ADDIS ABABA UNIVERSITY
SCHOOL OF GRADUATE STUDIES
DEPARTMENT OF BIOLOGY

Shearing Quotient based Ecomorphological Analysis of Cercopithecidae fossils from the Lower Omo Basin: Dietary Adaptation, Habitat Preference and Paleoenvironment Reconstruction

By

Mezgebu Ashagrie

A Thesis Submitted to the School of Graduate Studies of the Addis Ababa University in Partial Fulfillment of the Requirements for the Degree of Master of Science in Biology (Dryland Biodiversity).

Advisor: Solomon Yirga (D.Sc.)

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Approved by Examining Committee

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DECLARATION

I, hereby confirm that this thesis is my original work and has not been presented for a degree in any other University and that all resources of material used for this thesis have been duly acknowledged.

Name Mezgebu Ashagrie Demissie

Signature _____

Date of submission _____

This thesis has been submitted for examination with my approval as the research advisor.

Name _____

Signature _____

Date _____

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

ABSTRACT

This study was undertaken to reconstruct the Shungura cercopithecid assemblages' dietary adaptation, habitat preference and environmental changes. Their dietary adaptations were reconstructed through shearing quotient based ecomorphological analysis. Each species' trophic adaptation was compared to their locomotor adaptations and associated environmental evidences in the case of reconstructing their habitat preferences. Moreover, the proportions of their trophic adaptation across the stratigraphic members were taken to derive the paleoenvironmental changes. Reconstructed dietary adaptations show that except the *Theropithecus* lineage the rest of the cercopithecid taxa are adapted like that of their modern lineages, i.e., frugivory in cercopithecines (*Cercopithecus sp*., *Papio*, large papionini, small papionini A and B) and folivory in colobines (*Rhinocolobus turkanaensis*, *Paracolobus mutiwa* and *Colobus sp*.) have been observed. Exceptionally, the *Theropithecus* lineage shows different dietary adaptations along their successive temporal scale, i.e., frugivory (most likely soft fruit) in *T. brumpti*, hard food items (most likely seed or nut-like fruits) in *T. oswaldi* and more grass blades in *T. gelada* (the modern *Theropithecus*) are suggested. This trophic adaptation together with plausible previously documented environmental evidences indicate that *T. oswaldi* were living in open environment (habitats), while the rest of the fossil cercopithecids were dwelling in environments with more tree cover or forests to bushlands, particularly colobines and *Cercopithecus sp*. in forest, *T. brumpti* in closed woodland and the other papionini in closed to open woodland/bushland habitats. In addition to their habitat differences, the study showed that the Lower Omo valley was a closed environment at its basal members A and B. However, environmental changes have been observed at the later different stratigraphic members, particularly from closed to a mosaic of closed and open environment at member C (2.85 – 2.52 Ma) and progressively open and most probably extreme aridity at member H (1.90-1.74 Ma). These environmental changes coincide with the East African climatic change recorded from Marine records of African climate variability document as well as to the evolution of hominids such as *Paranthropus aethiopicus* and *Homo erectus*. These possible relations between faunal, environmental and climatic change in turn indicate that there exists temporal correlation between terrestrial and marine event sequences. Finally, the study suggests that the observed major late Pliocene-Pleistocene events in the Shungura Formation may have been climatically mediated.

Key words/ phrases: Ceropithecidae, Shearing crest/ quotient, Dietary adaptation, Habitat preference, Paleoenvironment, Shungura Formation.

1. INTRODUCTION

The old world monkeys (cercopithecoids) are a group of higher primates in which the extant members share at least one derived key character of adaptation, i.e. bilophodont dentition. This adaptation is also present in the fossil forms unequivocally assigned to the family (Delson, 1975, 1992). Bilophodonty of molars define the Old World Monkeys as a monophyletic taxon, but the development of bilophodonty in Victoriapithecidae is imperfect, and crista obliqua is observed in many maxillary molars, as well as primary molars (Benefit, 1999 and Fleagle, 1999).

From the point of view of morphology, the two catarrhine superfamilies' teeth shape and the occlusal (functional) surfaces show differences with high diagnostic value. Moreover, cercopithecoid monkeys are unique among anthropoids with respect to the distribution of maxillary sinus (MS). Unlike hominoids and platyrrhins, cercopithecoids except macaques completely lack maxillary sinus (Benefit, 1999; Rae et al., 2002 and Rae, 2008). Concerning their facial morphology, cercopithecoids' premaxillary suture contacts nasal (or frontal) superiorly, while in hominoids it contacts the nasal bone inferiorly. Furthermore as the other none hominoids, nasal bones are projecting anteriorly at the horizontal lines that represent the medial margin of the orbits (Rae, 1999).

Cercopithecids also differ from hominids postcranially in having a concave arcuate sulcus where limbs surround the sulcus rectus, rather than a frontal sulcus medial to the latter (Szalay and Delson, 1979). However, in the postcranial morphology of the two subfamilies of cercopithecidae, many characters are much more responsive for analysis of habitat adaptations than of heritage (Simons and Delson, 1978). For example, moderate to extreme terrestriality has arisen in parallel between earlier colobines and cercopithecines. This is suggested to represent homoplasies and reflect a shared terrestrial habitus rather than phylogenetic heritage (Leakey et al., 2003).

The old world monkeys are among the most successful of all primates, certainly of Neogene groups, and have a widespread distribution, except in Europe, which they had

occupied during the Pleistocene (Delson,1978). They are also varied in ecological, ethological, and locomotor adaptations, although their cranial and especially dental morphology is relatively stereotyped (Szalay and Delson, 1979).

Cercopithecoidea comprises the families Victoriapithecidae and Cercopithecidae with 11 still living and 13 known extinct genera, and well over 100 species (Delson, 1975; Szalay and Delson, 1979; Conroy, 1990 and Benefit and McCrossin, 1991). However, these numbers may vary depending on new findings. Victoriapithecidae includes fossil old world monkeys from the early to middle Miocene 15-20 Ma; (Ma = megannum = 1 million years ago), with known genera *Prohylobates* and *Victoriapithecus* (Conroy, 1990; Benefit, 1999 and Fleagle, 1999), which were formerly classified as *Cercopithecidae incertae sedis* (Delson, 1979 and Szalay and Delson, 1979).

Several features of the *Victoriapithecus* dental morphology (such as the occurrence of a crista obliqua on the upper molars and hypoconulid on the lower molars) are retentions of primitive features that are shared with apes. On the other hand, other characters including the relatively large anterior dentition, the high-flaring crowns of the molar teeth with little cusp relief, the closely approximated cusps, and the short-shearing crests are derived features that are shared with the later papionins (Leakey et al., 2003).

On the other hand, family Cercopithecidae is limited to the lineages that include living Old World monkeys. The Living Old World Monkeys' lineages are subsequently split in to two lineages of modern catarrhine monkeys that are assigned to subfamily colobinae and subfamily cercopithecinae.

Family Cercopithecidae is also the most successful group of nonhuman primates alive today (Xing et al., 2005). Taken as a whole, they account for over one quarter of the extant genera of primates and approximately 40% of the species (Disotell, 1996). They have also an extensive fossil record extending back to the early and middle Miocene of Africa (Delson, 1975). Despite this specific diversity and long evolutionary history, the fossil groups are argued to be relatively uniform in both their skeletal and dental anatomy

and this reflects that much of the current taxonomic diversity is a relatively recent phenomenon (Conroy, 1990; Fleagle, 1999; Frost, 2001 and Cachel, 2006).

The two subfamilies of cercopithecidae have developed their own adaptive mechanism to cope up with their feeding habit. Cercopithecinae has a buccal pouch, and colobinae has a complex, or sacculated stomach. In this ecomorphological adaptation it is thought that the buccal pouch is an adaptation for quickly putting sparsely available food like fruit into the mouth, and the complex stomach is an adaptation for eating leaves (Delson, 1975, 1992; Conroy, 1990 and Fleagle, 1999). In addition, this difference in dietary adaptations is related to differences between the subfamilies in morphology, such as the height of molar cusp and flare, the proportion of fore and hind limbs, size of the pollex, or thumb, behavior (foraging), habitat (forest/closed wood land or open grass land) and locomotion (arboreality or terrestriality) (Delson, 1975, 1992 and Fleagle, 1999).

1.1. Statement of the problem

An integral element to reconstructing the course of cercopithecoids' evolution includes understanding the kinds of environments in which they were living. The environment is a key component of most hypotheses regarding the pattern and process of cercopithecoidea and hominid biological and behavioral evolution (Degusta and Vrba, 2003). Accurate and precise reconstructions of paleoenvironments play a crucial role in the testing and refinement of such hypotheses. The morphological and behavioral adaptations of every species are in part a consequence of the selection pressures that operate within its specific environment (deMenocal, 2004). Moreover, more detailed reconstructions of Pliocene and Pleistocene environments helps to understand hominid evolution better.

However, it is important to note that superfamily cercopithecoidea have been sufficiently generalized in their locomotor and foraging behaviors that they potentially could have lived in and utilized a wider range of habitats (Eronen and Rook, 2004). The most useful environmental reconstructions are probably best if it is based on the understanding of the ecological parameters of the complete fauna as well as the physical aspects of the fossil locality.

Paleohabitat reconstructions based on cercopithecids are very popular because these animals are usually the most common element of the fauna in most Plio-Pleistocene fossil localities. The radiation of this family in the Plio-Pleistocene has been conspicuous that its members were evolving to inhabit a wide range of environments that stretch from forest (closed wood land) to arid desert (Eronen and Rook, 2004).

The great utility of fossil cercopithecids as habitat indicators has been demonstrated in the past by a number of studies. The earliest studies depended upon dental microwear (Teaford, 1993 and Benefit, 1999), molar flare and shearing crest (Benefit, 1999), correlating with other fossil records in the stratigraphic member like paleobotany and paleosol (Eck, 1977; Eck et al., 1987) and direct assessment of the taxonomic affinity of the fossils, followed by an extension of the habitat preferences of the living relatives back to the fossil taxa (Bobe et al., 2002; Zeresenay Alemseged, 2003; and Bobe and Behrensmeyer, 2004). In the later approach, relative abundance of different animal species permits a general characterization of habitat, assuming that certain taxonomic groups correlate with specific habitats in both the past and present (Potts, 1998). This approach of ‘‘taxonomic affinity’’ represents a type of substantive uniformitarianism (Kapplman et al., 1997). Even though the approach gets some support in the fact that some closely related cercopithecids (related at generic or even tribal level) share some of the same habitat preferences, it may not enable us to generalize for all phylogenetic groups. The obvious weakness of the method is that the habitat preferences are simply accepted with no need of testing for the adaptations of taxa. For example, monkeys particularly colobines, when present in fossil faunas, are conventionally taken to indicate forest or closed woodland environments (Gidey WoldeGabriel et al., 1994). However, if such conclusion does not hold true in different integrated approach or test, this approach may lead to biased paleoecological reconstruction and it may be very misleading.

Different arrays of methods use functional morphology to test for definitive morphological indications of the environment. This approach allows an ecomorphic, as opposed to a taxonomic, characterization of the biota and associated habitats without

assuming particular taxon-habitat correlations (Potts, 1998 and Eronen and Rook, 2004). Methods of ecomorphic analysis have increasingly been applied to the faunas of early hominin sites (Kappelman et al., 1997; Reed, 1997; Degusta and Vrba, 2003 and Eronen and Rook, 2004).

As a result of the aforementioned facts, ecomorphological approach have been developed to reconstruct habitat preferences as a means of understanding dietary and locomotor adaptations, and the way that these adaptations are linked to specific ecological or habitat parameters. Since this method relies on functional morphology, it offers the opportunity to build hypotheses that can be tested among living taxa. When these hypotheses are verified with strong correlations, the results can be extended with some confidence to the fossil record.

