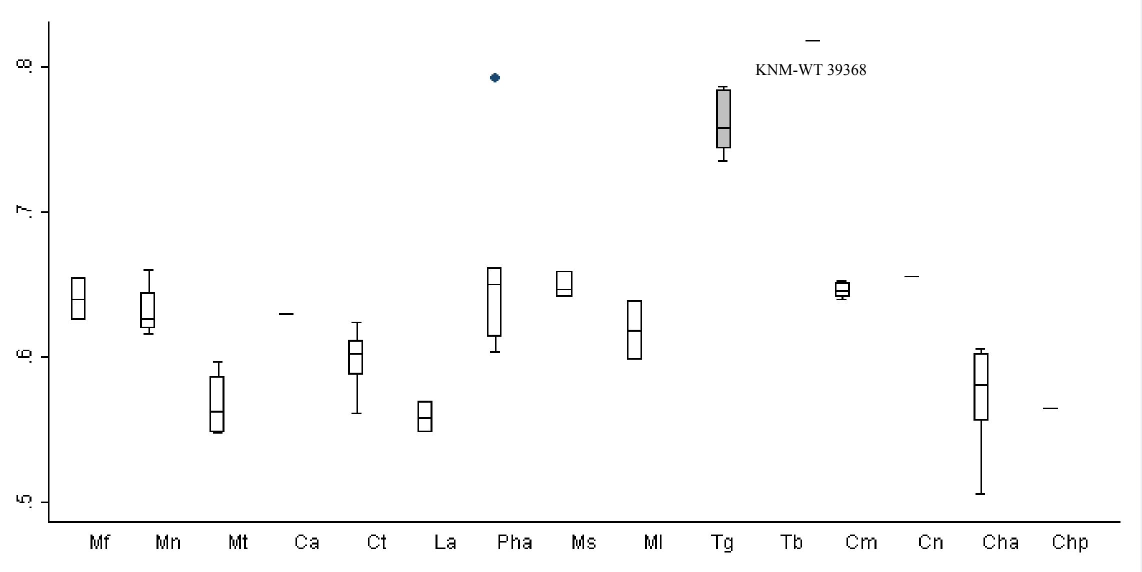
Jablonksi (Jablonski, 1986, 2002b), who found them all to be similar to *T. gelada* in morphology. Guthrie and Frost (2010) found that the proximal phalanges are all short, stout bones in extinct *Theropithecus* species. They are, in fact the shortest and the stoutest of all cercopithecines, although the phalanx robusticity index proved to be highly allometric (see Tabole 3.6). Terrestrial cercopithecids have relatively short proximal phalanges which act to increases the strength of the digits and may perhaps lighten the distal part of the limb enabling more efficient terrestrial locomotion (Jolly, 1972; Harrison, 1989; Patel, 2010). Such short, stubby fingers would preclude arboreal quadrupedalism, in fact modern geladas (which have identical hand structures) are poor tree climbers (Nina Jablonski, Personal Communication.)

Figure 5.11. Metacarpal Indices

a. Metacarpal III Robusticity (Index 23)



b. Relative Length of MC1 (Index 24)



Conclusions

The carpal elements were described herein and preliminary functional observations were made. Overall, the carpal bones are remarkably similar within cercopithecines. However, in the *T. brumpti* carpal suite there are a few features that appear to suggest terrestriality: 1)a slightly medially expanded head of the capitate, 2) flattening on the distal portion of the triquetral facet of the hamate (thereby liming range of exension) and 3) a hamate facet on the triquetral that is that is relatively long compared to width. Lastly, Whitehead (Whitehead, 1993) suggests a few features that may signal digitigrade locomotion which are present in *T. brumpti*: a lack of distinction between the MCIV facet and MCV facet on the distal hamate and large and hooked hamate hamulus. Among the extant primates, only the relatively terrestrial species adopt digitigrady, palmigrady (palm contacting the ground while walking) is associated with arboreal quadrupedalism (Patel, 2010).

The hand of *Theropithecus brumpti* is characterized by robust metacarpals and phalanges that are associated with a terrestrial habits (Guthrie and Frost, 2010; Jablonski 1986 and Jablonski et al., 2002). *T. brumpti* along with *T. oswaldi* have the most robust hand elements of all primates studied (Guthrie and Frost, 2010). An alternative implication for such stout and robust hand bones could be adaptation to cold habitats, following Allen's Rule, which may partially explain the very short and stout hand elements of *Macaca thibetana*. However, *Theropithecus* fossils are not known from such climates and thus their relatively stout and robust hand bones are, most likely, an adaption to terrestrial locomotion. This is of particular importance to the task in this dissertation, although subtle differences in the morophology of the hand and wrist are not well understood in cercopithecines, gross difference in size and shape are fairly consistent. In fact, phalanges and metacarpals should reflect the substrate more than other elements as they are in actual contact with the substrate. These facts, in combination with *T. brumpti*'s very large size, combine to make arboreality untenable. Therefore, the aspects of limb flexibility observed in other parts of the skeleton are unlikely to be due to arboreal substrate preference.

Mapped onto this terrestrial architecture of the hand, *T. brumpti* has a adaptations for precision grasping in the form of a thumb that is also robust, but nonetheless longer in comparison to the other digits than is the case in all other cercopithecids. This combination of manual features is striking. The proportionally long thumb is an adaption for manual foraging as often described in this genus. The presence of the structurally modified hand in *Theropithecus brumpti* has implications for understanding its ecology. Capabilities for precise opposition between the thumb and forefinger in *T. brumpti* demonstrated that the food harvesting and processing anatomy that distinguishes extant *T. gelada* was present in this early representative of the genus. This does not imply similar diets, however. Importantly, microwear studies have shown that *T. brumpti* was eating different foods than either *T. oswaldi* or *T. gelada* (Teaford, 1993). Rather powerful precision grips that permitted them to efficiently harvest and manipulate even the smallest foodstuffs. This anatomy should be considered in conjunction with the forelimb and hindlimb data and is discussed in Chapter VII.

CHAPTER VI

HINDLIMB

The forelimb is recognized as being more informative of modes of locomotion and manipulation than the hindlimb in cercopithecines (Napier and Napier, 1967). Nonetheless, several features of the cercopithecine hindlimb have been found to vary among taxa with different locomotor and substrate preferences (e.g. Jolly, 1972; Maier, 1972; Harrison, 1989; Frost and Delson, 2002). Additionally, although the hindlimb is generally considered to function mainly as propulsive thrust in locomotion, in *Theropithecus* it has some distinct features, which may relate to specific feeding and foraging behaviors (Krentz, 1993b; Jablonski, 2002b). Therefore, features of the hindlimb may be useful not only for estimating locomotor behavior and substrate preference, but also aid in identification of *Theropithecus* in the fossil record.

Only one study has looked specifically at the functional morphology of the hindlimb of *Theropithecus brumpti,* but this was done only with unassociated material from the Shungura Formation (Krentz, 1993b). Krentz's study suggested that *T. brumpti* possessed some features associated with extant *T. gelada* that are associated with its unique form of locomotion such as lateral angulation of the femur, strong anterior convexity and greater flexibility of the foot (Krentz 1993). These have been suggested to be related to feeding behaviors such as bipedal shuffling (Wrangham, 1980).

Jablonski et al. (2002) and Krentz (1993b) both describe two distinct features of the distal tibia in *Theropithecus brumpti*, the angulation of the medial malleolus and a prominent notch for the passage of the tendon of *M. tibialis posterior.* These features are thought to be related to greater flexibility and inversion of the foot during foraging and locomotion (Maier, 1972). If these features are indeed related to the unique shuffling behavior, then their presence in both *T. gelada* and *T. brumpti* could imply that this habit may be primitive for the genus.

The foot of *T. brumpti* is essentially undescribed. Krentz (1993) mentions the pedal material in passing stating that there is little variation, other than size, in the morphology of the astragalus or calcaneus and that they are similar to those of other terrestrial monkeys. He concludes that the morphology and function of the foot of *Theropithecus* varies little among species and has changed very little over time. Jolly has described pedal material of *T. oswaldi* (Jolly, 1972) and found that terrestrial animals had shorter and stouter proximal and middle phalanges in digits II-V (see Chapter V). Further, he found that those of *T. oswaldi* were stouter than other terrestrial primates. Jolly also discussed the relative size of the hallux and the muscles that power its movements and degree of abductability. These are larger in arboreal monkeys and relatively small in terrestrial monkeys. Unfortunately, the first metatarsal is not known from *T. brumpti*, neither is the first cuneiform which articulates with the hallux, so this trait could not be analyzed.

Associated hindlimb material of *T. brumpti* is now available (Jablonski, 2002b; Jablonski and Leakey, 2008; Gilbert et al., 2011) for analysis, which will be the focus of this chapter. As more material is found there is some confusion over specific morphological details of the hindlimb anatomy of *Theropithecus brumpti*. In Gilbert et al.'s (Gilbert et al., 2011) recent description of a partial skeleton from the Tugen Hills, aspects of the femur and tibia were described that differ from those previously published for the species. He concluded that *T. brumpti* was a terrestrial quadruped but was not clear about the degree of shuffling behavior and did not observe some of the traits historically used to recognize *T. brumpti*. This study is the first comprehensive functional analysis of *T. brumpti* hindlimb material (Table 6.1), and aims to shed light on locomotion and foraging behavior.

Table 6.1. *Theropithecus brumpti* hindlimb material used in study

	FEMUR	TIBIA	FIBULA	TARSALS
KNM-WT 39368		X	X	
KNM-WT 17554				X
KNM-ER 3119	X			
KNM-TH 46700	X	X		X
L 865-2				X

Hindlimb Material Results

Proximal Femur

Of the postcranial material associated diagnostic *Theropithecus brumpti* cranial remains there are 3 specimens which preserve proximal femoral elements: KNM-TH 46700, a complete right femur, and two fragmentary proximal elements KNM-ER 3084 and 3119 (Figure 6.1.). However, these latter two were too damaged to be measured, although qualitative variables were noted.

The femoral head in the associated *T. brumpti* material is round and as the femoral head shape index shows (Figure 6.2., Index 26), there is only modest variation in head shape in cercopithecines. *Mandrillus sphinx* and *Chlorocebus patas* have the most spherical heads (index closest to 100); however variation exists within these species. It appears that the femoral head of *T. brumpti* may be slightly wider than other *Theropithecus* species.

As Figure 6.1. shows the fovea capitis appears ovoid and horizontal. Gilbert et al. (Gilbert et al., 2011) notes that the fovea capitis in *T. brumpti* appears relatively shallow compared to *T. oswaldi* and *Papio.* Krentz also notes that *T. brumpti*, as well as *T. oswaldi*, have a relatively elongated fovea capitis relative to *T. gelada* (Krentz, 1993b). While this trait was not quantified, qualitatively the fovea capitis of *T. brumpti* did not seem particularly elongated. However, it does seem that this trait varies and some clearly round foveae were observed in modern *Theropithecus gelada*.

There are two aspects of the femoral neck in *Theropithecus* that are often discussed in the literature, 1) the extent of the articular surface onto the femoral neck (implying some lateral rotation of the thigh) and 2) the length and thickness of the neck itself (Krentz, 1993b; Frost, 2007). In these features *T. brumpti* conforms to the genus pattern of having an articular surface that extends onto femoral neck and a neck that is relatively short, broad, and flattened in the AP plane. The neck of the femur is also set at a low angle relative to the femoral shaft which would facilitate movements in the parasagittal place (Harrison, 1989).

Interestingly, *Theropithecus brumpti* has a relatively large maximum proximal femoral breadth, even though the femoral neck is relatively short. The proximal breadth of the femur appears to be relatively wider in the fossil *Theropithecus* species and *Macaca thibetana*. In the case of the latter species, this is likely due to its short and stout limbs, possibly related to Allen's rule. Species associated with more arboreal substrates (e.g. *Lophocebus albigena, Cercopithecus mitis*) have relatively narrower proximal breadths, ostensibly related to the shorter neck length. However, *Theropithecus* seems to create a relatively broad proximal femoral breadth by having robust greater trochanter, as neck length is relatively short.

In *T. brumpti* the greater trochanter projects well above (proximal or superior to) the level of the femoral head (Figure 6.2., Index 28), placing *T. brumpti* within the range of the other *Theropithecus* species and *Papio*. The *Theropithecus* species and *Papio* have greater trochanters that extend considerably proximal to the femoral head than is the case in other cercopithecines. Overall height of the greater trochanter does seem to separate *Theropithecus* from other cercopithecines. Large size and superior projection of greater trochanter is related to terrestrial quadrupedalism (Jolly, 1972). The longer greater trochanter produces longer lever arm for the *mm. gluteus minimus* and *medius* and therefore more power per stroke as well as contributing to greater stability at the hip joint (Fleagle, 1998). A large greater trochanter along with the anterio-posteriorly flattened neck suggests concentration of movement within the parasagittal plane (Harrison, 1989).

There is a large rugosity of the anterior surface of the greater trochanter in *T. brumpti* of for the insertion of *m. gluteus minimus,* and there is a relatively deep degree of excavation on the medial surface of the greater trochanter and gluteal fossa for the insertions of *mm. obturator internus* and *externus* (Birchette, 1982) and a prominent intertrochanteric crest as well. The anatomy of the greater trochanter is said to distinguish *Theropithecus brumpti* from other *Theropithecus* species in the vertical orientation of the tip of the greater trochanter (Krentz, 1993b), however, this does not seem to be the case among the associated material evaluated here. The tip appears to be medially projecting on the same fashion as other *Theropithecus* species (Gilbert et al., 2011).

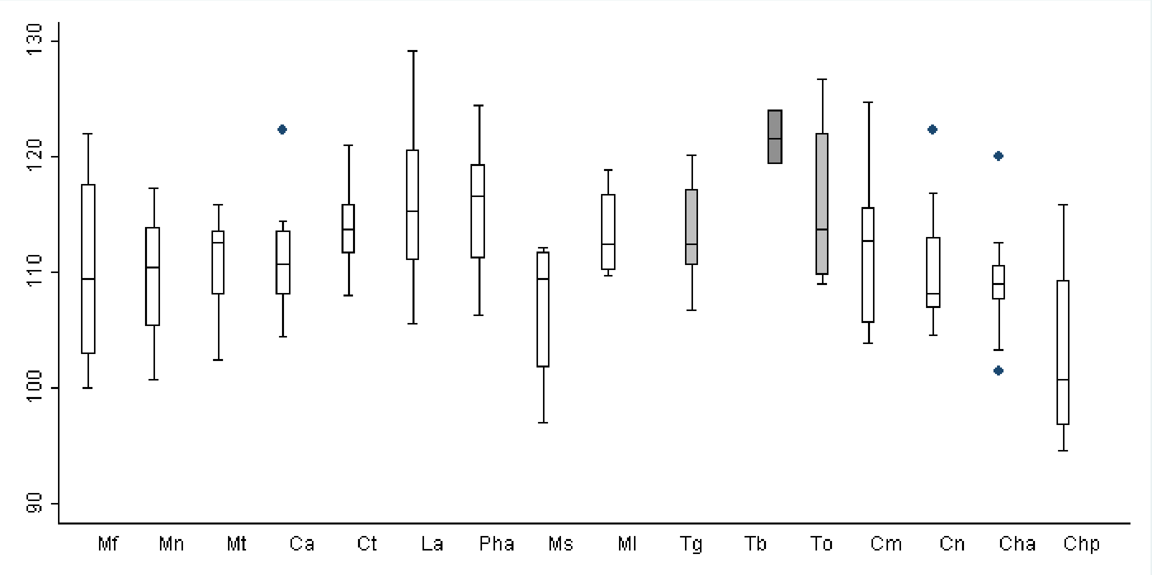
The orientation of the lesser trochanter is generally proximally oriented in all cursorial taxa (Bloch and Boyer, 2006). Figure 6.2. Index 29 shows the relative medial extension of the lesser trochanter. *T. brumpti* and the other *Theropithecus* species do not have very medially projecting lesser trochanters. As Gilbert and colleagues describe, the lesser trochanter in *T. brumpti* is oriented more posteriorly (Gilbert et al., 2011).

Interestingly, as in the forelimb, many of these distinct features are associated with arboreality in other primates especially in the femoral neck in its shortness and lateral excursion of the articular surface. Further, in terrestrial quadrupeds the femoral neck is usually long to facilitate stabilization of the hip joint (Fleagle, 1999). In *Theropithecus* the necks are shorter, relatively flattened and thick; all traits are usually associated with climbers and leapers. However, the short, anteriorly curved femur precludes possibility of leaping. Further, the morphology of the distal femur does not suggest climbing and the relative size of the greater trochanter to significantly limit the flexibility of the hip and the ability to abduct (Jolly, 1972).

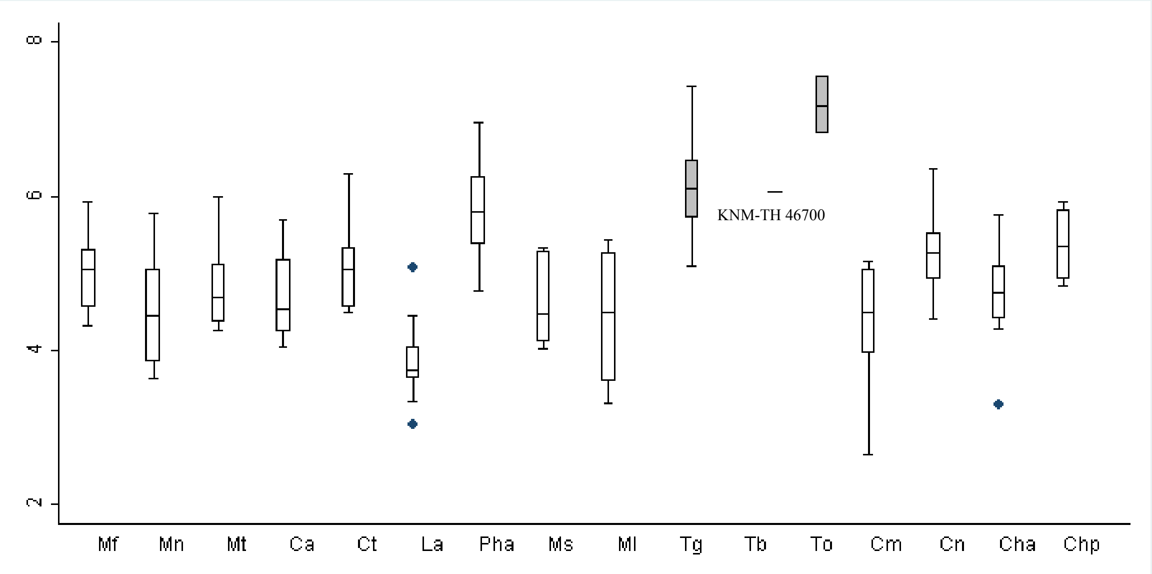
Figure 6.1. Proximal Femur**.** Anterior view of complete right femur of KNM TH 46700 (a), medial view of the greater tuberosity of KNM-ER 3084 (b) and superior view of KNM-ER 3119 (c)

Figure 6.2. Proximal Femoral Indices

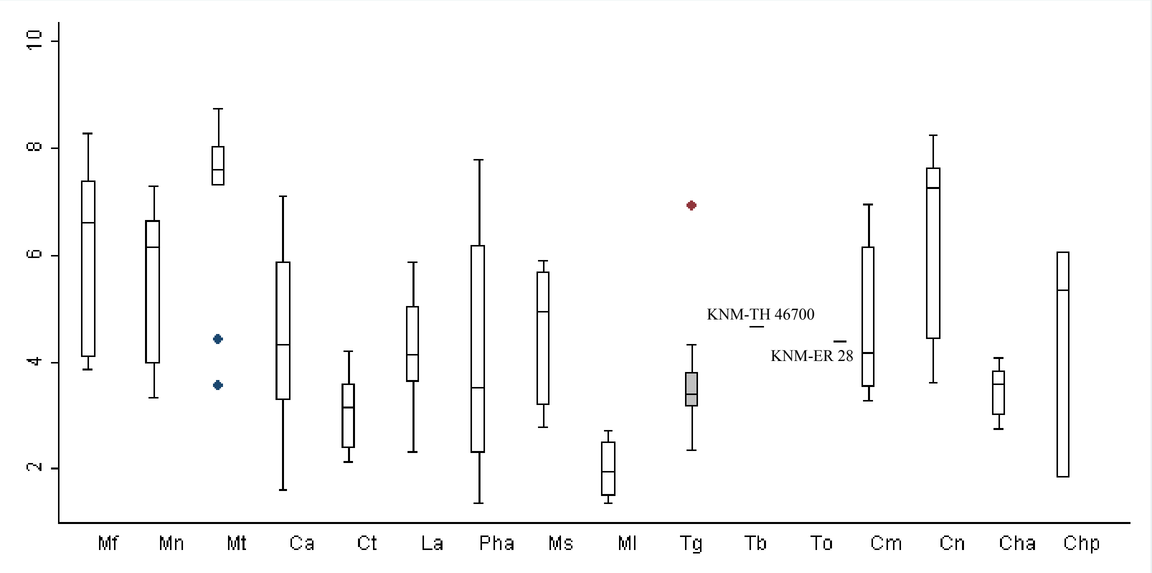
a. Femoral Head Shape Index (Index 26)



b. Greater Trochanter Projection (Index 28)



c. Lesser Trochanter Length Index (Index 29)



Distal Femur

The shaft of the femur was not analyzed quantitatively. The only available shaft is that of KNM TH 46700 (Figure 6.3.). The anatomy of the shaft was described by Gilbert (Gilbert et al., 2011), who found it to be strongly anteroposteriorly bowed, and generally similar to that of *T. oswaldi* (Jolly, 1972). The overall shape of the distal femur, as measured by the shape index (Figure 6.4., Index 30) varies little among cercopithecines, with only a few outliers. *Theropithecus brumpti* is typical. The femoral groove index (Figure 6.4.,Index 31) highlights a somewhat unusual feature, that the groove is deeper in *T. brumpti* than other *Theropithecus* species and deeper than other papionins. The only comparative species to also have this feature is *M. thibetana*. The function of this feature is unclear, but could be related to a habitually strongly flexed knee.

The patellar groove shape index (Figure 6.4., Index 32) is uninformative for cercopithecines, and most group together. The patellar sulcus is relatively narrow, the lips of the patellar groove are well developed, and the lateral lip is more prominent than the medial. These traits are all shared with *Lophocebus* and *Papio* (Fleagle and McGraw, 2002; Gilbert et al., 2011). In papionins prominence of the medial lip is associated with vertical climbing behaviors (Fleagle and McGraw, 2002) and therefore *T. brumpti* most likely did not engage in this behavior, unlike extant mandrills.