The linkage between certain morphological patterns and their functional expression in specific habitats (dietary adaptation) has generated a growing literature over the past several years (e.g., Kappelman et al. 1997; Benefit, 1999; Degusta and Vrba, 2003; Eronen and Rook, 2004 and Ankel-Simons, 2007). This approach is increasingly developed and known as ‘‘ecological functional morphology’’, ‘‘ecomorphology’’, or ‘‘eco-funk’’. This approach suggests several advantages over the uniformitarian or more simply a ‘‘nearest relative’s habitat preference’’ approach. The most important advantage of ecomorphology is its testability as noted above, as well as the fact that the exact taxonomic affinity of the fossil need not be known. In addition, ecomorphological approach can also contribute to see the evolutionary change with in the phylogenetic lineage if the taxonomic group is specified. McKee (2001) also support this idea by suggesting that ecological changes on the African continent played a role in shaping the evolutionary course of cercopithecids and other mammals during the Pliocene and Pleistocene.

On the other hand, combining a taxon free data set with the approach of ecological functional morphology permits the incorporation of unassigned (undetermined) or sometimes even unassignable specimens to specific taxonomic group into the

paleoecological reconstruction study. But, caution must be taken even at different taxonomic level here because taxonomic affinity may still partly control at least a portion of the expression of certain morphological traits (Degusta and Vrba, 2003).

The morphology of an organism is constrained and shaped by its evolutionary history, and is not developed specifically and solely for its current habitat. As such, phylogeny represents a potentially confounding variable in attempting to infer habitat preference from functional morphology. For example, the one forest-dwelling species that was open country subfamily is likely to retain some open-country dietary adaptations due to its evolutionary history. Similarly, a lineage that shifts from the forest to the plains may retain, at least for some time, a few adaptations associated with closed habitat dietary adaptation. So the use of functional morphology to infer paleohabitats is only 'taxon-free' in the limited sense that the method does not require taxonomic identification of the fossils used when the purpose does not need to consider the evolutionary trend.

The practical implementation of a functional morphological approach to paleohabitat reconstruction focuses on morphological characters, usually metric in nature but sometimes non-metric (shape defined according to descriptive criteria), that are potentially related to diet. One of the ecomorphological features that have proven useful in past habitat reconstructions is the cercopithecidae dental morphology. From such dental morphology, Leakey et al. (2003) revealed that the Pliocene and Pleistocene colobines were more likely primarily seed eaters living in more open country and eating leaves only seasonally when seeds were unavailable. The semiterrestrial rather than arboreal adaptations of the post-cranial anatomy of the fossil colobines (Frost, 2001) can support this suggestion. In essence, then, mature leaves may have been the original fallback food of colobines. Leakey et al. (2003) stated that the prevalence of arboreal monkeys in Africa today is a result of recent radiations of both arboreal forest-dependent colobines and the largely forest-inhabiting guenons. Consequently, they pointed out that this modern prevalence of forest and closed woodland cercopithecid habitats has led to biased views to the habitat reconstructions of fossil cercopithecid species. However, ecomorphological analysis enables us to search out the most probable paleoecology of

fossil cercopithecoidea which can be compared to the Lothagam fossils (Leakey et al., 2003) that show contrast to extant analogy outlooks.

Moreover, the cercopithecid fossil record shows a timely reminder that caution should be taken when interpreting past ecologies using the presence of taxa which today are associated with specific habitats. For example, the graminivorous *Theropithecus gelada* is today restricted to the grassy highlands of Ethiopia (Nowak, 1999). In the past, although *T. oswaldi* was suggested to be a habitual open country graminivore, studies of the postcranial anatomy (Krentz, 1993), the dental microwear (Teaford 1993), and the dental morphology of another species, *T. brumpti*, have shown that it had been an arboreal riverine gallery forest habitat dwelling species, possibly largely frugivorous (Eck et al., 1987; Gibert et al., 1995 and Leakey et al., 2003). Further more, as described above, Leakey et al. (2003) argued that the specialized arboreal folivorous colobinae known today are in sharp contrast to their fossil record of a long evolutionary history of semiterrestrial seed eaters.

Therefore, this study is primarily aimed at investigating the most probable dietary adaptation of different cercopithecids collected in the Lower Omo Basin, Shungura Formation, of Ethiopia. The investigation is made based on the relationship of shearing crest development and diet at their phylogenetic group. The study also aims to reconstruct their habitat preference and environmental changes on the basis of their dietary adaptation which can be reconstructed from the ecomorphological result and relative proportions of species compositions across stratigraphic members respectively.

1.2. Objectives of the study

1.2.1. General objective of the study

The general objective of the study is to investigate the dietary adaptation of different cercopithecoidea phylogenetic groups/lineages of the Shungura Formation on the basis of Shearing Quotient based Ecomorphological Analysis and reconstruct their habitat preferences along with paleoenvironmental changes.

1.2.2. Specific objectives of the study

The specific objectives of the study are:

- To reconstruct the dietary adaptation of different cercopithecidae groups on the basis of their shearing quotient.
- To evaluate dietary adaptation differences among the phylogenetic groups by comparing the shearing quotients of the different phylogenetic groups which occur together in different stratigraphic members of the Shungura Formation.
- To verify discernible dietary differences among the temporally successive phylogenetic groups by comparing the shearing quotients of cercopithecoids in higher stratigraphic members to that of cercopithecoids from earlier stratigraphic members;
- To reconstruct the cercopithecid habitat preferences and analyze the paleoenvironmental changes of the Lower Omo Basin from the results obtained in this study, in combination with other available evidences from previous studies.

1.3. Research questions

- Do different Plio-Pleistocene cercopithecidae taxa of the Shungura Formation reveal remarkable shearing quotient variations that characterize different dietary adaptations?
- Is there considerable shearing quotient difference between or among the phylogenetic groups?
- Is there significant shearing quotient difference between/among taxa across stratigraphic members?

- Do the broad dietary adaptation category and geological time show some trend of relation?
- Do the cercopithecids that occur in different stratigraphic members show mosaic of habitat preference ranges?
- Can the proportion of species of different dietary category show relation to changes in Paleoenvironmental evidences?

1.4. Significance of the study

The palaeodiet and palaeohabitat reconstruction trends based on assumptions of taxonomic uniformitarianism oversimplify the true extent of naturally occurring ecological variability and evolutionary changes. However, this ecomorphological study of cercopithecidae with its long time scale (3.6-1.16Ma) enables to see the morphological and behavioral adaptation that can ultimately show the behavioral variability and ecological diversity as well as the causal factor for their diversity and evolutionary changes. In addition, the implications of this study also can be used to test habitat-specific hypotheses or environmental hypotheses of Hominin evolution, (i.e. hominin adaptive evolution are habitat-specific or adaptations that arose to meet the special demands of a particular type of environmental setting). This is because Hominids and cercopithecids are phylogenetically closely related and undoubtedly shared the same ecological conditions and competed for similar resources, and were hunted by the same predators.

2. LITRATURE REVIEW

2.1. Paleodietary Adaptation and Evolutionary Success of Cercopithecoids

Fossil Cercopithecids are known from the Miocene through the Pleistocene epoch of the tertiary, and only this time span is mostly considered for paleobiology and evolutionary reconstruction, or radiation of old world monkeys (Delson,1978). In this period, old world monkeys have a long history of sharing their environments with hominids and competed for the same resources (El-Zaatari et al., 2005 and Carter, 2006).

In primate evolution, there have been several successive radiations, of which two are still flourishing, one of them being the cercopithecidae (Delson, 1979). Cercopithecidae, are the most successful family of living primates in terms of species diversity and by their tolerance of different ecological/environmental situations, which is surpassed only by *Homo* (Delson, 1978). They might have evolved from the early Miocene to middle Miocene, and their diversity was in fact low during the early to middle Miocene (Delson, 1975, 1978; Szalay and Delson, 1979; Hill et al, 2002; Reed and Bidner, 2004 and Delson and Tattersall, 2006). In the late Miocene, even though, the family was sparsely represented by four or five species, they became a dominant element of the Old World primate faunas (Delson, 1979). Consequently, they had an explosive diversification by the late Miocene to early Pleistocene (Frost, 2001). On the other hand, Hominoids seem to have been out competed in most habitats, both forested and more open, from later Miocene into Pleistocene times, and only a few genera maintained isolated footholds in Asia (Delson, 1978 and Conroy, 1990).

Though, it is not yet possible to be definite about the dietary adaptations of ancestral cercopithecoids, the *Victoriapithecus* dental morphology with its similarities to that of the papionini may be the ancestral adaptation to frugivory. Two monkey species that were considered to show evidence of the differentiation of the colobines and cercopithecines were recovered in the middle Miocene at Maboko (Andrew, 1985 and Benefit, 1999). However, among these large collections of dentitions in which *Victoriapithecus* has been

identified from Maboko, there is no indication of dental colobine adaptations. This can be interpreted as either because the ancestral colobines may not have shared dental character with their ancestor, victoriapithecine, or a closer colobine ancestor simply was not present at Maboko for ecological reasons. Therefore, it can be noted that the time of emergence of the colobine dentition in the evolutionary record is not clear (Leakey et al., 2003). Nevertheless, the earliest known preserved colobine is *Microcolobus tugenensis* whose molar teeth show the typical colobine morphology. In addition, as indicated in Leakey et al. (2003) there is no evidence, earlier than *Microcolobus,* for the divergence of the two subfamilies.

In the plio-Pleistocene cheek teeth cusp relief of cercopithecidae increased, especially as representatives of a relatively derived conditions within the group, have been observed (Benefit, 1999). This feature is known to provide longer marginal shearing crests which are usually signal to folivory in primates (Ungar and Kay, 1995; Benefit, 1999; Teaford and Ungar, 2000 and Swindler, 2002). But, the concurrent trend toward terrestrial life was also detected and this is unexpected for a habitual leaf-eater of such dental morphology. Probably, these paradoxical events may instead reflect a dietary adaptation closer to mixed diet or coupled with expansion into a range of habitats and substrates, which eventually flourished into the immense range of niches occupied by Plio-Pleistocene cercopithecids (Delson, 1979; Frost, 2001 and Swindler, 2002).

Plio-Pleistocene cercopithecids show more diversity. For instance, mangabey and guenon fossils have been found in addition to macaques, baboons and *Theropithecus* fossils. Mouri (2003) speculated that the diversity of the present species is a relatively new phenomenon (since 1 Ma. at present). Cercopithecoids are a highly successful group, having the greatest number of species and broadest geographic and ecological distributions of all living nonhuman primates (Andrews, 1985; Conroy, 1990 and Fleagle, 1999). As stated in Andrews (1985) and Conroy (1990) the adaptive radiation of old world monkeys especially in the middle Miocene to late Miocene parallels the apparent evolutionary decline of many hominoid species from Eurasia and Africa. These authors suggested that there is a causal relationship between these evolutionary trends.

The possible explanation for this evolutionary trend or change lies in the relationship between the dietary and habitat preferences of each group. The retention of frugivorous diet in most hominoids (the “primitive” dietary condition) and the associated primitive character of their dentition can generally be associated with forest habitats (Andrews, 1985b; Conroy, 1990 and Benefit, 1999). Therefore, the primitive teeth and diets in hominoids contrast with the specialized teeth and diets in cercopithecoids. As Conroy (1990) and Swindler (2002) stated, the derived adaptations of cercopithecoids’ digestive tract give these primates an advantage over hominoids in terms of dietary availability. For instance, colobine stomach is specialized to digest cellulose, a vast new food source not available to hominoids. In addition, the cercopithecines can also tolerate eating unripe fruit while hominoid’s stomach can not. Consequently, the monkeys can explore the food resources earlier in their growths than the hominoids can, even though cercopithecines and hominoids may eat similar fruit from the same trees.

On the other side, Swindler (2002), Benefit (1999), Blue et al. (2006), and Cachel (2006) associated the radiation of cercopithecoid monkeys with their specialized bilophodont molars. Bilophodont molars give an adaptive advantage to cercopithecoids than nonbilophodont Miocene hominoids since cercopithecoids are able to shear tough, mature leaves that could not be consumed by hominoids. In addition, leaves are generally available and easier to obtain than fruits, which are typical ape foods. Thus, cercopithecoids are able to exploit a dietary resource which is unavailable to primates that lack such specialized molar lophs or shearing crests such as most hominoid species. This ability of primitive cercopithecoids to do so gave them an evolutionary advantage over ancestral apes by allowing them to survive during periods of shortage of fruits. Therefore, this may have been critical for evolutionary success of cercopithecoids over hominoids during the late Miocene, under condition of increasing seasonality in which the forests began to vanish (Eronen and Rook, 2004). According to these authors, the cercopithecoids seem to have been able to adapt to wide range of environments including the more open and dry environments.

2.2. Dental Evidence for Dietary Adaptation

The predominance of teeth in the primate fossil record is prominently important both in studies of phylogenetic affinity and paleodietary reconstructions (Ungar and Kay, 1995; Benefit, 1999; Fleagle, 1999; Ungar and Williamson, 2000; Leakey et al., 2003; Singltone, 2003; El-Zaatari et al., 2005; Carter, 2006; Grine et al., 2006; White, 2006 and Procter, 2007). Thus, a close examination of the dental evidence variation is crucial to the accurate reconstruction of fossil primate paleobiology. For example, dietary adaptation of the fossils, which is very important for paleoenvironmental reconstruction, can be developed from five sources: analyses of tooth size, tooth shape, enamel structure, dental microwear, and jaw biomechanics (Teaford and Ungar, 2000). In such studies, comparative analyses of extant and fossil primates have yielded many useful generalizations concerning relationships between dental evidences and diet.

Early reconstructions of primitive cercopithecoid dental and dietary adaptations indicate that Old World monkeys use their bilophodont teeth differently than do other lophodont mammals because they do not shear food directly between their transverse lophs. Instead, shear takes place along the margins of cusps, known as shear crests (Benefit, 1999). Among bilophodont Old World monkeys, frugivory is as common as folivory. Field studies on extant cercopithecidae indicate that many colobines once assumed to be folivorous, especially *Colobus, Procolobus, Semnopithecus, Presbytis,* and *Nasalis,* actually consume as many seeds as they do leaves (Benefit, 1999). These seeds are not hard seeds rather they are undried with their coats. Yet frugivorous and seed-eating Old World monkeys are as bilophodont as the folivorous cercopithecoids are.

Grine et al. (2006) point out that morphological attributes may reflect the efficiency with which teeth can process different types of food, and inform us about the range of foods a species is capable of fracturing, but they do not provide direct evidence for “what an animal actually ate?”. Dental adaptations may reflect preferred dietary items, fallback resources, or both, but they might be biased towards those foods that are difficult to fracture or puncture. Therefore, imprecise functional relationship between teeth form and diet is even more difficult to interpret when analyzing morphologies (or combinations of

morphologies) that is unique to the fossil record. In essence, the anatomical record may speak to specific adaptations of a species or lineage, but these may or may not be useful to what individuals actually consumed at any given time (Grine et al., 2006).

Nevertheless, Ankel-Simons (2007) points out that it may be possible to hypothesize with great caution that certain occlusal tooth morphologies did evolve in response to specialized dietary habits. In this hypothesis dental morphology varies in relation to their active role in mastication. The correlations are as the scoop-shaped, chisel-edged incisors with the consumption of soft food item, crested molars with the slicing of tough food items, or flat and low-cusped molars with the crushing of food items.

Therefore, whether a monkey eats fruits, seeds, or leaves its diet is usually correlated strongly with its shear-crest length (longer in folivores) (Ungar and Kay, 1995; Ungar, 1998; Benefit, 1999 and Ungar and Wiliamson, 2000), degree of cusp relief (greater in folivores), thickness of enamel (thinner in folivores) and proximity of cusp tips in both a mesiodistal and buccolingual direction (closer in frugivores, leading to greater flare of the sides of the crown relative to the smaller occlusal area, as well as to a longer mesial shelf) (Singleton, 2003). In addition, diet is also related to incisor size and implantation of the upper central incisors (more procumbently implanted and broader in frugivores).

Morphological features of the occlusal surface and the difference in the size of the anterior dentition indicate the dietary differences in the two subfamilies of cercopithecidae. As indicated in Benefit (1999) and Leakey et al. (2003) the colobines, with their small anterior dentition and prominent transverse loph(id)s were probably adapted to eat leaves and some seeds, whereas the cercopithecines, with their large anterior dentition and large cheek teeth with less occlusal relief were eating mainly fruits.

Tooth size differences, especially the incisors, among cercopithecoidea reflect dietary differences. This is suggested because the primary function of incisors for primates is the preparation of food items for mastication. Higher primates that feed primarily on large objects (e.g., fruit) often have larger incisors than primates that eat small and harder

objects (e.g., seeds, leaves, grasses) because it is necessary for them to reduce the size of their food so that they can chew it between their molars (Teaford and Ungar, 2000 and Ankel-Simons, 2007). As such, it is speculated that large incisors in fossil cercopithecidae imply the same dietary adaptation as in the extant ones.

On the other hand, the shapes of primate molar teeth reflect the fracture properties of foods that these animals eat. This is suggested in a view that variations in tooth shape are considered as a means of adapting to changes in the internal characteristics of foods, such as their strength, toughness, and deformability (Teaford and Ungar, 2000). Taxa that often eat tough leaves, for example, have more occlusal relief and longer shearing crests than do species adapted to consume hard objects (Singleton, 2003 and Walker and Murray, 1975). Such crests are much better suited to cut up or chop up tough food items such as leaves than are teeth that lack shearing crests. Therefore, from such justification it can be suggested that dental topography differences between cercopithecidae species track diet even for worn teeth.

Tooth enamel thickness has also been argued to be an adaptation to protect teeth against breakage given a diet including hard, brittle foods requiring high occlusal forces to be cracked (Daegling and McGraw, 2007). On the other hand, thinner enamel facilitates quicker dentin exposure, which can increase surface sharpness. Therefore, this might suggest another adaptation for efficient fracturing of tough foods (Teaford, 2000).

Ancestral monkeys that occupied mixed leaf-and-fruit niche in the early Miocene might have diverged by the mid-Miocene into the source groups for the two subfamilies. Early colobines tend to develop specialized dentitions and digestive tracts to consume leaves, whereas early cercopithecines retain the earlier food preferences or re-emphasizing fruits, as well as concentrating on development of terrestrial locomotion with concomitant evolution of longer faces and cheek pouches (Delson, 1978).

Dietary reconstructions for Late Miocene-Pleistocene colobine and cercopithecine monkeys indicate that both subfamilies evolved from a frugivorous ancestor (Leakey et

al., 2003). Nonetheless, Miocene colobines could masticate leaves more efficiently than victoriapithecids could, but this adaptation was not shared by cercopithecines. Late Miocene and Pliocene colobine monkeys possessed all of the dental features that separate colobine from cercopithecine monkeys: taller shear crests, stronger occlusal cusp relief, and larger central basins. However, their molar teeth were less specialized for folivory than are those of some modern forms. Plio-Pleistocene colobines were as derived as their modern counterparts in having high occlusal relief, but tended to have shorter shear crests and a greater degree of flare as compared to their modern counterparts. For example, as shown in Benefit (1999) the annual diets of *Paracolobus* from Laetoli and Omo and *Rhinocolobus* from Koobi Fora are reconstructed as having included more fruits than leaves when it is made on the basis of lower second-molar shear quotients and flare, even though the opposite is true when diets are reconstructed based on their high cusp relief.

The fossil evidences from the above example and additional indication in Leakey et al. (2003) can suggest that the evolution of cercopithecoid bilophodonty was probably related to an adaptation for the consumption of hard fruits and seeds rather than leaves. Teaford (2000) suggests that cercopithecoid loph(id)s evolved to produce cusps with a distinct wedge shape not seen in other catarrhines. Such wedges are efficient at producing initial fractures on tough items such as seeds, while the blade-like crests on the margins of the wedges are preadapted for slicing. In addition, formation of the lower molar distal lophid increased the number of distinct grinding facets on victoriapithecid lower molars relative to those of other catarrhines (Benefit, 1999).

2.3. Phylogenetic Relationship of Cercopithecidae

Cercopithecidae represent one of the largest and most diverse primate families. They have diagnostic features, especially in dietary adaptations apart from craniofacial morphology described in different literatures (e.g. Delson, 1975, 1979, 1992; Szalay and Delson, 1979; Strasser and Delson, 1987 and Fleagle, 1999). On the basis of diagnostic features, cercopithecidae can be divided into two ecologically and morphologically distinct subfamilies: cercopithecinae (cheek-pouched monkeys) and colobinae (leaf-eating monkeys) (Delson, 1992; Disotell, 1996; Fleagle, 1999; Swindler, 2002; Xing et

al, 2005 and Delson and Tattersall, 2006). The distinct dietary adaptations of the two subfamilies are the specialized digestive tract in colobines and the buccal pouches in cercopithecines. The colobines eat leaves, which they digest in specialized stomachs convergently similar to those of ruminant artiodactyls such as cattle, while cercopithecines have much wider food choice, but often concentrate on fruit. Dietary preferences are also reflected in teeth as it has been discussed in dental morphology. These dietary adaptive features and dental morphology are also two of the several potential morphological synapomorphies that define the colobine and cercopithecine clades (Disotell, 1996). Moreover, colobines are distinctive among catarrhines in the early eruption of their molars relative to anterior teeth; however, this feature is primitive, and a common pattern in lemurs, and platyrrhines (Harvati and Frost, 2007).

In turn the subfamily cercopithecinae encompasses the tribes cercopithecini and papionini. Papionini is further classified into subtribes macacina and papionina. Cercopithecini includes genera *Cercopithecus, Allenopithecus, Miopithecus, Erythrocebus,* and *Chlorocebus* (Disotell, 1996 and Groves, 2004). On the other hand the tribe papionini includes subtribe macacina with only one genus *Macaca*, and subtribe papionina includes genera *Cercocebus*, *Lophocebu*s, *Theropithecus*, *Papio*, *Parapapio*, *Pliopapio* and *Mandrillus* (Delson, 1978; Szalay and Delson, 1979; Eck et al., 1987; Strasser and Delson, 1987; Disotell, 1996; Fleagle, 1999; Frost, 2001 and Xing et al., 2005).

There are also perspectives that split the colobines biogeographically into African and Asian clades. With this view, subfamily colobinae is divided into African colobines (subtribe colobina) and Asian colobines (subtribe presbytina) (Disotell, 1996, Fleagle, 1999). The African colobines are generally placed in to genera, including *Colobus, Procolobus, Piliocolobus, Paracolobus, Rhinocolobus, Micorcolobus, Libypithecus, Cercopithecoides and Kuceracolobus* (Delson, 1975; Eck et al., 1987; Frost, 2001 and Hlusko, 2006). The Asian leaf-monkeys are classified in to genera, *Mesopithecus, Dolichopithecus, Nasalis, Presbytis, Pygathrix, Rhinopithecus, Semnopithecus, Simias,* and *Trachypithecus* (Delson, 1975 and Strasser and Delson,1987), but latter *Presbytiscus*

(Disotell, 1996) is considered as a separate genus. In addition, Xing et al. (2005) indicate as there is debate in consideration of *Presbytiscus* and another genus, *Allochrocebus* as separate genera.

3. MATERIALS AND METHODS

3.1. Materials

The fossil record of cercopithecidae from the Shungura and Usno Formations of Southwestern Ethiopia is one of the richest that includes approximately 6,500 specimens. Eck et al. (1987) indicate the allocation of these specimens to at least four genera and seven species of cercopithecines and three genera and three species of colobines, making the sample one of the most diverse as well. The specimens were recovered from localities of thoroughly documented stratigraphic provinces by the American and French contingents of the International Omo Research Expedition between 1967 and 1976.