Distally, the femoral condyles in *T. brumpti*, and *Theropithecus* as a genus, are deep and highly asymmetrical. This pattern is reflected in several indices. The first (Figure 6.4., Index 33) looks at the relative depth or anteriorposterior dimension of the condyles. The medial condyle is relatively deeper than the lateral in *T. brumpti, Theropithecus* generally, and in other terrestrial papionins including *Papio hamadryas anubis* and *Macaca thibetana.* The femoral condyles are also asymmetrical in proximo-distal length (i.e. height) (Figure 6.4., Index 34), with the lateral condyle being longer than the medial. Finally, they are asymmetrical in medio-lateral width as well (Figure 6.4., Index 35) with a relatively wide medial condyle.

In summary, *Theropithecus*, including *T. brumpti*, is characterized by relatively deep and wide medial condyles and relatively long lateral condyles. In Elton's (2002) reappraisal of the locomotor behavior of *T. oswaldi* she described features of the femoral condyles that she found to be the most informative in distinguishing among taxa of different habitat and locomotor categories. She found that a medial condyle that is deeper and wider than the lateral, as seen in *T. brumpti*, is associated with 'open terrestrial' habitats. Furthermore, the stout presentation of the medial condyle relative to the lateral is associated with an "increased length in the moment arm for the *m. quadriceps femoris* with powerful extension of the knee which is important in terrestrial travel" (Elton 2002, pg. 265).

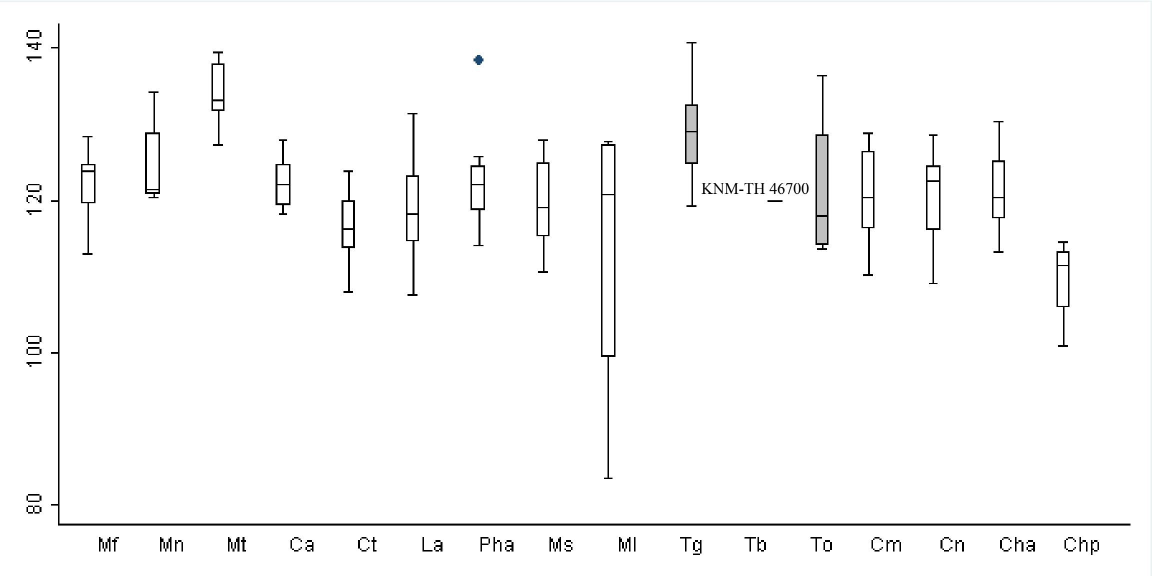
Theropithecus has been described as having a "reverse" carrying angle of the femur (Krentz, 1993b). This is a trait that has proven difficult to define and to quantify. According to Krentz (Krentz, 1993b) this is produced by the femoral shaft angling laterally onto the condyles (see Krentz, 1993: figure 14.8, p. 393). Gilbert (Gilbert et al., 2011) did not observe this lateral excursion in KNM-TH 46700 and found the angling of the shaft to be within the range of variation of other large bodied terrestrial papionins (see Gilbert et al., 2011: figure 9, p. 358). However, it should be noted that the distal extension of the lateral condyle, as seen in KNM-TH 46700 would produce lateral excursion in a different sense, lateral excursion on the articulation with the tibia. This would produce a hindlimb that would effectively be splayed laterally, but, apparently, in a different manner than Krentz described. As described above, *Theropithecus brumpti* does have more distal projection in the lateral condyle than other papionins (Figure 6.4., Index 34).

Krentz (1993) has attributed this morphology as a byproduct not of locomotion but rather for sitting during long periods of food gathering with hips splayed laterally. Therefore, it does seem that the unusual morphology in the distal femur has been present in the *Theropithecus* lineage since *T. brumpti* diverged from other *Theropithecus* species. However, it is not possible to tell if this same sitting and shuffling behavior was utilized. It could also be that this morphology, originally evolved for some other purpose of use in a woodland environment was co-opted by the modern form for splaying of the hindlimb during foraging and shuffling in a grassland environment.

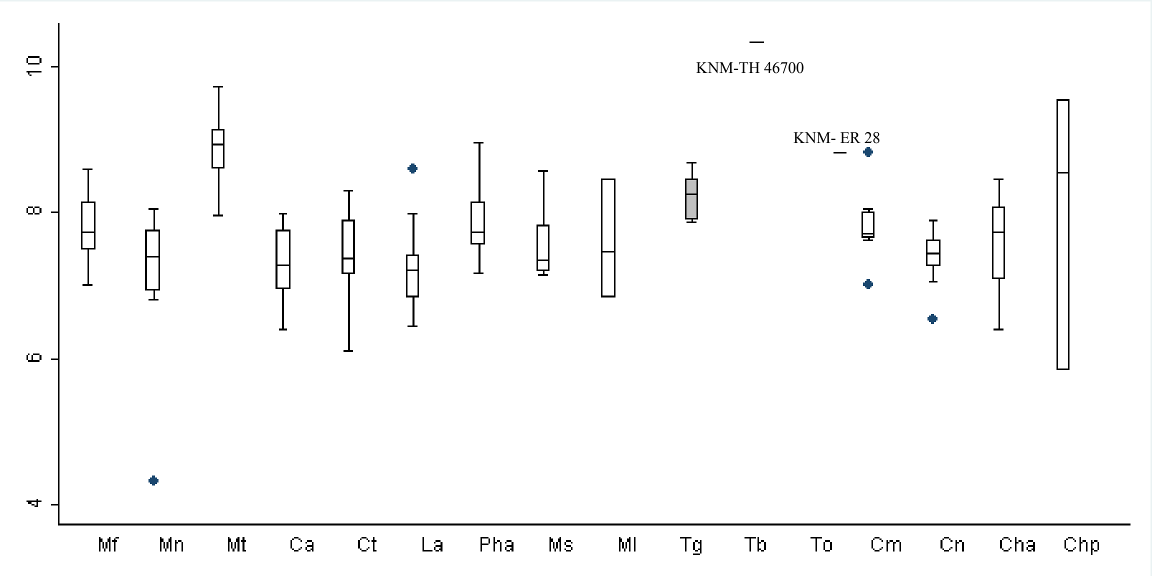
Figure 6.3. Distal Femur**.**Posterior (a) and anterior (b) views of KNM-TH 46700

Figure 6.4. Distal Femur Indices

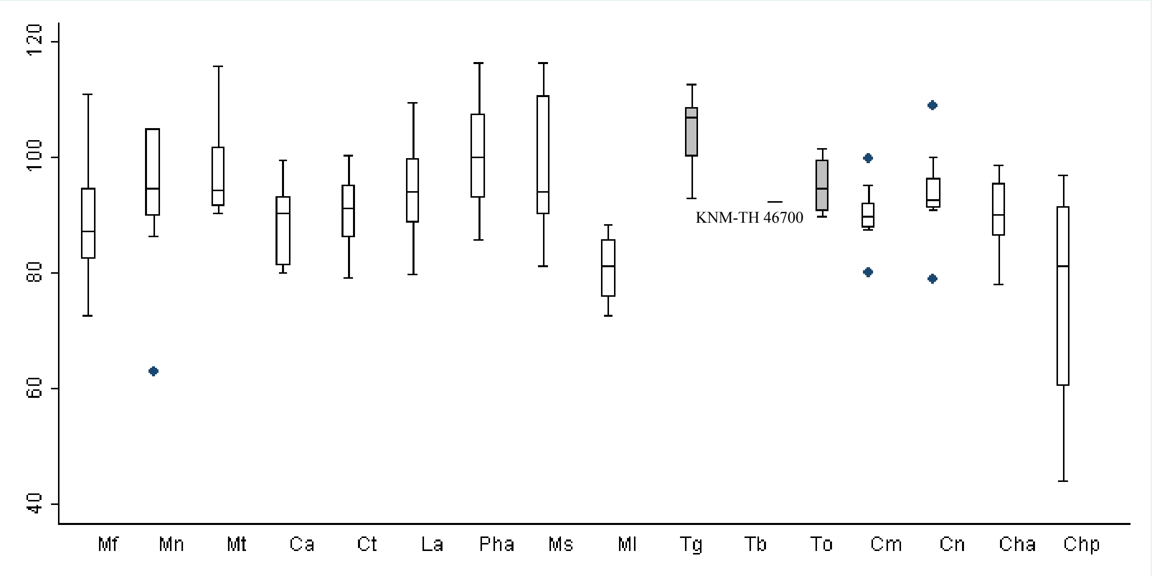
a. Femoral Distal Shape Index (Index 30)



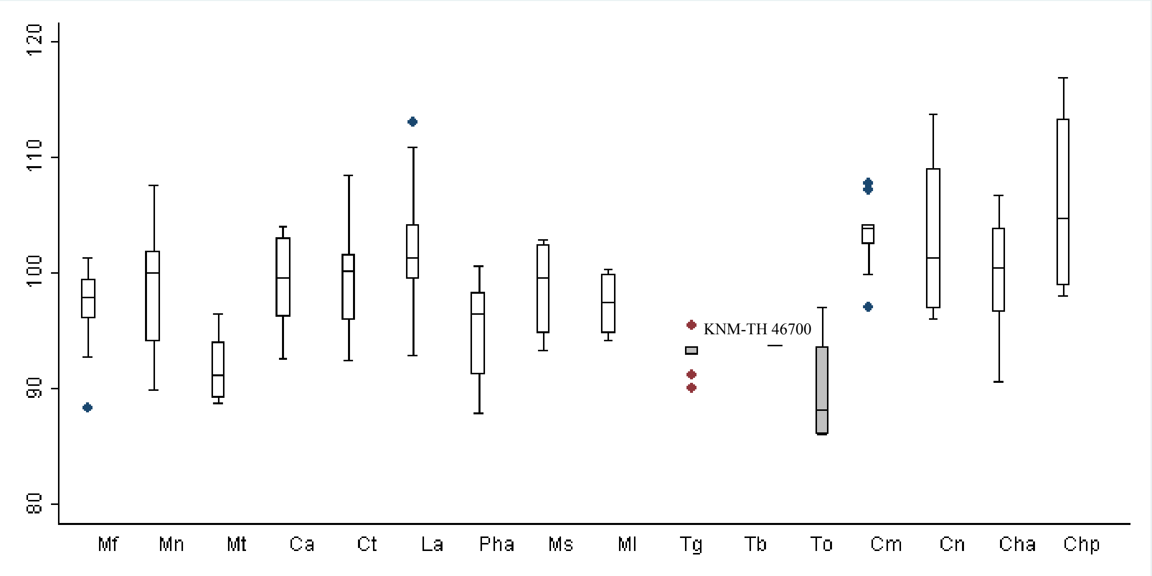
b. Femoral Groove Index (Index 31)