From the Omo cercopithecidae collections this study considered only the cercopithecid specimens from the Shungura Formation since in either case (faunal or floral), a relatively firm stratigraphic framework is a necessary prerequisite for the development of an evolutionary and environmental history. In this case the stratigraphic framework of the Shungura Formation is well developed as shown in figure 1 and described in different previous studies (e.g. Bobe et al., 2002; Zeresenay Alemseged, 2003 and Bobe and Behrensmeyer, 2004). The cercopithecids in the data source are grouped in to *Cercopithecus sp.*, *Papio*, small papionini (group A and B), large papionini, *Theropithecus* indent, *Theropithecus brumpti*, *Theropithecus oswaldi*, colobinae indent, *Paracolobus mutiwa*, *Rhinocolobus turkanaensis* and *colobus sp.*. The detail systematics descriptions of these taxonomic groups are provided in Eck et al., 1987. And their distribution in the stratigraphic members (A-L) (geological time) is summarized in table 1. However, for the convenience of environmental change analysis, *Theropithecus* indent are considered to either of the two species according to their evolutionary time. As Eck (1977) indicated that small papionini group (A) and small papionini group (B) have affinities to genus *Cercocebus* and genus *Parapapio* respectively, even though it is not documented in the data source. This level of taxonomic diversity presents an invaluable opportunity to gain insight into the cercopithecidae dietary adaptation and paleoecological conditions that existed in the lower Omo basin during the Plio-Pleistocene. Apart from this taxonomic diversity, comparison of body parts preservation through time, of fossil assemblages, indicate that the specimens are recovered with

isotaphonomic (similar taphonomic) biases (Zeresenay Alemseged, 2003) and this also increase the probability that observed similarities and differences in biological responses to be a reflection of original ecological or evolutionary factors rather than disparate taphonomic histories.

Table 1. Distribution summary of cercopithecids across stratigraphic members of the Shungura formation or geological time intervals

Taxa	Stratigraphic members with their Time intervals in Ma										
	A 3.6-3.4	B 3.4 – 2.85	C 2.85 – 2.52	D 2.52 – 2.4	E 2.4-2.36	F 2.36-2.33	G 2.33-1.90	H 1.90-1.74	J 1.74-1.53	K1.53-1.39	L 1.39-1.16
Cercopithecus	+	+	+				+		+		
Papio	+	+	+	+	+	+	+		+	+	
Small Papionini A	+	+	+						+		+
Small Papionini B		+	+		+	+	+			+	+
Large Papionini		+									
T. brumpti		+	+	+	+	+	+				
T. oswaldi			+	+	+	+	+	+	+	+	+
P. mutiwa		+	+	+	+	+	+				
Rhinocolobus	+	+	+	+	+	+	+				
Colobus sp.										+	+

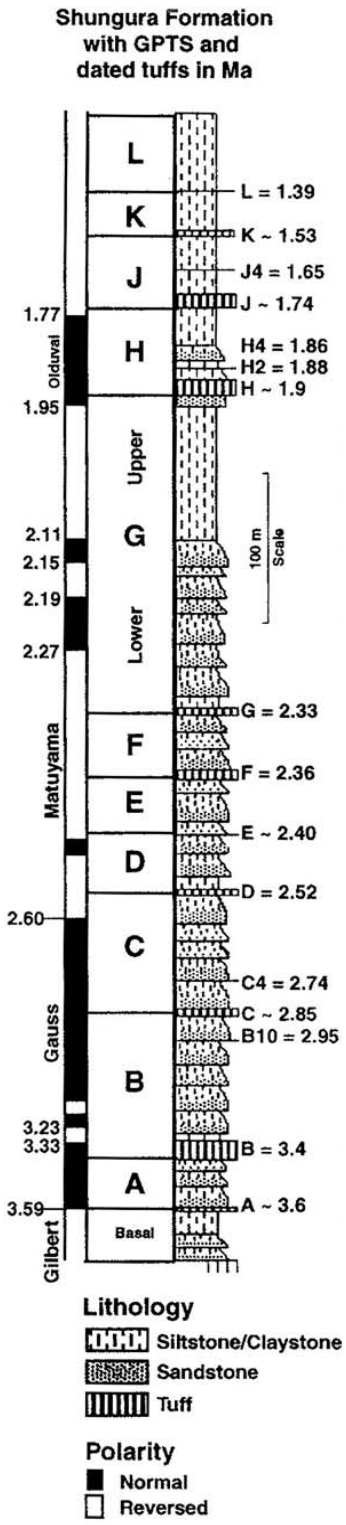

Figure 1. The Shungura Formation stratigraphy showing Members A–L with magnetostratigraphic and radiometric dates (adopted from Zeresenay Alemseged, 2003).

This study is carried out by using the Omo Paleontological faunal collection database which is catalogued in the National Museum of Ethiopia (NME) as a reference. Here the cercopithecid catalogue is used to select second lower molars (study materials) with their corresponding taxonomic group and stratigraphic members as well as to made stratigraphic member distributions summary of the taxa indicated above in table 1. And the specimens that are considered in this ecomorphological study are only unworn or nearly unworn specimens and they are listed in appendix 1.

In addition to the fossil cercopithecidae specimens listed in appendix 1, the extant frugivorous cercopithecine monkeys (*Cercopithecus mitis*, *Cercopithecus sp*., *Chlorocebus aethiops*, *Chlorocebus sp*., *Papio anubis* and *Papio hamadryas*) were used for allometric scaling purpose from frugivorous genera and also *Theropithecus gelada* to draw comparative data that are used to compare in the apparent course of dietary reconstruction and evolution of the Lower Omo cercopithecids. These extant monkey specimens were accessed from the Zoological Natural History Museum of Addis Ababa University (AAU), Zoological laboratory of biology department AAU, NME and Personal collection (Dr. Solomon Yirga) AAU biology department. Additional information of these extant specimens is summarized in appendix 2.

3.2. Methods

Shearing quotient (SQ) is a measure of the relative shear potential of a tooth and it can be used to study dietary adaptations of fossil cercopithecidae (Ungar and Kay, 1995; Ungar, 1998 and Benfit, 1999). SQ studies have been applied to the fossil record by superimposing extinct primate values on an extant primate regression plot. In this way, results for fossils can be compared with those for a baseline series of living primates. Shearing crests are measured as distances from cusp tips to the notches between cusps as well as mesial and distal ends. Crest lengths change with attrition, and quickly become impossible to measure as cusp tips are obliterated by wear. Thus, SQ studies are limited to unworn teeth. As in other SQ studies, this study has not focused on worn teeth because of difficulties in measuring and comparing crest lengths for variably worn specimens. In addition, as a tooth wears, changing of occlusal relief that affect shearing crest length can be expected (Ungar and Williamson, 2000).

In this diet inference method, for measuring the shear potential of a tooth: the lengths of mesiodistally running shearing crests (1-8) connecting the main cusps of unworn or nearly unworn lower second molars (M_2) were measured as distances from the cusp tips to the notches between cusps and/or mesial and distal ends. In addition to the shearing crest lengths, its mesiodistal length was also measured from mesial to distal occlusal ends by following previous protocols (Benefit and McCrossn, 1990; Ungar and Kay, 1995; Ungar, 1998; Benefit, 1999 and Ungar and Williamson, 2000). A total of 9 linear length measurements were taken for each individual specimen (figure 2). The measurements were taken three times for each length with a digital caliper and recorded to the nearest tenth of a millimeter (0.01mm). Mean values for the shearing crest lengths (1-8) and mesiodistal length were computed for each measured specimen and mean values of the shearing crest lengths (1-8) were summed to obtain the total shearing crest length. The mean total shearing crest length and mesiodistal length of the extant frugivore taxa were transformed in to $\log_{10}$ and their mean are summarized in table 2. Then a least-squares regression line that can fit for these groups of frugivorous extant cercopithecine species (*Cercopithecus* spp., *Chlorocebus* spp. and *Papio spp*.) alone with M_2 length as the independent variable and total shear crest length as the dependent variable were used to

scale for allometric analysis of the extinct taxa under study (figure 3). The only frugivorus extant cercopithecine is used to control for allometric changes since the late Miocene through Pleistocene colobine and cercopithecine monkeys were believed to be evolved from a common fruigivorus ancestor, *Victoriapithecus* (Benefit, 1999).

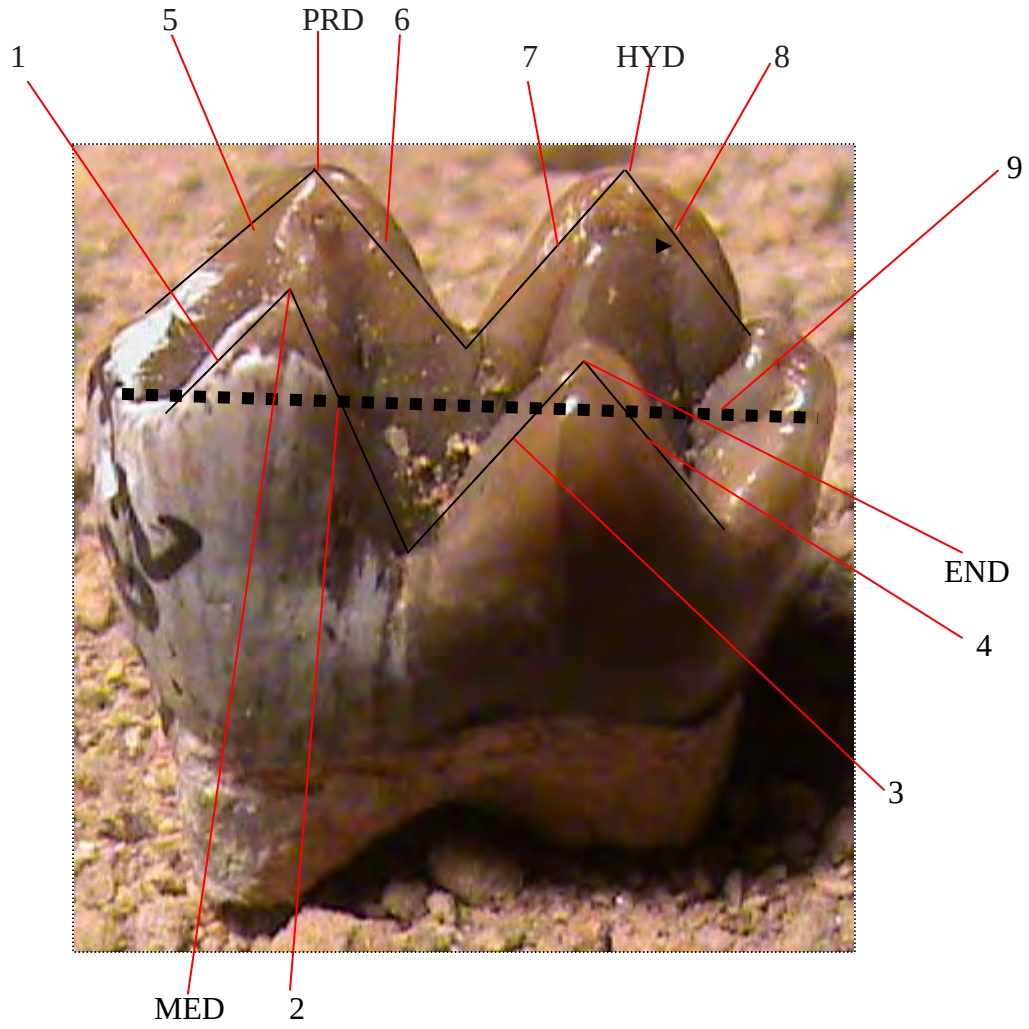

Figure 2. Measurement of shearing crest lengths (solid line) (1-8) and mesiodistal occlusal table length (broken line) on a *Theropithecus* molar. MED, metaconid; END, entoconid; PRD, protoconid; HYD, hypoconid cusps.

Table 2. Descriptive statistics summary of logarismic transformed values of Shearing crest and mesiodistal length of Extant frugivore cercopithecidae.