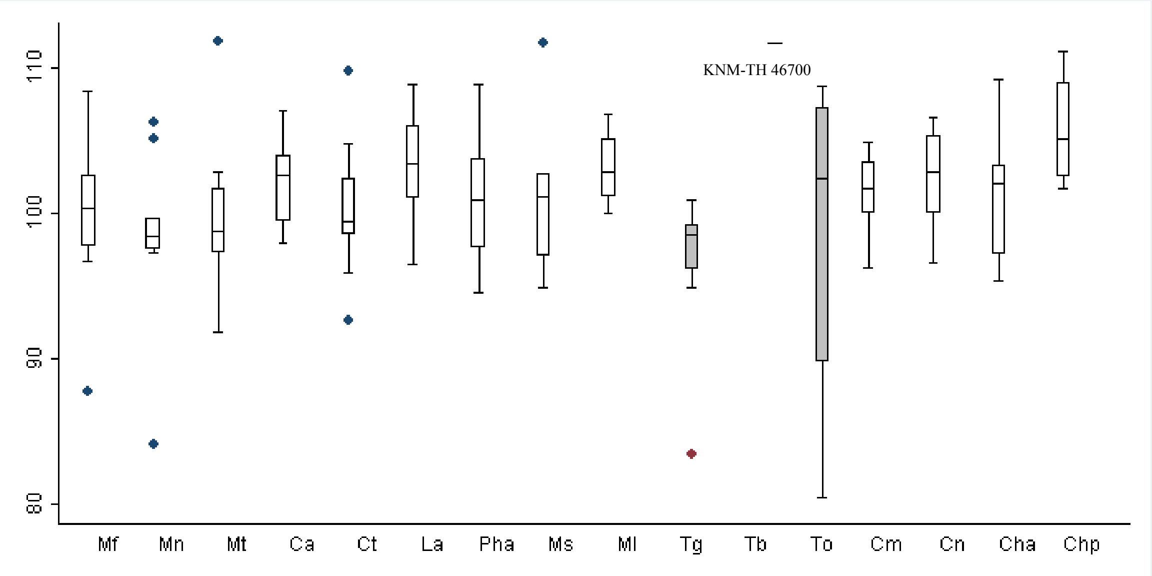
c. Patellar Groove Shape Index (Index 32)



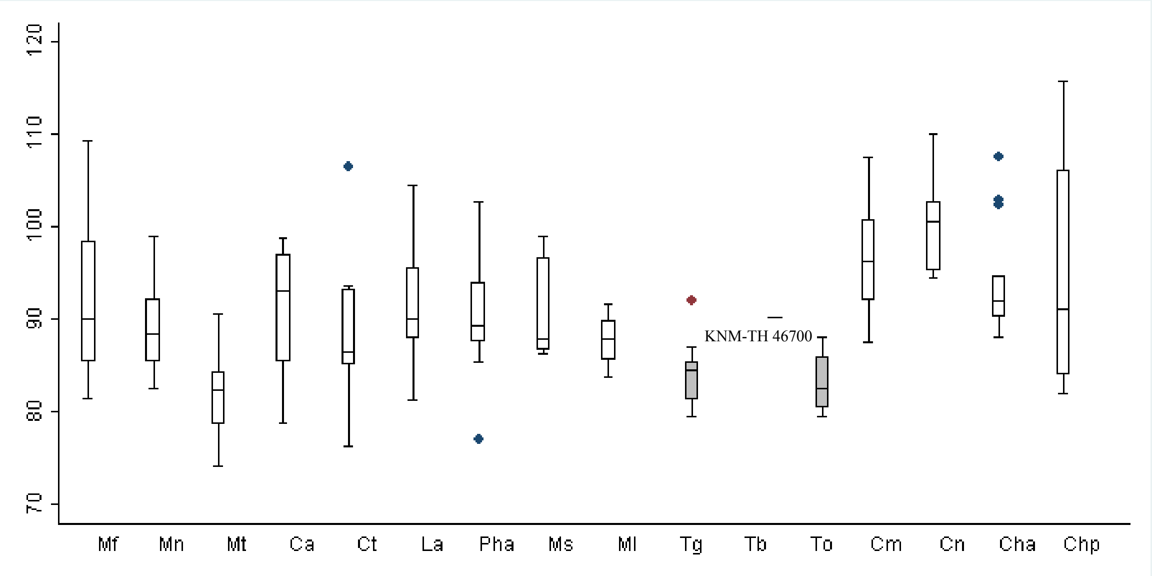
d. Femoral Condyle Depth Index (Index 33)



e. Femoral Condyle Length Index (Index 34)



f. Femoral Condyle Width Index (Index 35)



Tibia

Of the associated *Theropithecus brumpti* material there are 2 specimens with tibiae. These include the complete and reconstructed right tibia KNM-WT 39368 EZ and the complete right along with portions of the left from KNM-TH 46700 (Figure 6.5.)

General anatomy of the tibia is conservative within and among primates and the differences in the morphology of the tibia of cercopithecoids is minimal (Turley et al., 2011). The Tibial Proximal End Shape Index (Figure 6.6., Index 36) captures the variation in gross proximal tibial shape. Macaques appear to have relatively broad proximal ends while some of the guenons have anterio-posteriorly longer proximal ends. *Theropithecus* as a genus is intermediate in this trait.

The relative sizes of the tibial condyles differ in *Theropithecus* reflecting the influence of unequal femoral condyles. While the widths are similar across cercopithecines, fossil *Theropithecus* is distinct in having short lateral condyles (Figure 6.6., Index 37 and 38). Furthermore, the lateral condyle is more proximally positioned than the medial and the tubercle for the attachment of the cruciate ligaments is strongly raised.

Overall tibial shaft shape was examined qualitatively. The shape of KNM- WT 39368 is hard to discern because the shaft has been crushed and reconstructed. However, that of KNM-TH 46700 well preserved, and it is strongly laterally bowed. The tibial shaft of KNM-TH 46700 is also elongated in the anterio-posterior direction similar to *Papio* and *Lophocebus* (Fleagle and McGraw, 2002). It is hard to know if this bowing always characterizes *T. brumpti*, but similar extreme bowing is seen in some *T. oswaldi* specimens, such as MCK II from upper Bed II Olduvai gorge (ca. 1.5 Ma) and the possible *T. oswaldi darti* specimen AL431-1o from the Denen Dora Member, Hadar (3.2 Ma).

As in the femur, traits that have been used to identify the distal tibiae of *Theropithecus* are traits associated with arboreal primates. Krentz (1993b) notes that *Theropithecus* and *Colobus* both share a medial malleolus that is angled medially and a pronounced sulcus for the tendon of *m. tibialis posterior*. Jablonski *et al.* (Jablonski, 2002b) also found these features in the *Theropithecus brumpti* skeleton KNM-WT 39368. These features have been interpreted as indicating more flexibility of the talo-crural joint than in other cercopithecines and perhaps related to the inversion of the foot of *Theropithecus* while feeding (Maier 1972).

However, the medial malleolus in *T. brumpti* does not appear to be angled at 45 degree as described by Krentz (Krentz, 1993b). Agreeing with Gilbert's assessment, the level of angulation of the medial malleolus of KNM-TH 46700 appears similar to *Papio* and that other *Theropithecus* species appear to have only slightly more angulation (Gilbert et al., 2011). Furthermore, while there is a distinct groove on the distal tibia for the tendons of the long digital flexors and *m. tibialis posterior,* this does not seem to be distinct for *T. brumpti* or *Theropithecus* in general, but rather a fairly distinct and large groove appears to be present on most cercopithecid distal tibiae.

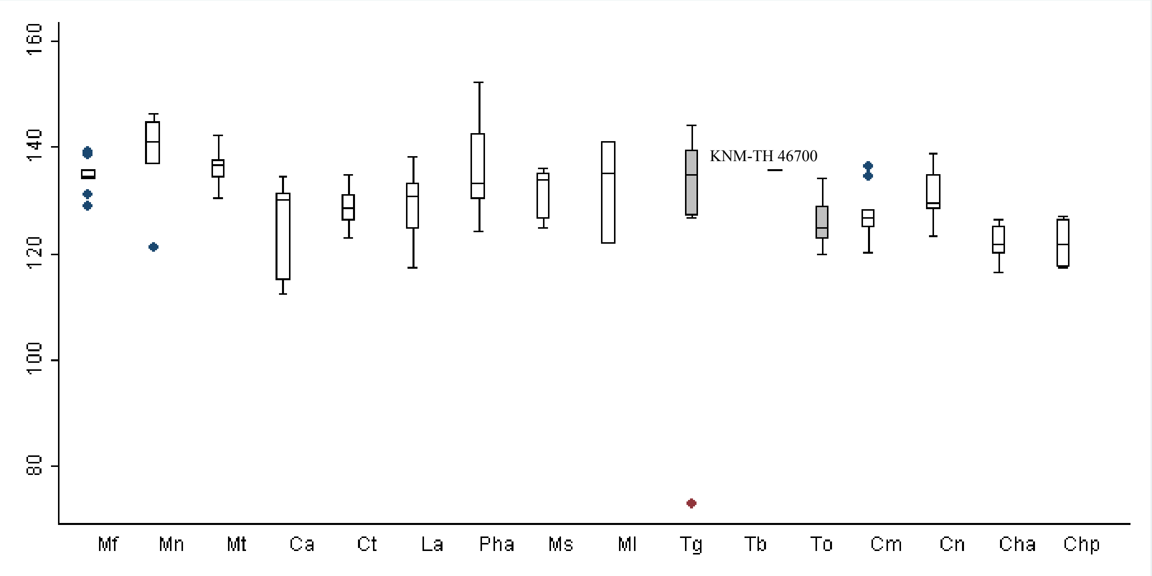
In terms of overall shape, the length of the medial malleolus does not seem to vary widely (Figure 6.6., Index 39). However, *T. brumpti* as well as other *Theropithecus* species, *Papio* and *Mandrillus*, seem to have a slightly longer medial malleolus than *Macaca* or guenons. However, in width (Figure 6.6., Index 40), the medial malleolus of the extinct *Theropithecus* species is distinct in being relatively medio-laterally wide. In fact, it is wider than all cercopithecids sampled. *T. oswaldi* appears to be even slightly wider than *T. brumpti.* A relatively large medial malleolus has been associated with habitual inversion of the foot during feeding (Krentz, 1993b; Jablonski and Leakey, 2008). However, it is not clear if “large,” as used by these authors, refers to proximo-distal length or medio-lateral width. In primates, a relatively wide medial malleolus is associated with arboreal taxa, especially apes, where there is an increase in the range of dorsiflexion and inversion, and an increase in flexibility (DeSilva, 2008). Further, a wide medial malleolus in some apes many be related to stability in vertical climbing with larger body masses (DeSilva, 2009; Turley et al., 2010). As other aspects of the postcrania (especially digital length and body mass; see chapter V) preclude true arboreality or climbing as habitual behaviors for *T. brumpti*, the suggestion that the foot of *T. brumpti* is highly flexible seem the most likely scenario.