Taxa		Log sum of shearing crests 1-8	Log second lower molar length
Chlorocebus aethiops	Mean	1.2761361	.78848480
	N	4	4
	Std. Deviation	.03280950	.00654685
Cercopithecus mitis	Mean	1.2945397	.78390357
	N	1	1
	Std. Deviation	.	.
Cercopithecus sp.?	Mean	1.2781436	.77935595
	N	1	1
	Std. Deviation	.	.
Cercopithecus sp.? (zoo. Lab.)	Mean	1.2715318	.77766843
	N	1	1
	Std. Deviation	.	.
chlorocebus sp.?	Mean	1.2912208	.78342711
	N	1	1
	Std. Deviation	.	.
Papio anubis	Mean	1.5580924	1.0936757
	N	2	2
	Std. Deviation	.00985408	.02391996
Papio hamadryas	Mean	1.5619923	1.1030399
	N	2	2
	Std. Deviation	.00628631	.00621715

Different studies on dietary reconstruction of fossil (extinct) primates have recognized that comparisons of occlusal form between species require a quantitative approach. Accordingly, studies of SQ have been applied to a wide range of fossil primates, leading to important dietary inferences for many extinct species (Kay, 1977; Benefit and McCrossn, 1990; Ungar and Kay, 1995; Ungar, 1998; Benefit, 1999). Thus, to reach at the dietary adaptation category of the taxa, SQs were computed as deviations from the frugivore regression line. As indicated in Ungar and Kay (1995) shearing quotients (SQs)

are expressed as the difference between the observed and expected shearing-crest lengths for a given mesiodistal tooth length. Expected shearing-crest lengths were computed from the M_2 mesiodistal length for all taxa by using the regression line equation of the frugivorous extant taxa (figure 3):

$\text{Log}_{10}\ \text{Se} = 0.879 * \log_{10} M_2\ \text{length} + 0.594$,

Where, Se- is the expected summed shearing-crest length for a given M_2 length.

0.879- is slope of the regression equation of the frugivorous living taxa

0.594- is the intercept of the same regression equation

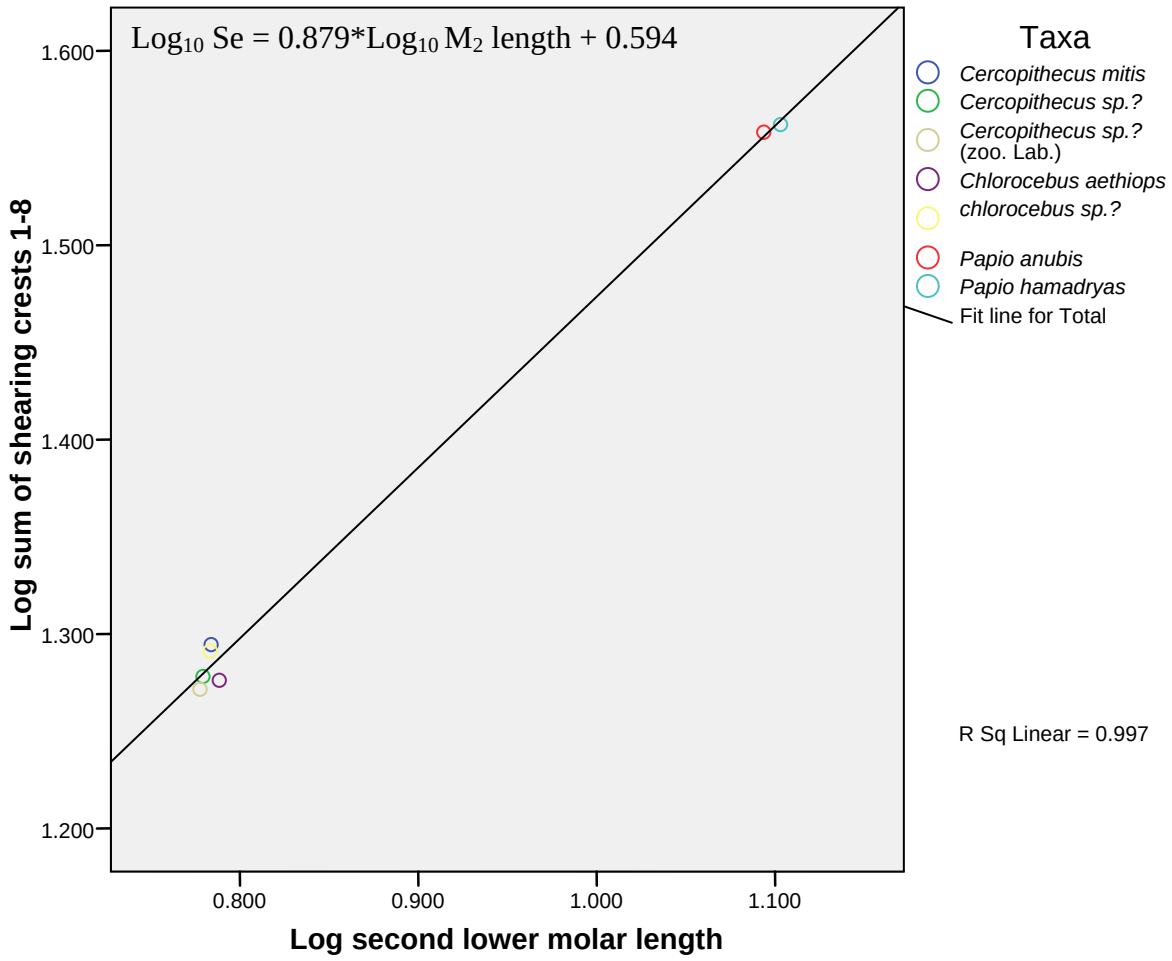

Figure 3. Regression plot of summed shearing crest lengths (mm) versus second lower molar mesiodistal length (mm) of extant frugivore cercoipthecine at 95% degree of confidence and r = 0.98.

Therefore, SQ is computed using the formula as:
SQ = 100(So-Se)/Se, where So is observed shearing crest length which is equal to the sum of the lengths of the eight shear crests, and Se is expected shearing crest length which is calculated from the previous formula.

In such analysis, higher SQ indicates the longer shearing crests relative to expectation of the typical frugivorous extant cercopithecidae, while lower SQ value denotes the shorter shearing crest development (Ungar and Kay, 1995; Ungar, 1998; Benefit, 1999 and Ungar and Williamson, 2000).

Finally, to test for environmental change through time, the broadly defined habitat preferences of cercopithecids has been assigned from their dietary adaptation and related ecomorphological and other evidences. Thus, from this analysis changes in relative proportion of taxa associated with open and closed habitat have been used to reconstruct members of the spectrum of the Omo paleoenvironments.

3.2.1. Statistical Analyses

To determine the dietary adaptation of the phylogenetic groups under consideration descriptive statistics, correlation and regression analyses were conducted. Moreover, for the analyses of shearing quotient variation between or among the phylogenetic groups descriptive statistics were used. To compare groups for statistical significance differences, the Kruskal-Wallis H Test, the nonparametric analog of one-way analysis of variance, particularly asymptotic significance and Monte Carlo approximation with 95% confidence level were used since the data are not normally distributed. Finally for paleoenvironmental reconstruction relative proportions of cercopithecids on the basis of their dietary adaptation were analyzed across time scale (stratigraphic members) and presented through line graph. The entire data analyses were made by using SPSS version 15 and Excel 2003 software programs.

4. RESULTS AND DISCUSSION

4.1. Results

4.1.1. Reconstruction of dietary adaptation

The result observed from shearing quotient analysis of this study revealed highly significant differences among the colobine and cercopithecine genera and /or species in their shearing crest development at P = 0.00 (table 3). Except *Cercopithecus sp.* the entire cercopithecinae groups considered in this study (e.g., *Papio*, large papionini, small papionini A and B, *T. brumpti* and *T. oswaldi*) have lower shearing quotient, while the whole colobinae groups (*Colobus sp*., *P. mutiwi* and *R. turkanaensis*) showed higher shearing quotient (fig., 4).

Table 3. Statistical significance test summary of cercopithecine and colobine shearing quotients.

Test Statistics(b,c)

			SQ
Chi-Square			38.340
Df			9
Asymp. Sig.			.000
Monte Carlo Sig.	Sig.		.000(a)
	95% Confidence Interval	Lower Bound	.000
		Upper Bound	.259

a Based on 10 sampled tables with starting seed 2000000.

b Kruskal Wallis Test

c Grouping Variable: Taxa

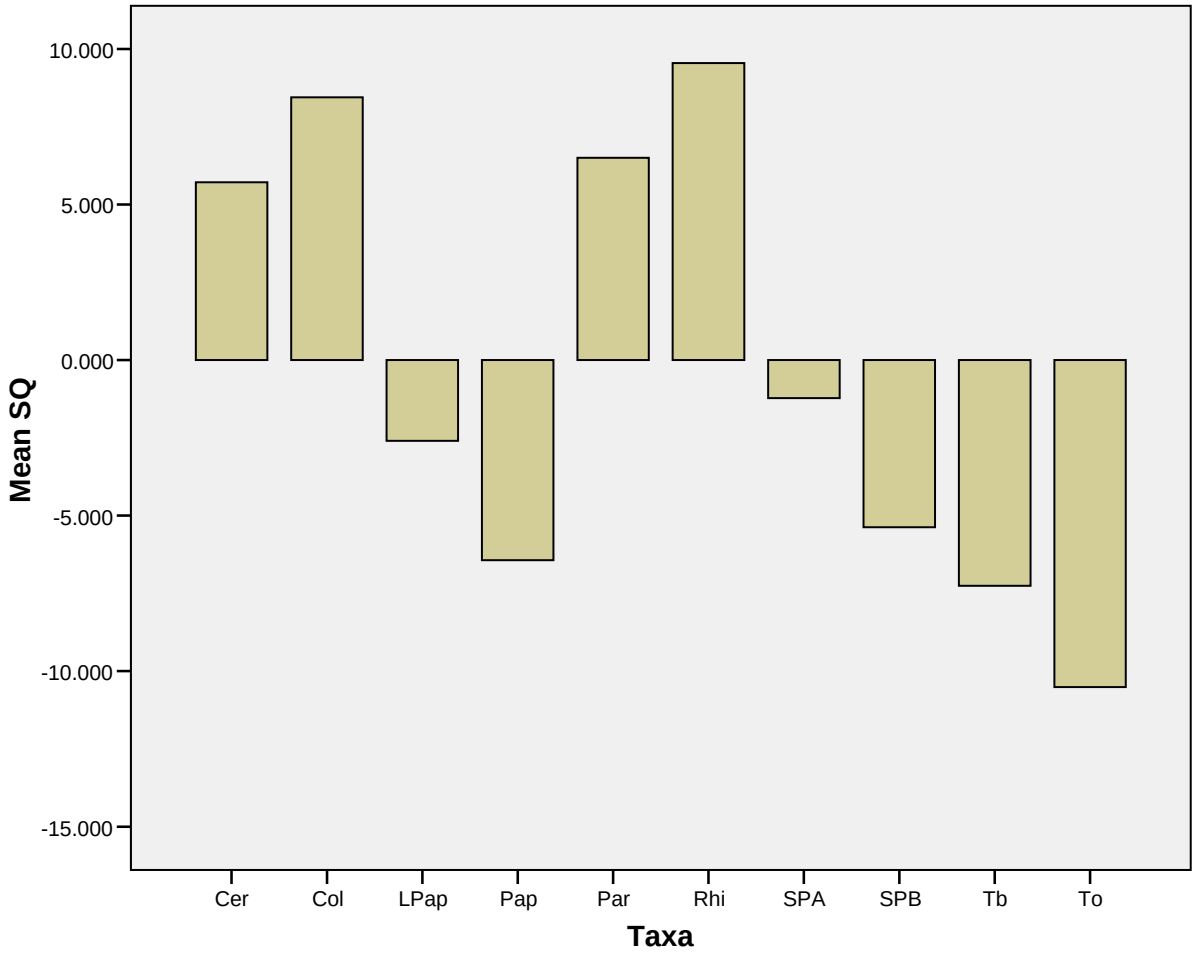

Figure 4. The shearing quotient values that indicate the length of shear crest development of the lower Omo valley cercopithecidae taxa that are coded as Cer, Col, Lpap, Pap, Par, Rhi, SPA, SPB, Tb and To. Note the taxa represented by the code nomination are *Cercopithecus sp*., *Colobus sp*., Large papionini, *Papio sp*., *P. mutiwa*, *R.. turkanaensis*, Small Papionini (A), Small Papionini (B), *T. brumpti* and *T. oswaldi* respectively.