The shape of the astragalar facet is also related to the function of the ankle. However, its morphology in all cercopithecids appears to be quite similar, and *T. brumpti* is not distinctive. Another study, using 3D geometric morphometrics, found more functional signals in this joint, but did not look at *Theropithecus* (Turley et al., 2010). This would be an interesting future project.

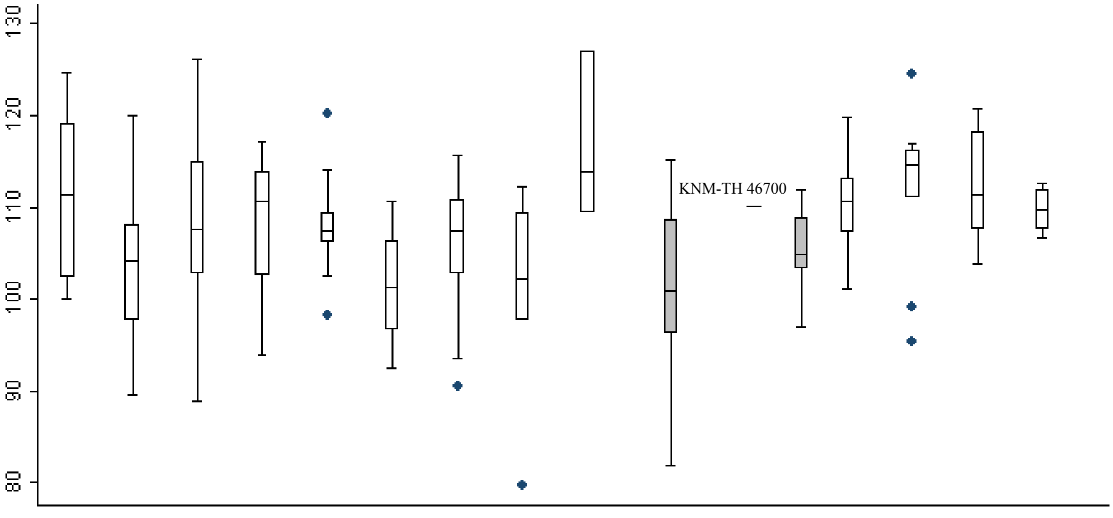
Figure 6.5. Tibia. Anterior view of KNM-WT 39368 (a) and KNM-TH 46700 (b).

Figure 6.6. Tibia Indices

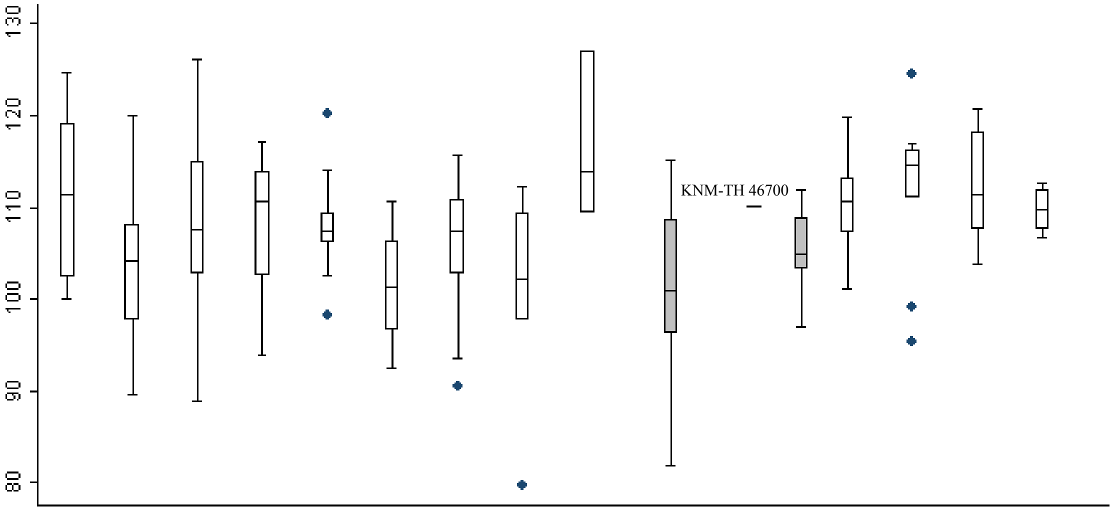
a. Tibial Proximal End Index (Index 36)



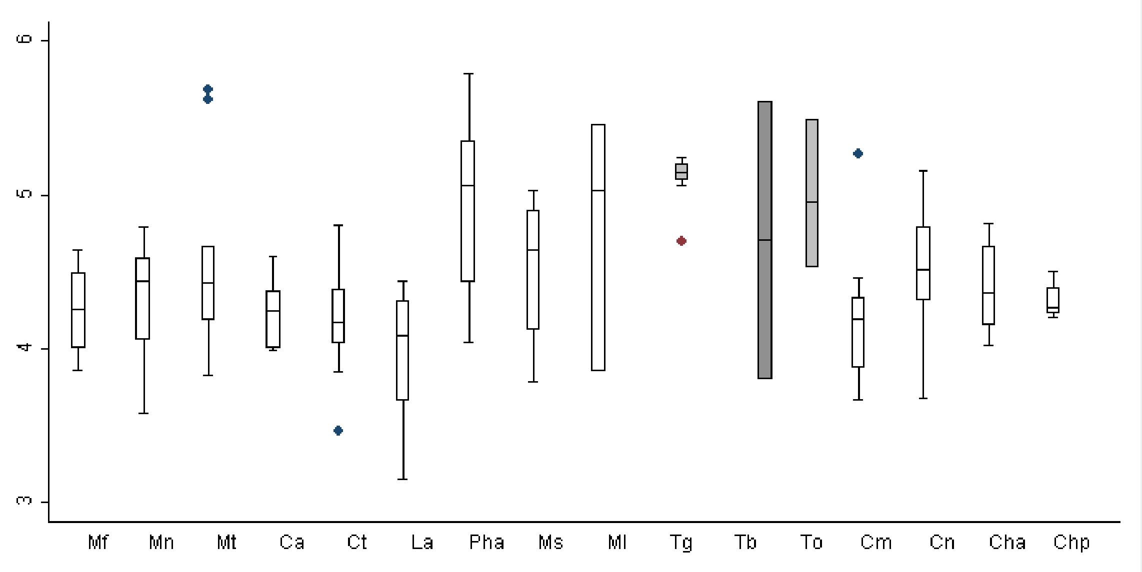
b. Tibial Condyle Width Index (Index 37)



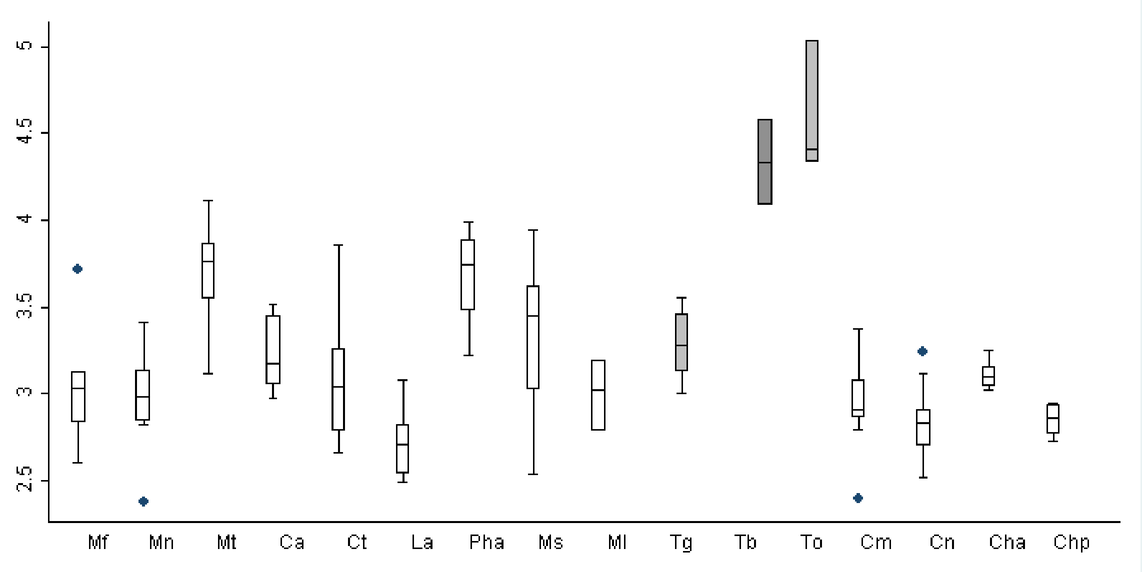
c. Tibial Condyle Length Index (Index 38)



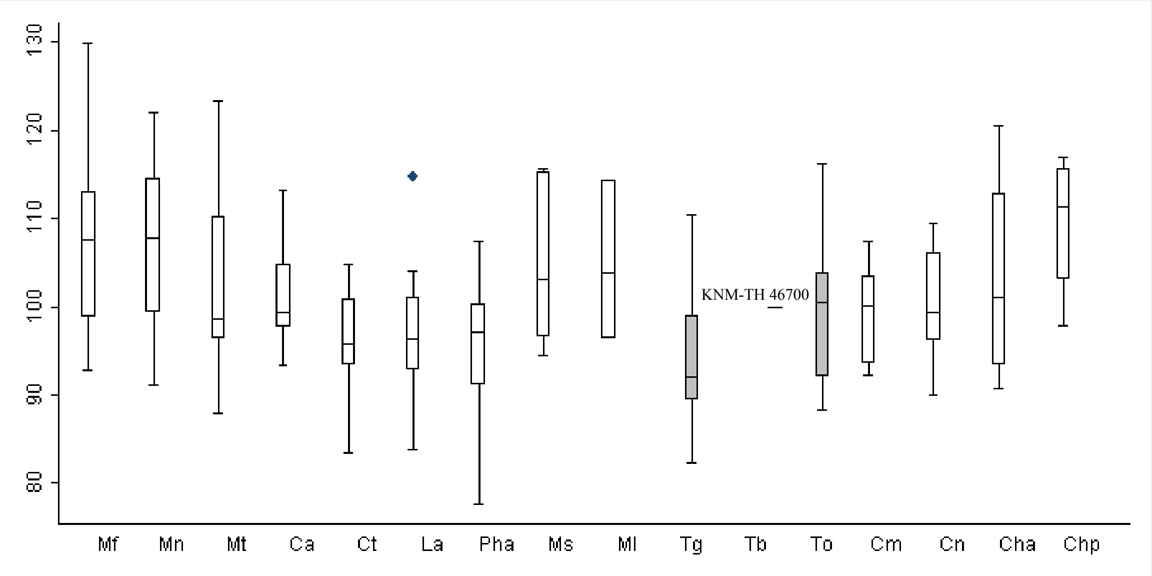
d. Medial Malleolus Length Index (Index 39)



e. Medial Malleolus Width Index (Index 40)



f. Tibial Distal Articular Suface (Lateral Astragalar Facet) Shape Index (Index 41)



Foot

Talus

Two tali (KNM-WT 17554 and L865-1t) are known for *Theropithecus brumpti* (Figure 6.7.). Both are completely intact and well preserved. The talus of *T. brumpti* preserves a number of features that are similar to those of other papionins and associated with terrestrial locomotion. These include: a sellar astragalar surface which is strongly trapezoideal in outline being widest anteriorly and narrower posteriorly, with a strongly raised lateral margin of the trochlea, vertical lateral malleolar surface, relatively deep fossa medially ("malleolar cup") for the medial malleolus of the tibia and a head and neck which are stout and directed anteromedially (Strasser, 1988; Harrison, 1989; Jablonski and Leakey, 2008).