As pointed out in Ungar and Kay (1995) and Ungar and Wiliams (2000) the higher the shearing quotients (SQ) indicate longer shearing crests and more occlusal relief than expected from a species with the diet considered in allometric scaling (regression plot), i.e. frugivore, and the lower SQ indicate shorter shearing crests and less occlusal relief than expected. From this point of reference, *Colobus sp.*, *P. mutiwa* and *R. turkanaensis* have longer shearing crest. On the other hand, all the cercopithecine groups, except *Cercopithecus sp*., namely, *Papio* sp., large papionini, small papionini A and B, *T.*

brumpti and *T. oswaldi* have short crest. If the shearing crest development is compared at the subfamily level, the cercopithecine groups including *Cercopithecus sp*. have shorter shear crest development than the colobine groups (table 4).

Table 4. The shearing quotient descriptive statistics of the lower Omo fossil and extant cercopithecidae

Taxonomic Group	Mean	N	Std. Deviation
Cercopithecus sp.	5.71622	1	.
Colobus sp.	8.44483	1	.
Large Papionini	-2.59604	1	.
Papio sp.	-6.43104	10	3.26127985
P. mutiwa	6.50074	7	7.21728506
R. turkanaensis	9.54356	9	8.38799907
Small Papionini (A)	-1.22662	2	.056884808
Small Papionini (B)	-5.37391	5	2.89915126
T. brumpti	-7.25623	32	6.63391730
T. oswaldi	-10.5115	3	2.11302256
*Cercopithecus spp.**	.36347	3	2.090447
*C. aethiops**	-1.45642	5	6.066901
*Papio spp.**	.14461	4	1.609164
*T. gelada**	38.4479	4	7.339412

Note: the astric (*) symbol represents extant taxa.

Apparently, the shearing quotient pattern of fossil *Cercopithecus sp.* and *T. gelada* are closer to the fossil colobines rather than other fossil and extant cercopithecines (table 4 and fig. 5). This is notably due to a large shearing crest development on their teeth in contrast to their counterparts.

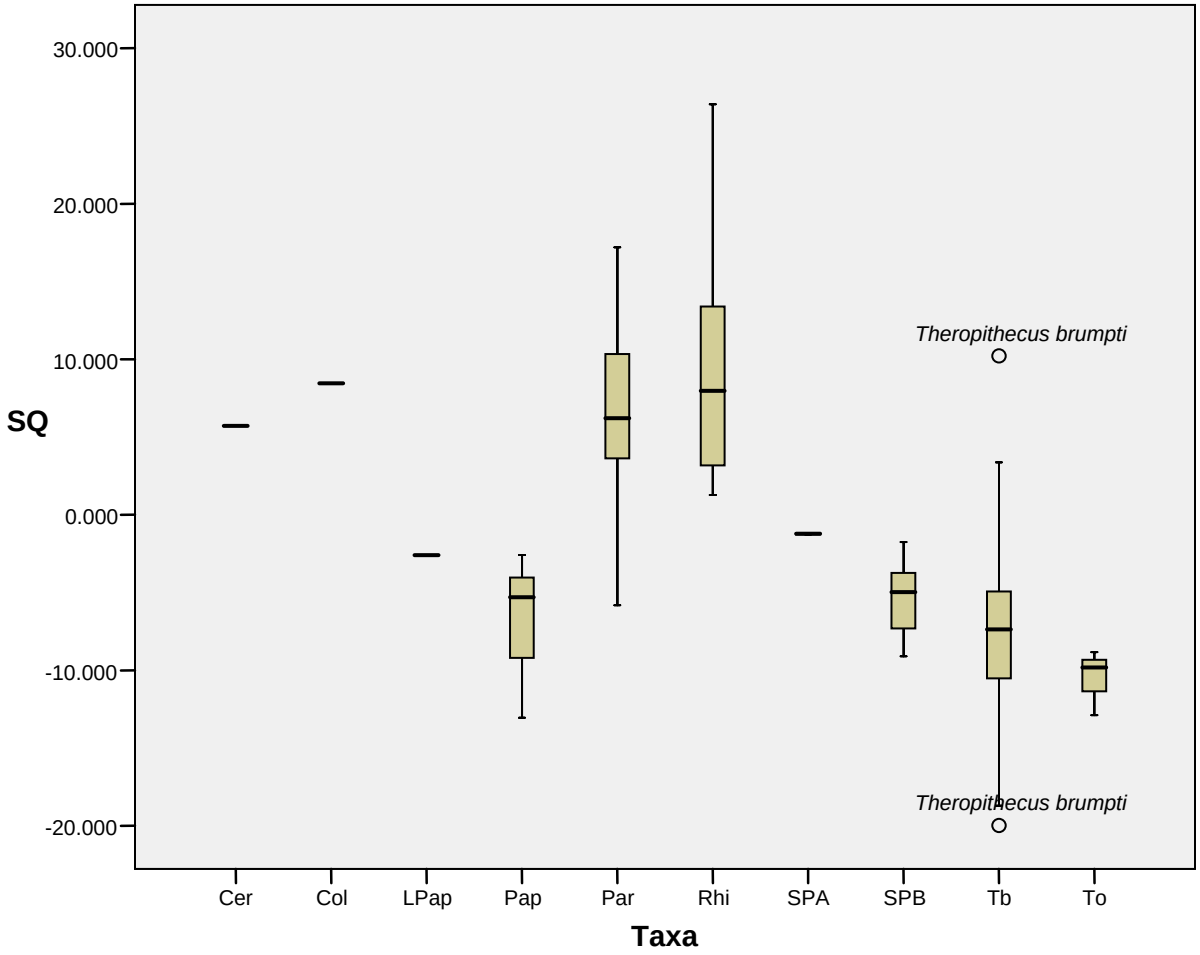

Figure 5. A comparison of the shearing crest development (quotient) of the lower second molars of colobine and cercopithecine genera or species from the Plio-Pleistocene Omo vally cercopithecidae. The taxa represented here are the same as figure 4. The mean, range and 95% confidence limits are indicated by the solid horizontal line, vertical bar and top and bottom horizontal lines, respectively.

Comparative studies have confirmed that folivores have higher SQs than closely related frugivores, and that among frugivores, hard-object specialists have the lowest SQ values (Ungar and Kay, 1995 and Ungar, 1998). Therefore, the entire Plio-Pleistocene colobines (*Colobus sp., P. mutiwa* and *R. turkanaensis*) of the Shungura Formation are folivores rather than frugivores or seed eaters since they have high shearing quotient or longer crest length that can be associated to a better adaptation for slicing of tough foods. On the

other hand, the cercopithecine groups (large papionini, *Papio sp*., small papionini group A and B, *T. brumpti* and *T. oswaldi*) are frugivores as they have low shearing quotient or shorter shear crest length which can be associated to crushing of foods rather than slicing. However, the *Cercopithecus sp.* has intermediate shearing quotient or shear crest length between the colobines and other cercopithecine groups (fig. 5). This intermediate crest length development may indicate that *Cercopithecus sp.* supplements its fruit dietary preference with leaves and/ or insects as a fallback diet. In addition as shown in table 4 and figure 5, *T. oswaldi* has the lowest shearing quotient as compared to the whole cercopithecidae species/ genera. This can also enable to suggest that *T. oswaldi* was mostly seed eater even it could have been graminivore.

4.2. Discussion

4.2.1. Reconstruction of Dietary Adaptation

Primate tooth form reflects the mechanical properties of their diet, since the main relationship between teeth and diet is mechanical processing. In order to break down foods, teeth must stress the food to the point of fracture such that new surfaces are created for further digestion in the gut. This implies, differences in tooth form can be related to differences in mechanical properties of the foods they are adapted to feed on. Thus, focusing on relationships between tooth shape and strength, toughness, and deformability of foods are very important in dietary reconstruction. Fleagle (1999) also emphasized this by stating that the dietary categories accord well with the structural characteristics of primate foods, and thus cercopithecids with defined (specified) dietary category have characteristic features of teeth and guts that enable them to process their different diets.

Much research has focused on such relationships between aspects of dental morphology and diet. For example, Benefit and McCrossin (1990), Benefit (1999), Singlton (2003) associated specific dental morphologies in primates with different physical properties (tough or fiberous, soft and hard or abrasive) of their diet. In these studies, long molar crests have been related to food toughness which is associated with folivorous or insectivorous diets and food hardness has been linked to both thick enamel and short crest, low, rounded cusps. Understanding these relationships allows us to infer dietary adaptations from the teeth of fossil forms.

Tooth shape reflects diet in cercopithecids because foods with different physical properties require different actions to break them down for further processing in the stomach. For example, sharp blade-like teeth would better slice more tough food items like mature leaves with their fibrous nature than would blunt, hammer-like teeth suited to crushing hard, brittle foods. Among such relationships between tooth shape and diet, this study used shear crest to infer dietary adaptations of fossil cercopithecids.

The dietary adaptation differences of the two cercopithecid subfamilies are shown by the relative size of their shear crest length (fig.4) and this is also in agreement with their anterior and posterior dentitions that are suggested to be correlated with dietary adaptations (Fleagle, 1999). Colobines have large posterior teeth and relatively small incisors, whereas most cercopithecines have both large anterior teeth and large cheek teeth. As Jolly (1970) and Hylander (1975) revealed, the relative size of cercopithecids' incisors is highly correlated with diet. Cercopithecids that feed primarily on large food objects (large fruits) have larger incisors than those that feed on smaller food objects (leaves). This difference reflects that larger food objects need more extensive incisal preparation before mastication.

- **Colobines**

Colobines are one subfamily of Old World monkeys and easily distinguished from cercopithecines by their sharp-cusped cheek teeth and relatively narrow incisors (Fleagle, 1999). As indicated in figure 5, the entire colobines of this study site have long shear crest lengths and this suggests that they were folivores. Among these colobine monkeys the *Colobus sp.* which is recorded in the latter stratigraphic members K and L (table 1) has the longest shear crest length next to *R. turkanaensis* and this indicates that *Colobus sp*. can be closest to the living folivorous colobine in its dietary adaptation. As Eck et al. (1987) pointed out, the teeth of this *Colobus sp*. are indistinguishable from both *C. badius* and *C. guereza* in their size and morphology. This size and morphology proximity can corroborate the folivorous dietary adaptation of fossil *Colobus sp*. which is suggested from its shear crest.

On the other hand, the shear crest of *P. mutiwa* is shortest among the colobine species and closest to *Cercopithecus sp*., while *R. turkanaensis* has the longest shear crest among the rest fossil cercopithecids. The lengthy molar shearing crests on the molars of colobine monkeys provide relatively high molar shearing capacity. As a result, they are highly suited for processing of foods with high fracture toughness. When we consider fracture toughness of food, leaves might be tougher than most fruits since most leaves, except the youngest, are toughened by sclerenchyma fibers that are usually arranged around veins in

the form of a sheath. Such tough foods require precise, scissor-like cutting or shearing to be efficiently processed (Lucas, 2004). Thus, the overall long shear crest development of colobine species of the Shungura Formation as compared to the cercopithecine monkeys of the same site can show their folivore dietary adaptation. Based on dental morphological comparison of these species to extant Colobus, Eck et al. (1987) and Fleagle (1999) suggested that both *P. mutiwa* and *R. turkanaensis* are largely adapted to folivorous dietary adaptation. The cusp relief analysis of these species from Benefit (1999) also corroborates the consumption of more leaves than fruits in their diet, even though the opposite is true when diets are reconstructed based on their molar flare.

Since the cusp relief is measured from the lingual cusps of lower molars and these cusps wear less rapidly than the cusps on the opposite side of the tooth, cusp relief has the advantage of being measurable on both unworn and moderately worn molars. This in turn enables to infer more plausible dietary preference of fossil cercopithecids than molar flare which can be more influenced by tooth wear. Benefit (1999) pointed out the relationship of shear crest and cusp relief as greater shear crest length on the molars of folivorous colobine monkeys is accomplished by a decrease in the height of the central basin, mesial fovea and distal fovea above the cervix. This height reduction can also contribute for long crest development as crest lengths are measured from the cusp tips to the base of the notchs (basins) and the same pattern holds true for cusp relief. Therefore, folivorous dietary adaptation of these species which is inferred from their long shear crest length is more plausible.

In addition to dental morphology, from their postcranial elements Leakey (1982), Eck et al. (1987) and Fleagle (1999) indicate that *R. turkanaensis* was an arboreal monkey; while *Paracolobus* is suggested to display some traits that are intermediate between arboreal colobines and terrestrial cercopithecines even if most features are typical of arboreal colobines. The shear crest of *P. mutiwa* which is closest to *Cercopithecus sp*. together with the suggested locomotor behavior may signify that the species included more fruits in its diet compared to *R. turkanaensis* and *Colobus sp.*

- **Cercopithecines**

In contrast to colobine monkeys, the cercopithecine molars have shown short shear crest length development (figure 5). This result is also supported by the combination of low cusp relief and close cusp proximity dental morphologies which can affect their crest development (Benefit, 1999). Even though shear crests of cercopithecines are shorter than colobines, the shear crests of cecopithecines are wider in range. Therefore, their dietary adaptations are analyzed in three relatively closer phylogenetic groups.

Cercopithecus sp.

The fossil *Cercopithecus sp*. shows shear crest development that is closer to fossil colobines, rather than its extant counterparts (table 4). This result is also in agreement with fossil cercopithecine molar microwear patterns which are suggested in Leakey et al. (2003) to be like those of extant colobines. This indicates that Plio-Pleistocene *Cercopithecus sp.* was probably feeding on foods closer to those eaten by extant colobines.

Fruit pulps are easier to ingest and digest than are leaves. In addition, most fruit pulps are high in sugars, even though they are low in fat and protein contents. On the contrary, even if, eating and digesting leaves undoubtedly present the biggest dietary challenges to primates, leaves are not a 'low-quality' resource in absolute terms. On a per weight basis, leaves are often richer in protein than other primate vegetable resources (Lambert, 2007), and the potential energy density is very high as the major component of leaves, cellulose, is nothing more than a polymer of sugar molecules.

Thus, because of the nutritional deficiencies and inaccessibility, or slow ripening rate of fruit as a diet, every predominantly fruit-eating cercopithecid species may supplement their diet with either leaves or insects or both as fall back food.

For the same reason stated above, the observed *Cercopithecus sp.* shear crest being closer to colobine in this study, might be attributed to an adaptation for obtaining protein and minerals from leaves by selecting low-fiber parts of plants, which can be processed in the

gut relatively quickly to extract soluble carbohydrates, proteins and minerals. Moreover, as Wahungu (1998) pointed out, niche differences among fruit-eater species are less obvious and when the Shungura formation is considered the papionini that coexist with *Ceropithecus sp.* were mainly fruit eaters. Thus, moderately developed shear crest of *Cercopithecus sp*. together with its smaller size might be correlated to adaptation to minimize competition with other coexisting frugivore cercopithecines.

Accordingly, the *Cercopithecus sp*. molars' long crests can suggest that *Cercopithecus sp.* was less frugivore specialist than other Omo cercopithecine monkeys*;* instead it was capable of accommodating a diet which included a greater proportion of more fibrous materials, such as young leaves or fruits with differing physical properties. However, in a highly frugivorous diet specialized cercopithecine monkeys' cusps and occlusal crests are low and rounded (Harrison, 1989).

Papionini (excluding *Theropithecus*)

Shear crest estimates for fossil cercopithecids of the Shungura Formation are summarized in table 4 and fig. 5. These table and figure indicate that the papionini in general possess shear crest that is intermediate between fossil *Cercopithecus* and *Theropithecus spp*. The intermediate shear crests between the two extreme cercopithecine groups can suggest that papionini were predominantly frugivorous cercopithecine groups. The reconstructed frugivorous dietary adaptation of the eastern Africa fossil papionins from their dental morphology (Benefit and McCrossin, 1990) also corroborates the Shungura fossil papionins to be highly frugivorous. On the other view, the lack of large pits on the molars microwear of the Lothagam papionins evidenced that East African Plio-Pleistocene papionins were not hard object feeders (Leakey et al., 2003). Therefore, as shown by Benefit and McCrossin (1990) dental morphology, and Leakey et al (2003) molar microwear analyses, the shear crest of the Shungura papionini might reveal that they had better access to soft and easily processed foods, unlike, extant savanna baboons that are often forced to rely on grass corms (under ground storage organs) during the dry season when the preferred foods are not available (Alberts et al., 2005).

Moreover, in contrast to modern savanna baboons that are known to be highly opportunist feeders, using any available resources to different degrees (Wahungu, 1998; Alberts et al., 2005 and Codron et al., 2005), the Shungura papionini adaptation to soft fruits can suggest that their habitats were suitable for production of fruits.

Dietary Adaptation of *Theropithecus*

From the Shungura Plio-Pleistocene *Theropithecus*, *T. oswaldi* has shorter shear crest than *T. brumpti* that have had relatively longer shear crest. And this result indicates that *Theropithecus oswaldi* had a better adaptation for hard, tough or abrasive dietary items that are found commonly on the ground than *T. brumpti*. As Benefit and McCrossin (1990) pointed out, this possible dietary adaptation is substantiated by the presence of thicker enamel on the molars of *T. oswaldi* than on molars of *T. brumpti* from the same site. Thicker molar enamel indicates that molars of *T. oswaldi* have better adaptation for a diet including hard, brittle foods such as seeds or underground storage organs that require high occlusal forces to initiate fracture, since development of thicker enamel has been argued to be an adaptation to protect teeth against wear that can be created due to hard diet abrasion (Kay, 1985; Lambert et al., 2004 and Ungar et al., 2006). On the other hand *T. brumpti* has shear crest length which is closer to *Papio sp*. than *T. oswaldi*, and this points out that *T. brumpti* included more soft fruits in their diets than do the *T. oswaldi*. The rapid rate of cusp deformation and close proximity of the molar cusps observed from the molars of *T. brumpti* also supported more consumption of fruit than leaves (Benefit and McCrossin, 1990).

Modern *Theropithecus* (*T. gelada*)

The molar shear crest length of *T. gelada* is apparently quite distinct as compared to the other cercopithecines. As summarized in table 4, the shear crest of *T. gelada* is extremely longer than the other cercopithecine monkeys. This distinctive shear crests length of *T. gelada* is supported by its dental morphological adaptations (Delson, 1979). High crowns and lophs combined with deep fovea to provide considerable occlusal relief and relatively long-lasting enamel cutting edges to functional analogs in the teeth of other mammals with a large grass component in their diets (Delson, 1979).

The characteristic microwear pattern of *T. gelada* also shows its distinctiveness from the fossil *Theropithecus* species (Teaford, 1993). The average proportion of pits on teeth is low and this is most similar to leaf-eater colobines (Teaford, 1993). Thus, the shear crest result of *T. gelada* can correspond well with the microwear results. The distinctive strong shearing crest development pattern and low pit proportion of this species is convincingly related to the heavy emphasis on grass-eating indicated in different field studies. Therefore, the long shear crest result of this study together with Teaford's (1993) analyses of molar microwear can suggested that the *T. gelada* molars are adapted to grass eating. This suggestion is in turn supported by the high-altitude grasslands biogeographic distribution of the species in Ethiopia.

The gelada have not evolved any of the complex digestive mechanisms for extracting nutrients from the cell walls of grasses. The best they do in this direction is to masticate the grass blades heavily prior to ingestion, but they do not thereafter ferment them using specialized gut flora to break down the structural material as do the ruminant-like colobines (Dunbar, 1983). Therefore, extremely long shear crest development can be attributed to efficient mastication to the fact that the gelada are able to exploit the abundant grass species. This indicates just how highly evolved the gelada's own specializations for grass blades have become.

Comparisons of *T. brumpti* and modern *T. gelada*

The shearing crest development patterns exhibited by *T. brumpti* form an interesting contrast to those exhibited by modern *Theropithecus* (*T. gelada*). *T. brumpti* possess shorter shearing crest than *T. gelada*. This is also in agreement with the more frequent molar pit of *T. brumpti* than *T. gelada* (Teaford, 1993). The combination of shorter crest length and more pits show that *T. brumpti* was more frugivorous than *T. gelada*. Since pits may be formed by adhesive wear, i.e., in repeated tooth-tooth contacts in the mastication of soft food, the more frequent pits and shorter shear crest indicate that *T. brumpti* included significant amounts of soft fruit in its diet. Therefore, with this result it is impossible to suggest the possibility that leaves formed a significant part of the diet of

T. brumpti. Teaford (1993) also noted that no modern primate leaf-eater has shown an incidence of pitting as high as that is observed in *T. brumpti*. In addition to shear crest and microwear information, the possession of a large anterior dentition of *T. brumpti* also supports its fruigivore dietary adaptation (Fleagle, 1999).

Comparisons of *T. oswaldi* and modern *Theropithecus* (*T. gelada*)

The shear crest development of *T. oswaldi* is also quite contrasting to *T. gelada*. In this study, it is shown that the shear crest length of *T. oswaldi* is extremely shorter than any other cercopithecids, while shear crest length of *T. gelada* is extremely longer than the other cercopithecids. However, in contrast to their shear crest development, microwear pattern of *T. oswaldi* is more similar to that of *T. gelada* than to *T. brumpti* (Teaford, 1993). *T. oswaldi* and *T. gelada* show consistently low proportions of pits on their molars than *T. brumpti*. In addition to their molar microwear pit proportions, their relatively small, vertically implanted incisors bear resemblance in the two species (Cronin and Meikle, 1979 and Fleagle, 1999). Their relatively small, vertically implanted incisors can show that both *T. oswaldi* and *T. gelada* are mainly adapted to dietary items like seeds and grasses/ leaves that do not need more incisal preparation. In spite of their similarity in microwear pits proportion and incisor size, their shear crest variation implies that the dietary adaptation of *T. oswaldi* is different from *T. gelada*. This difference also agrees with the dietary reconstruction from Carbon isotope that showed more C_3 foods that manifests dicotyledonous fruits in the diet of *T. oswaldi* than their living relatives, *T. gelada* (Codron et al., 2005).

Comparisons of *T. brumpti* and *T. oswaldi*

Even though the shear crests of *T. brumpti* is closer to *T. oswaldi* than *T. gelada*, shear crest of *T. oswaldi* is shorter than *T. brumpti*. These fossil *Theropithecus* species also show differences in their molar microwear features (Teaford, 1993), i.e., *T. brumpti* showed significantly more pits than *T. oswaldi* even when they are from the same stratigraphic members. Their shear crest differences together with their microwear features show that *T. brumpti* and *T. oswaldi* were adapted to different dietary preferences. These differences are in agreement with other morphological analysis. Based

on analysis of dental morphology, Benefit and MacCrossin (1990) suggested that *T. brumpti* had less abrasive diet than did *T. oswaldi*.

In addition to these molar features, Krentz (1993) noted that the post cranial morphology of *T. brumpti* indicates a more arboreal adaptation than is apparent in the highly terrestrial *T. oswaldi* and *T. gelada.* Besides the morphological differences, their distribution in different stratigraphic members with different paleosol, paleoclimatology and Paleoecology can support their dietary adaptation differences. *T. brumpti* is found primarily in the lower (basal) strarigraphic members (deposition) of the Shungura sequence (table 1) and also more closed habitat than *T. oswaldi* that preferred open woodland and grassland habitats (Eck, 1977; Wesselman, 1984; Eck et al., 1987 and Gibert et al., 1995). This habitat difference can also add information to infer *T. brumpti* to be more soft fruit eater (frugivore) and *T. oswaldi* to be hard object feeder. Hardness refers to the context of resistance to be crushed or puncture resistance.