T. brumpti tali are virtually indistinguishable in morphology from the available *T. oswaldi* material (Jolly, 1972). A slightly wedge-shaped, highly asymmetrical astraglar trochlear facet with the lateral border rising substantially above the medial is most marked in the large-bodied terrestrial primates (Strasser, 1988). This morphology should increase the amount of abduction with accompanies dorsiflexion. The trochlear shape index (Figure 6.8, Index 42) highlights the marked posterior/anterior breadth asymmetry of the trochlea. In this feature *T. brumpti* is even more narrow posteriorly than other terrestrial cercoptihecines, and *T. oswaldi* more marked still. The 'extreme' narrowness could be a result of the relative width of the medial malleolus and the deep medial fossa of the trochlea. Therefore, this could be a reflection of the inverted posture of the grasping foot associated with the flexible aspects in the tibia.

Calcaneus

Two calcanei (L-865-1r and KNM-ER 30385) are associated with *Theropithecus brumpti*. The calcanei of cercopithecids appear to be surprisingly uniform and the morphology of *Theropithecus brumpti* conforms to the general cercopithecid pattern (Birchette, 1982; Strasser, 1988). There are, however, a few notable features, mainly in the segmentation of the superior surface. The anterior segment of the calcaneus (from anterior-most point of the posterior talar facet to the cuboid facet) is markedly abbreviated in *T. brumpti* and *T. oswaldi* (Figure 6.8., Index 43), while the posterior talar facet is relatively anteroposteriorly long (Figure 6.8., Index 44). The length of the anterior talar facet is within range of most papionins, but appears to be much shorter than in *Papio* (Figure 6.8., Index 45). This arrangement, especially the length of the posterior facet, is related to movement about the tale-calcaneal joint and suggests potential for a large degree of movement. Again, these features accord with the generally mobile ankle joint that may be related to inverted foot postures seen in *T. gelada* during terrestrial feeding.

Cuboid

Only one cuboid, a left, (KNM-TH 46700) is associated with *Theropithecus brumpti*. Notably, the lateral facet for the sesamoid in the tendon of *m. peroneus longus* is present, which is typical for cercopithecids. The shape of the cuboid in *Theropithecus gelada* and *T. oswaldi* is distinctive in that the lateral border is much shorter than the medial border, giving the bone a wedged shape (Jolly, 1972). *T. brumpti* has this same morphology, although less exaggerated than seen in *T. oswaldi*. The expanded medial border would accommodate large distal and proximal articulations with the lateral cuneiform more distally and the navicular more proximally. This is distinct from the African colobines where the only distal articulation is between the lateral cuneiform and the cuboid. The expansion of the medial border seen in *Theropithecus* is an expansion of the navicular facet and is therefore related to midfoot flexion (DeSilva, 2008). Modern cercopithecoids dorsiflex the midfoot region while climbing (DeSilva, 2009). This asymmetry of the cuboid is more pronounced in all species of *Theropithecus* than it is in *Papio*.This feature may be related to the climbing ability seen in the modern fauna, which is not true vertical climbing on trees but rather dexterity in uneven terrain such as is the case in *T. gelada*.

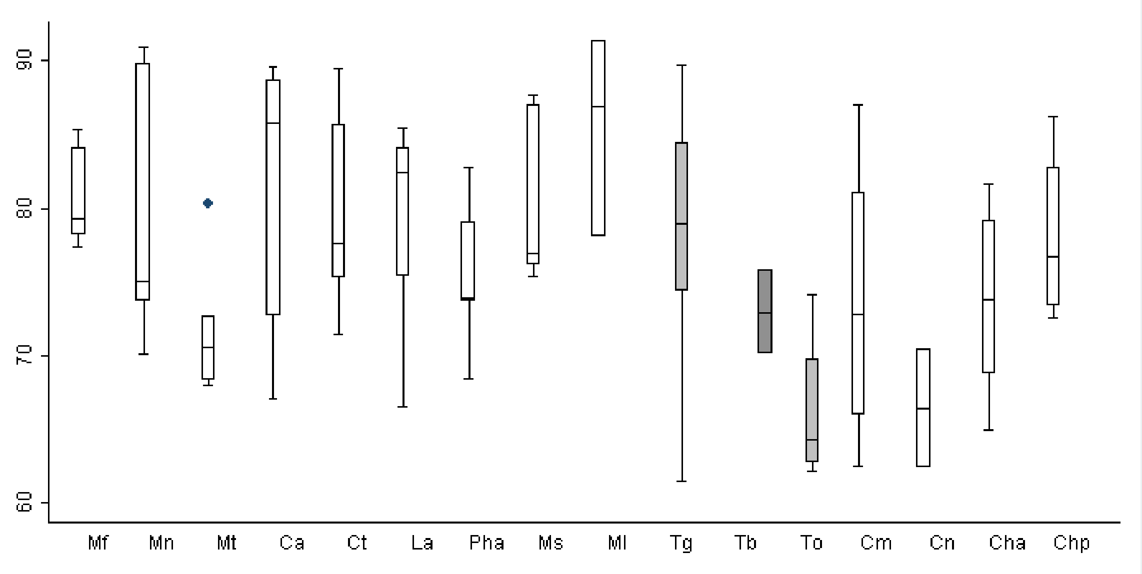
Metatarsals

Two metatarsals are known for *T. brumpti*, a proximal left fifth metatarsal and a proximal right third metatarsal, both are from KNM-TH 46700. Both elements are broken and robusticity indices could not be calculated. Both appear to be, from visual analysis, typical terrestrial papionin elements. The third metatarsal is relatively narrow and deep. The arrangement of the facets on the lateral and medial surfaces of the base for the fourth and second metatarsals respectively is typical. The dorsal surface of the base extends proximally in a wedge-shaped process which is long and pointed similar to *T. gelada*. Shaft is robust with strong ligamentous tubercles at the proximal end. The fifth metatarsal is also robust compared to the modern gelada. Based on what is preserved of the shaft, the metatarsals would have been relatively short and stout compared to the modern *Theropithecus* in which the metatarsals are relatively slender. Facet for the fourth metatarsal is typical for cercopithecids. The tubercle for the insertion of *m. peroneus brevis* is very large, which would presumably be related to inversion of the foot.

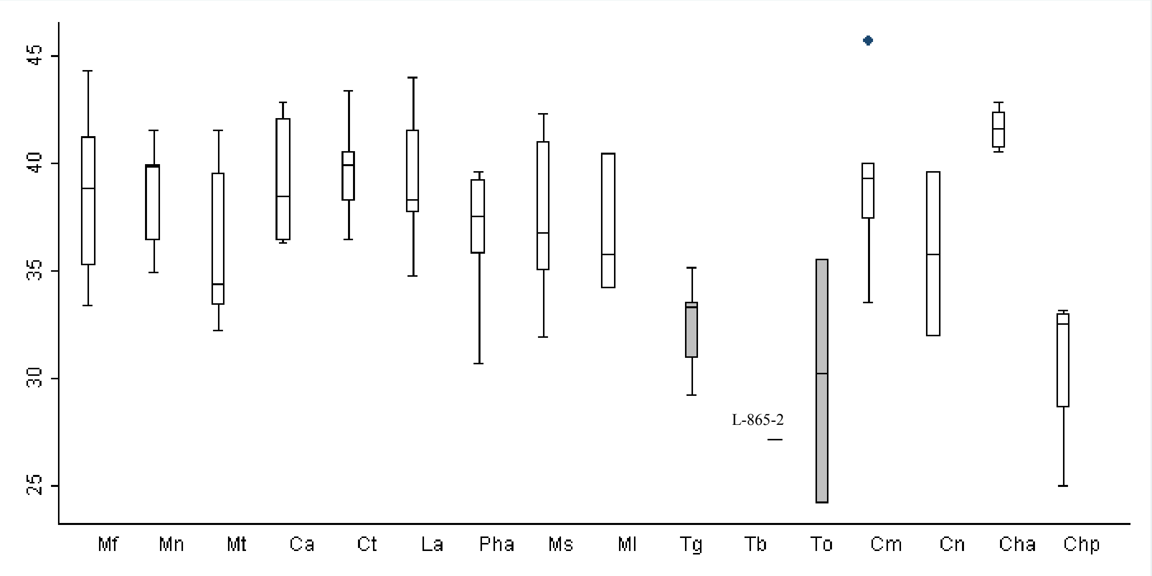
Figure 6.7. Foot. Talius a. KNM-WT 17554 and b. L865-1; Calcanei c. L865-1 and d. KNM-ER 30385; Cuboid e. KNM-TH 46700; Metatarsals f and g. KNM-TH 46700

Figure 6.8. Foot Indices

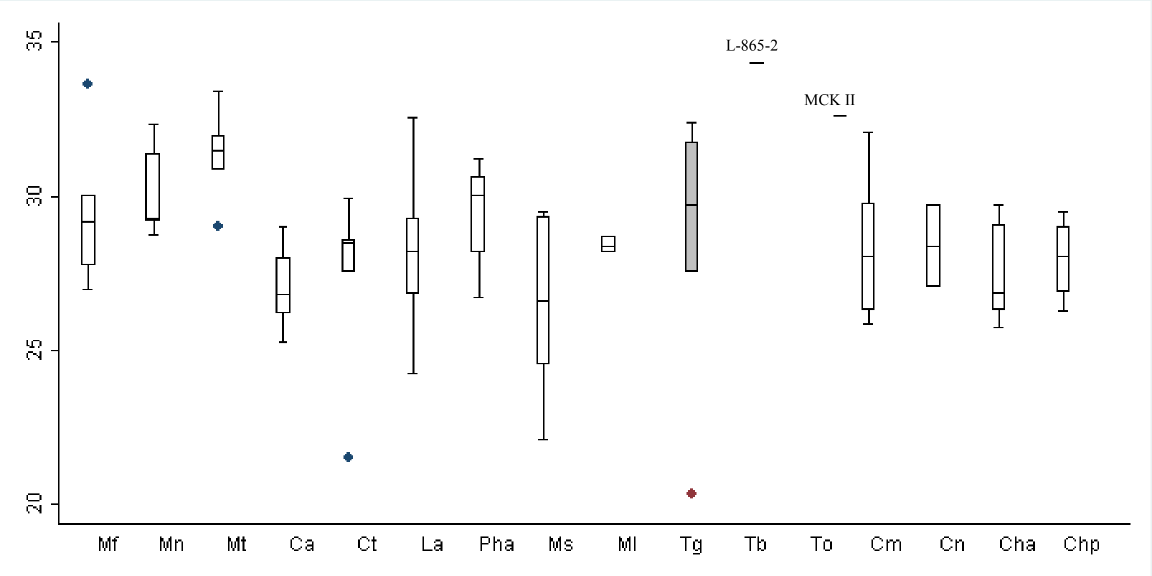
a. Trochlear Shape Index (42)



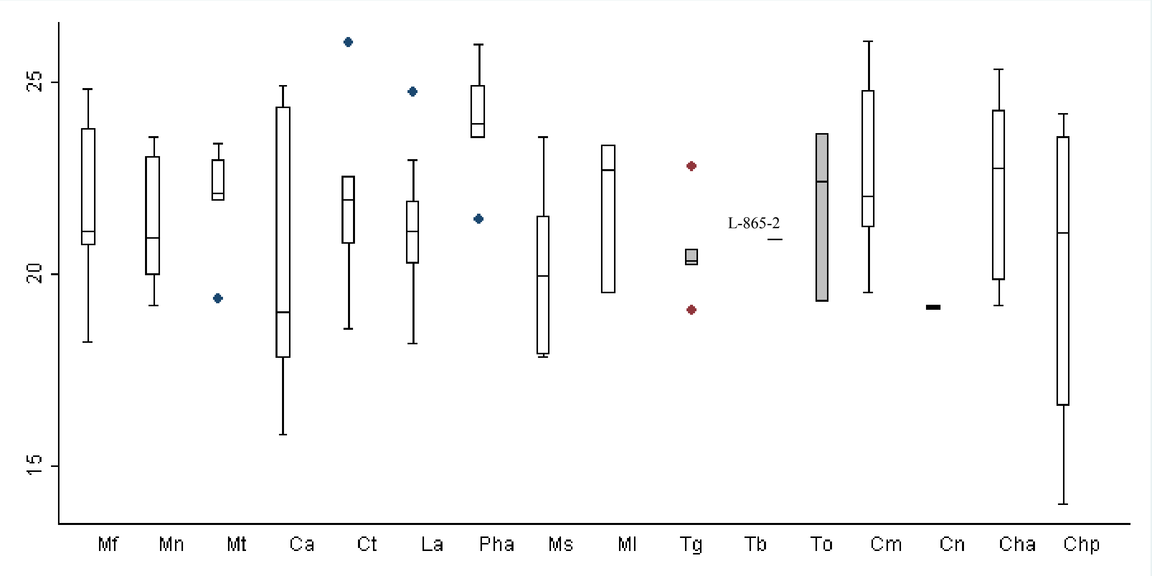
b. Calcaneus Anterior Index (Index 43)



c. Calcaneus Posterior Facet Index (Index 44)



d. Anterior Facet Index (Index 45)



Conclusions

When all the *T. brumpti* hindlimb material is analyzed and compared with other cercopithecines, it is clear that *T. brumpti* is a terrestrially adapted baboon with signals of flexibility possibly related to feeding and foraging. Hindlimbs of primates are conservative, and papionins in general are characterized by morphology associated with terrestrial quadrupedalism. *T. brumpti* also exhibits these features including a relatively high greater trochanter, deep and wide medial condyles of the femur, a typical terrestrial papionin presentation of the talus and calcaneus, and short and stout metatarsals.

As in the forelimb, however, *T. brumpti* also retains a degree of flexibility in the hindlimb also seen in other members of the genus. This is seen in all three main joints: the hip, knee and ankle. At the hip, the relatively short femoral neck and extension of the articular surface onto the posterior surface of the femoral neck are usually features associated with more arboreal taxa. These features have historically been associated with the unique foraging behavior in *Theropithecus,* as the modern species has these traits in spite of being a relatively poor arborealist. At the knee the posterior extension of the lateral condyle would create a ‘reverse carrying angle’ or lateral splay of the femur at the knee. Again, as this is seen in the modern *T. gelada* it is also associated with its unusual habitual sitting and shuffling feeding behaviors. Finally, at the ankle, the strikingly wide medial malleolus in the extinct species of *Theropithecus* is intriguing. As with several other aspects of the postcranium of *T. brumpti* described in the forelimb, that the broad medial malleolus is associated with arboreal primates. Furthermore, it is associated with arboreal primates that engage in vertical climbing. Taken in isolation this feature would give an interesting signal of climbing in *T. brumpti*. However, taken in concert with the rest of the hindlimb, this appears to be a signal of increased flexibility of the foot, or at least, more inversion and dorsiflexion than other cercopithecids. This use of the foot is also indicated by the highly asymmetrical cuboid.

In summary, while *T. brumpti* has numerous post-cranial features associated with the unique feeding behavior of the modern gelada, it is not likely that they were using them in the same manner (i.e. a different biological role *sensu* Bock and von Wahlert, 1963). Studies of the masticatory apparatus have hypothesized that the emergence and early diversification of *Theropithecus* was linked to the evolution of a feeding apparatus specialized for grazing (Jablonski, 1993a). This does not appear to be supported by the postcranial material. Rather, manual foraging appears to define the early evolution of the clade.

In all known species of *Theropithecus,* the forelimb presents numerous traits associated with manual foraging. Therefore, this suite of traits that characterize the genus were most likely present in their last common ancestor. The presence of these hindlimb traits in *T. brumpti* confirms the presence of autapomorphic *Theropithecus* traits in the fossil record near the origin of the genus. The modern *T. gelada*'s specialized diet cannot explain these traits in *T. brumpti*. Therefore, we must reconsider how these specializations are interpreted, which could have implications for the origin of the *Theropithecus* lineage.

Gilbert et al. (Gilbert et al., 2010) recently suggested that manual terrestrial foraging may have been primitive for papionin monkeys and so perhaps these traits are better interpreted as foraging adaptations related to forest floor locomotion and gleaning which may be primitive for *Theropithecus* and possibly for papionins. Further, if the common ancestor of *Theropithecus*, *Papio* and *Lophocebus* was arboreal, perhaps then the features that allowed for flexibility in that ancestor were co-opted for fine manipulation of food objects on the ground in *Theropithecus*. However, it is also possible, that these traits did, indeed emerged for gramnivory, and retained that function in *T. oswaldi* and *T. gelada*, but in *T. brumpti* they were co-opted for a different diet.

CHAPTER VII

CONCLUSIONS AND IMPLICATIONS

This dissertation is a reappraisal of the functional morphology of the postcrania in *Theropithecus brumpti* based on associated material. Contrary to previous findings, this dissertation concludes that *Theropithecus brumpti* was a terrestrial primate. *T. brumpti* has many traits that are clear signals of terrestriality in large-bodied papionins including: a relatively narrow scapula, retroflexed medial epicondyle, retroflexed olecranon process, short and robust metacarpals and phalanges, a relatively high greater trochanter and deep, wide medial condyles of the femur.

However, there are numerous traits in the *T. brumpti* postcrania that are unusual in a large-bodied terrestrial papionin including: moderately indented glenoid fossa, variation in relative humeral head height, relatively well developed rotator cuff musculature, relatively short trochlear flange and large radial tuberosity, relatively short femoral neck and extension of the articular surface onto the posterior surface of the femoral neck and a relatively wide medial malleolus.

Some of these traits have been used previously to support the hypothesis that *T. brumpti* was arboreal. While *T. brumpti* retains a degree of flexibility (at the shoulder, elbow, hip, knee and ankle), this is not exceptional when compared to other members of the genus, notably *T. oswaldi*. Not only are traits similar in both species, but there is a wide range of variation and overlap in both. There is no truly terrestrial primate and all primates spend some amount of time in the trees. The large size of *T. brumpti* does preclude its being truly arboreal quadruped. There are large arboreal taxa (e.g. *Pongo* and *Gorilla*), but they accomplish their arboreality through suspensory postures and not above-branch arboreal quadrupedalism. No cercopithecines show any adaptations for suspensory locomotion or posture. Further, the relatively stubby digits render arboreal quadrupedalism even more unlikely. As this is the part of the organism that is in direct contact with the substrate, the short, robust hand elements are so stubby as to render climbing difficult. Therefore, retention of traits that have been used to signal arboreality is better interpreted as flexibility. It is likely that *T. brumpti* may have spent some time in trees, perhaps in the way modern *Papio* does. It should be noted that modern *Papio* does not have any signals of arboreality or any of the papionin signals of 'flexibility' outlined in this paper. Therefore, *T. brumpti* (and *T. oswaldi*) were interacting with the environment in a fundamentally different way.

Features historically used to reconstruct *T. brumpti* as more arboreal are interpreted here as part of a suite of traits that characterize early *Theropithecus* in general. This suite of traits may instead be adaptations to manual terrestrial foraging, in particular adaptations related to forest floor locomotion and gleaning, which may be primitive for *Theropithecus* and possibly for papionins.

One additional goal of this dissertation was to outline postcranial differences in closely related groups. Among fossil *Theropithecus* species, this proves to be a difficult task. This dissertation shows that the overlap in range and variation of the postcranial morphology of *T. brumpti* and *T. oswaldi*. Therefore, it may be impossible to allocate isolated postcranial to species. Unfortunately, the suite of feature used by Krentz (1993a; 1993b) to identify *T. brumpti* must now be revised.

Further, postcranial differences between *Theropithecus* and *Papio* may be a matter of degree. However, there are some features that, with the current material, seem to be unique to *Theropithecu*s as a genus. These may aid in identification of isolated postcrania:

- Distal extension of the deltoid pectoral crest of the humerus
- Distinct depression on the distal-most portion of the deltoid pectoral crest
- Crest on superior surface of the olecranon process of the ulna
- Furrowed groove on the radial tuberosity
- Deep excavation on the medial surface and prominent interosseous crest of the radius
- Long MCI relative to MCII
- Very robust phalanges
- Strong lateral deviation of the femoral shaft

These traits are distinct the genus and are present in the earliest representatives for whom we have postcranial material. Although tentative, we may draw some conclusions as to the ancestral *Theropithecus* morphotype. As discussed, many traits seen in *Theropithecus* are also seen in arboreal papionins. Although they are retained in a terrestrial primate, perhaps these traits are retained from an arboreal (or more arboreal) ancestor. Fossil evidence from *Victoriapithecus* (an early primate thought to be contemporaneous to the colobines/cercopithecine split) suggests a semi-terrestrial mode of locomotion including manual terrestrial foraging and vertical climbing. The trait which seems to indicate this (a proximally-extending brachioradialis flange) is also present in some extant papionins which still exhibit this behavior (*Mandrillus* and *Cercocebus*) (Fleagle and McGraw, 2002; Gilbert et al., 2010).

The proximally extending brachioradialis flange has been suggested to be primitive for papionins. As this is seen in *T. brumpti* to some extent, it suggests 1) similar behavior in the fossil *Theropithecus* and 2) that such a behavior (and related morphology) would have been part of the ancestral morphotype. This particular trait is not seen in modern *Theropithecus* and *Papio*, suggesting that a more distally restricted crest is the derived condition; presumably as these groups became ever more terrestrial. In a related implication, if the common ancestor of *Theropithecus*, *Papio* and *Lophocebus* is arboreal (or semi-terrestrial in a more woodland environment) perhaps in the *Theropithecus* lineage the ability to manipulate arboreal environments was co-opted for fine manipulation of food objects on the ground.

In conclusion, what is clear is that, unfortunately, interpretation of locomotor morphology cannot be done with only part of the puzzle (that is, isolated postcrania). Any one element of *T. brumpti*, taken alone, would suggest a far more 'arboreal' lifestyle than seem to actually be the case. A point which Birchette (1982) discusses at length as *Paracolobus chemeroni* (a fossil colobine) appears to also more terrestrial than initially thought.

Hopefully, this project will help interpret postcranial morphology of other fossil cercopithecines. Future work with these data include: discriminant function analysis for habitat correlates present within papionins, further discernment of morphological correlates of the cercopithecoid postcrania using the large comparative database now collected and finally, if possible, reappraisal of the unassociated *Theropithecus* postcrania from the Shungura Formation originally used to characterize *Theropithecus brumpti*.

Finally, as an anthropological thesis, how fossil primates can help interpret human evolution or help inform human evolution is of intrinsic interest. This re-interpretation of the paleobiology of *T. brumpti* compared to that of *T. oswaldi* may offer a direct parallel with hominins as new fossil evidence suggests use of terrestrial substrates in more woodland habitats for late Miocene to early Pliocene hominins, in contrast to more open habitats associated with later hominins. Therefore, this dissertation helps develops a framework for understanding the woodland to grassland transition among large bodied primates including hominins.

APPENDIX A

THEROPITHECUS BRUMPTI MEASUREMENTS

Scapula

	S1	S2	S3	S4	S5	S6
KNM-WT 39368	137.12	111.33	28.24	20.98	25.41	82.3
KNM-WT 17554						
KNM-WT 17560						
KNM-ER 30385			25.88	17.9		
KNM-ER 3084			26.02	18.32		
KNM-ER 3119						
KNM-TH 46700						
L 865						

Humerus

	H1	H2	H3	H4	H5	H6	H7	H8
KNM-WT 39368	227.59	227.91		40.11	33.42	26.75	31.91	116.62
KNM-WT 17554								
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084				34.89	34.07	27.47	27.96	
KNM-ER 3119								
KNM-TH 46700								
L 865								

	H9	H10	H11	H12	H13	H14	H15	H16
KNM-WT 39368				16.01	22.93	60.29	47.42	36.62
KNM-WT 17554								
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084								
KNM-ER 3119								
KNM-TH 46700								
L 865							44.49	31.05

	H17	H18	H19	H20	H21
KNM-WT 39368	42.03		31.17	13.66	15.42
KNM-WT 17554					
KNM-WT 17560					
KNM-ER 30385					
KNM-ER 3084		16.19			
KNM-ER 3119					
KNM-TH 46700					
L 865	39.7	19.52		12.79	16.15

Ulna

	U1	U2	U3	U4	U5	U6	U7	U8
KNM-WT 39368			24.62	21.59	18.15			
KNM-WT 17554								
KNM-WT 17560			18.24	17.13	17.1	14.5	19.66	
KNM-ER 30385								
KNM-ER 3084			21.64	20.27	17.09	12.77	22.08	
KNM-ER 3119								
KNM-TH 46700								
L 865								

	U9	U10
KNM-WT 39368		8.45
KNM-WT 17554		
KNM-WT 17560		
KNM-ER 30385		
KNM-ER 3084		
KNM-ER 3119		
KNM-TH 46700		
L 865		

Radius

	R1	R2	R3	R4	R5	R6	R7	R8
KNM-WT 39368			11.83	28.73	19.56	22.22		
KNM-WT 17554					15.02	16.13		
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084								
KNM-ER 3119								
KNM-TH 46700								
L 865								

Femur

	F1	F2	F3	F4	F5	F6	F7	F8
KNM-WT 39368								
KNM-WT 17554								
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084								
KNM-ER 3119						14.75	28.59	23.06
KNM-TH 46700	216.12	210.43	46.6	41.05	13.07	10.09	23.48	19.68
L 865								

	F9	F10	F11	F12	F13	F14	F15	F16
KNM-WT 39368								

KNM-WT 17554								
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084								
KNM-ER 3119	28.59							
KNM-TH 46700	24.67	18.14	16.37	24.15	22.31	42.23	35.25	37.08
L 865								

	F17	**F18**	**F19**	**F20**	**F21**	**F22**
KNM-WT 39368						
KNM-WT 17554						
KNM-WT 17560						
KNM-ER 30385						
KNM-ER 3084						
KNM-ER 3119						
KNM-TH 46700	34.78	14.9	13.45	22.01	24.6	22.31
L 865						

Tibia

	T1	**T2**	**T3**	**T4**	**T5**	**T6**	**T7**	**T8**
KNM-WT 39368	221.82	213.39				30.23		17.27
KNM-WT 17554								
KNM-WT 17560								
KNM-ER 30385								
KNM-ER 3084								
KNM-ER 3119								
KNM-TH 46700	196.88	185.83	41.25	30.37	19.65	26.53	17.76	16.12
L 865								

	T9	**T10**	**T11**	**T12**
KNM-WT 39368		10.15		
KNM-WT 17554				
KNM-WT 17560				
KNM-ER 30385				
KNM-ER 3084				
KNM-ER 3119				
KNM-TH 46700	26.36	8.04	17.3	17.3
L 865				

Talus

	TL1	**TL2**	**TL3**	**TL4**	**TL5**	**TL6**	**TL7**
KNM-WT 39368							
KNM-WT 17554	30.69	20.86	22.67	21.5	16.89	11.85	16.91
KNM-WT 17560							
KNM-ER 30385							

KNM-ER 3084							
KNM-ER 3119							
KNM-TH 46700							
L 865	35.39	25.52	32.9	26.69	18.23	14.2	18.74

	Calcaneus					
	C1	**C2**	**C3**	**C4**	**C5**	**C6**
KNM-WT 39368						
KNM-WT 17554						
KNM-WT 17560						
KNM-ER 30385						
KNM-ER 3084						
KNM-ER 3119						
KNM-TH 46700						
L 865	51.52	13.98	32.11	17.69	10.76	29.83

	Cuboid	
	CB1	**CB2**
KNM-WT 39368		
KNM-WT 17554		
KNM-WT 17560		
KNM-ER 30385		
KNM-ER 3084		
KNM-ER 3119		
KNM-TH 46700	19.19	17.67
L 865		

APPENDIX B

CATALOGUE OF EXTANT COMPARATIVE SAMPLE

Abbreviations for museum/collections are as follows: **AMNH**: American Museum of Natural History; **FMNH**: Field Museum of Natural History; **HERC**: Human Evolution Research Center; **KNM**: National Museums of Kenya; **NHML**: Natural History Museum London; **NMNH**: National Museum of Natural History; **RCMA**: Royal Museum of Central Africa and **UMT**: University of Minnesota Tappen Collection

Macaca fascicularis	AMNH	175460	M
	AMNH	193654	F
	AMNH	103659	M
	AMNH	30622	F
	NMNH	573504	M
	NMNH	458727	?
	NMNH	308723	?
	NMNH	308725	?
	NMH	1910.12.24.1	F
	NMH	1847.121.11.5	M
	FMNH	FMNH 65451	F
Macaca nemistrina	AMNH	282256	M
	AMNH	106564	M
	AMNH	106563	M
	NMNH	305069	F
	NMNH	49691	M
	NMNH	49696	M
	NMNH	49874	M
	NMNH	258230	F
	FMNH	FMNH 105658	F
	FMNH	FMNH 99688	F
Macaca thibetana	AMNH	60160	M
	NMNH	241162	?
	NMNH	258651	M
	NMNH	254800	M
	NMNH	258650	F
	NMNH	258686	M
	NMNH	241163	M
	NMNH	258649	M
	FMNH	FMNH 39500	F
	FMNH	FMNH 39499	M

Cercocebus agilis	AMNH	81250	M
	AMNH	52641	M
	AMNH	52634	M
	RMCA	RMCA 23497	M
	RMCA	RMCA 23495	M
	RMCA	RMCA 23496A	F
	RMCA	RMCA 36971	M
	RMCA	RMCA 5999	M
Cercocebus torquatus	LNMH	1938.7.7.3	M
	LNMH	1948.45	M
	LNMH	1938.12.6.1	F
	LNMH	1938.7.7.5	F
	LNMH	1938.7.7.2	M
	LNMH	1938.7.7.4	F
	FMNH	FMNH 73809	F
	FMNH	FMNH 73807	M
	FMNH	FMNH 73806	M
	FMNH	FMNH 51812	?
Lophocebus albigena	AMNH	52596	F
	AMNH	52598	M
	AMNH	52603	M
	AMNH	52627	M
	NMNH	452502	M
	NMNH	452500	M
	NMNH	452501	F
	NMNH	164578	F
	NMNH	164580	F
	NMNH	452498	F
	NMNH	164579	M
	KNM	452499	M
	NMNH	452503	M
	RMCA	RMCA 37572	M
	RMCA	RMCA 12250	M
	RMCA	RMCA 5969	M
	RMCA	RMCA 1282	F
	RMCA	RMCA 1782	M
	RMCA	RMCA 27746	M
	RMCA	RMCA 29107	M
	RMCA	RMCA 5998	M
	RMCA	RG 6002	M

Papio hamadryas anubis	AMNH	52668	F
	NMNH	236976	M
	NMNH	239743	?
	NMNH	384228	M
	NMNH	384234	M
	KNM	KNM OM 6271	F
	KNM	KNM OM 5068	M
	KNM	KNM OM 6264	F
	KNM	KNM OM 3141	F
	KNM	KNM OM 5061	M
	RMCA	RG 2230	M
	RMCA	RG 6149	M
	RMCA	RG 1285	M
	LNMH	1962.12.14.6	F
	LNMH	1901.8.9.23	F
	LNMH	72.127	M
	LNMH	1940.1.20.21	M
	LNMH	35.2.14.1	M
	LNMH	1948.8.3.2	M
	FMNH	FMNH 18868	M
Theropithecus gelada	AMNH	201008	M
	HERC	HERC 108	M
	HERC	HERC 113	F
	HERC	HERC 110	F
	HERC	HERC 109	M
	FMNH	FMNH 27040	M
	NME	MCA 442	M
	NME	MCA 443	F
	NME	MCA UID F.1.	F
Mandrillus sphinx	AMNH	89365	F
	AMNH	89364	M
	AMNH	89358	F
	AMNH	89367	F
	AMNH	170364	M
	AMNH	170366	?
	NMH	30.12.15.9	M
	LNMH	1948.7.6.2	M
Mandrillus leucophaeus	LNMH	1944.85a	F
	LNMH	49.82	M
	LNMH	49.83	F

	LNMH	82.492	M
	LNMH	1949.86	F
Cercopithecus mitis	AMNH	52420	M
	AMNH	52368	M
	NMNH	452550	F
	NMNH	452557	F
	NMNH	452551	M
	RMCA	RG 5994	F
	RMCA	RG 11329	F
	RMCA	RG 27963	M
	LNMH	72.66	F
	LNMH	72.65	M
Cercopithecus neglectus	AMNH	52429	M
	AMNH	52421	M
	NMNH	452524	M
	NMNH	452525	F
	NMNH	452520	F
	NMNH	452523	M
	NMNH	452522	F
	RMCA	RG 11526	F
	RMCA	RG 1287	M
	LNMH	72.48	F
Chlorocebus aethiops	LNMH	72.27	F
	LNMH	72.29	M
	LNMH	72.25	M
	LNMH	72.31	M
	LNMH	1977.3148	M
	LNMH	72.36	F
	LNMH	72.28	M
	LNMH	72.32	F
	LNMH	1977.3149	F
	LNMH	72.3	F
	UMT	UMT 265	F
	UMT	UMT 246	F
	UMT	UMT 223	M
	UMT	UMT 245	M
	UMT	UMT 137	M
Chlorocebus patas	AMNH	38738	M
	AMNH	34714	M
	AMNH	34713	M

NMNH	164684	M
RMCA	RMCA 569	?
LNMH	1968.5.11	F

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