The general implication of these overall evidences can indicate that different *Theropithecus* species are differently adapted to their dietary preferences. Nevertheless, the second lower molar shear crest development pattern of *T. brumpti* and *T. oswaldi* is comparable to each other than to the modern *T. gelada*. In view of comparison, *T. gelada* show extremely longer shear crest not only to the fossil *Theropithecus* but also to all of the cercopithecids. This distinctive shear crest of *T. gelada* can be correlated to its unique grass dietary adaptation among primates. Despite the fact that comparable shear crest of *T. brumpti* and *T. oswaldi* can imply that the two fossil *Theropithecus* species are closer in their dietary adaptation than to *T. gelada* with reference to the physical properties of their diet that needs crushing or grinding rather than shearing (slicing).

Moreover, on the basis of baboons' analogy Grine (1981) attributed the shorter shear crests of *A. robustus* to their hard fruits (small and nut-like dry adapted fruits) dietary adaptation. Further more, as stated in Ungar (1998), among frugivores, hard-food specialists have even lower SQs than do soft fruit eaters, indicating that hard-food feeders have extremely blunt teeth designed for crushing. This relationship between SQ and diet

holds for all major extant cercopithecoids. If this analogy can hold true for fossil *Theropithecus* species, shorter shear crest of *T. oswaldi* can be attributed to hard fruit or seed dietary adaptation. This analogy can also be supported by the logic that seeds are likely to be less resulting in plastic deformation and high fracture resistance due to their high density. With these physical features blunt cusps can be more durable than sharp ones.

4.2.2. Habitat Preferences and Paleoenvironmental Reconstruction

Habitat preferences of the Shungura cercopithecids

Cercopithecids mainly depend on plants for their diet and shelter. Thus, their existence and species composition in the ecosystem can be a predictor of vegetation physiognomic structure. It can also be true for plant species diversity if they do not compete strongly for resources. Accordingly, the relative proportions of fruits, leaves and seeds or grasses in the diets of fossil cercopithecids is related to their habitats, i.e. forest or woodland versus open or treeless savanna habitats they dwell in. This is by no means disregarding the relationship of food plant diversity to primate species diversity even though the relationship is a complex matter (Lambert, 2007). Such diet and habitat association is also observed in extant baboons. Extant baboons exploiting forested habitats tend to eat higher quantities of fruits than grass or herbs, while the opposite is true for baboons living in scrub savannah (Dunbar, 1983). On the basis of uniformitarian principle, the relationship between diet and habitat observed from extant cercopithecids is assumed to be the same for fossil cercopithecids.

Based on diet- habitat association observed in extant cercopithecids and strong association of availability of fruits and leaves on trees, the Shungura Formation cercopithecids which are adapted to fruigivory and folivory are generally suggested to indicate closed environments (woodlands or forests). Therefore, the colobines (*R. turkanaensis, P. mutiwa* and *Colobus sp*.) and frugivore cercopithecines were closed environment dwellers. Arboreal adaptation of the colobine (Leakey, 1982 and Eck et al., 1987) and T. brumpti (Krentz, 1993) also support their forest habitat preferences

However, the hard food dietary adaptation of *T. oswaldi* most likely dietary items that are found commonly on the ground implies that *T. oswaldi* is expected to inhabit relatively open woodland-grassland plant communities like *T. gelada*. Its terrestrial locomotor adaptation (Krentz, 1993) also agrees with the reconstructed habitat preference. Moreover, relatively complex vegetational mosaics those are pointed to be dominated by relatively open woodland-grassland or open grassland plant communities of the habitat associated in the depositions where *T. oswaldi* was preserved (Eck et al., 1987) also corroborate this reconstructed open habitat preference of *T. oswaldi.*

As it is stated in Jolly (1972) and Gibert et al. (1995), *T. oswaldi,* is commonly found in sites of later Pliocene and Pleistocene age over much of Africa and such wide distribution might not support the edaphic grassland habitat preference of the species. Shear crest result of this study also suggests that *T. oswaldi* is mostly adapted to be hard food feeder (seeds or underground storage organs) rather than grass blades that constitute significant proportion of the T. gelada diet (Iwamoto, 1993). This dietary adaptation does not show special relation with edaphic grasslands even if the species can be collected in waterside environmental geological settings. Instead its dietary adaptation might be related to savannah open grasslands or open woodlands. Thus the greatest differences in preferred habitats between *T. gelada* and *T. oswaldi* appear to be related to altitude and size of area of distribution. In contrast, the frugivory dietary adaptation of *T. brumpti* can verify that the habitat preferences of *T. brumpti* have differed significantly in some respects from those of these two species. Some other authors (Jablonski et al., 2002) considered that *T. brumpti* as a species thought to be restricted in distribution to the Lake Turkana basin through its existence.

Analysis of environmental change across stratigraphic members

Comparisons between stratigraphic members in terms of relative proportions of cercopithecid species which are adapted to different dietary category groups (fig. 6) show comparable pattern to the expected food availability from vegetational (botanical) and other associated environmental evidences.

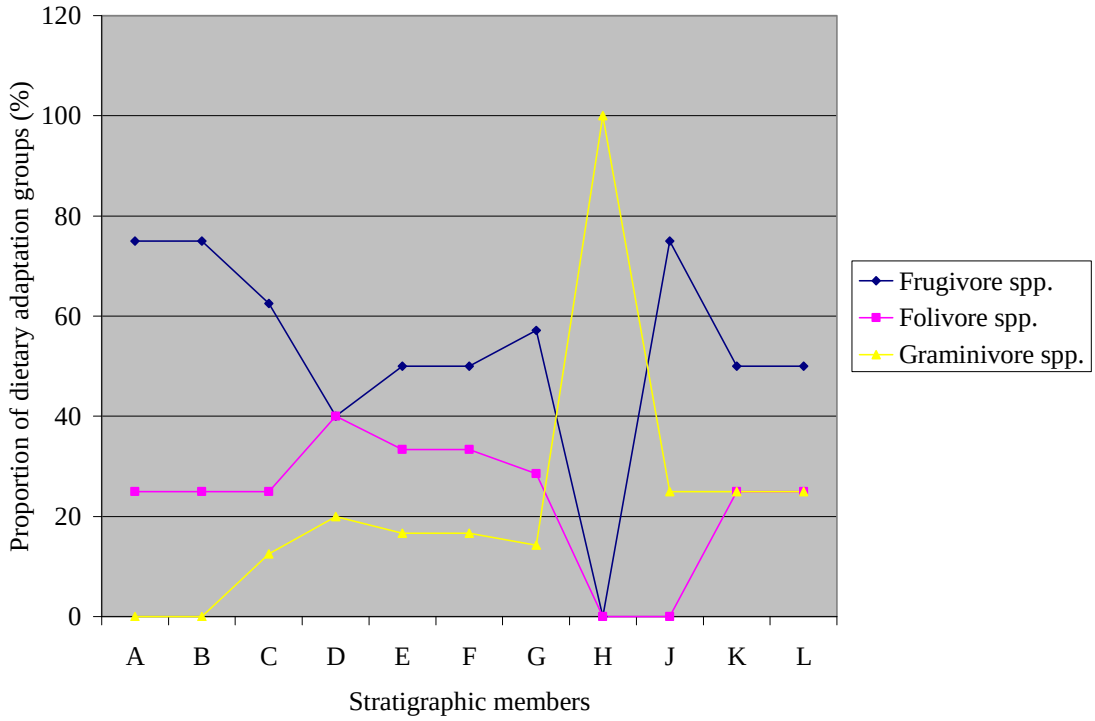

Figure 6. The relative proportion trends of different dietary adaptation groups through the Omo sequence. The relative proportions of frugivore, folivore and graminivore spp. reflect the availability of fruits, leaves and hard food items (grain, seeds or small hard fruits, etc.) as their dietary resources and the concomitant wide spectrum of habitats ranging from forests to open grasslands that can provide the resources.

The high percentage of frugivorous and folivorous species at member A and B together with arboreal locomotory adaptation of the colobine species indicate the stratigraphic members A and B to be a habitat of mostly closed woodland with riverine forest. Other habitat reconstructions also include a riverine forest based on pollen analysis (Bonnefille, 1984), more closed woodland based on low bovid abundance (Bobe et al., 2002) and a wooded savanna and forest based on micromammals (Wesselman, 1984). Thus, habitat reconstruction from the dietary adaptation of cercopithecids presented here agrees with these reconstructions.

On the other hand, at member C the manifestation of open environment adapted species (*T. oswaldi*) and increment in its proportion at member D as well as a relative reduction in the total proportion of the frugivorous and folivorous cercopithecids indicate the shift of dominantly closed habitat (most likely woodland with riverine forest) to a mosaic of closed and open vegetational zone. In the same way, even though members E, F and G showed some variation in the proportion of differently adapted cercopithecids (fig. 6), the variations at these members might not indicate significant ecological changes which can be different from members C and D. Therefore, the entire deposits C to G appear to contain an overall mosaic of closed to open habitats (probably bushland–woodland regime with a riverine forest and open grasslands habitats that can support fruigivores, folivores and open environment adapted species). A woodland-grassland habitat noted by Bonnefille (1984) from the pollen recovered in these members supported the reconstructed habitat changes at these members as compared to the basal members A and B. Moreover, an increased pattern of bovids' abundance in these members (Bobe et al., 2002) also shows the trend of environmental changes towards open environment.

At member H the terrestrial and hard food adapted cercopithecids proportion increases considerably from the previous members, while the reverse is observed for arboreal folivorous and frugivorous cercopithecids (fig. 6). Thus, this evidence indicates that the stratigraphic member was characterized by less tree cover or dominantly open grassland and arid conditions. On the other hand, the revival of frugivorous cercopithecids at member J and additional folivorous cercopithecids at members K and L indicate the restoration of tree covers at the habitats of these members. At these members the tree covers of the habitats seems to have been restored, or the forests appeared to be expanded again. Nonetheless, the relative high proportion of open environment adapted species as compared to the previous members (A-G) indicates that open environment (woodland-grassland communities) remained to be a significant component of the ecosystem.

In addition to the implication of habitat types (vegetation cover types), fruit availability is related to the amount of rainfall and soil fertility. This association is expected since higher soil fertility and rainfall allow more fruit production, which can support more

frugivores and may encourage greater dependence on fleshy fruits as opposed to the mechanically well-defended, non-fleshy species that are typically found in low-nutrient, low-productive areas of the tropics (Wahungu, 1998).

Thus, the highest proportion of frugivory at members A and B indicate that the lower Omo valley was characterized by high rainfall and well developed soil at these members, while the reduction of frugivory proportion in the later members other than member J suggest a decline in precipitation and soil quality. This suggestion which is made in correspondence to the pattern of food resource availability of cercopithecids coincides with the evidences from clay minerals and fossil soils. Clay minerals and fossil soils indicate higher in amount and less seasonally variable precipitation during the deposition period of Members A and B than the depositional periods in the later members that are suggested to show progressively decreasing in amount and seasonally variable precipitation (deHeinzelin, 1983).

Had the local precipitation been higher and less variable during the earlier range of time, more extensively and continuously distributed riverine forests and woodlands that supply more fruit could be expected in the lower Omo valley ecosystem. In the same pattern, as precipitation decreased in amount and became more variable, more open, drought resistant plant communities could be expected. As a result, an environment parallel to a decline in riverine forest coverage and an increase in vegetational mosaic complexity of the environment would have been possible. The precipitation and soil fertility pattern which are inferred from the proportion of cercopithecids adapted to different dietary resources (expected food resource availability) across the stratigraphic members shows such a pattern of change in the distribution of plant communities in the Shungura Formation.

Apart from the overall alignment of this research results to the terrestrial evidences, the first appearance of open environment and extreme aridity observed at member C and H respectively coincides with shifts to more arid and open conditions near 2.8 Ma and 1.7 $\pm$ 0.1 Ma (deMenocal, 1995) which are recorded from Marine records of African climate

variability document. As noted in deMenocal (1995), these climatic change events can be interpreted more plausibly by the development of periodically cooler and drier African conditions after 2.8 Ma, and their subsequent intensification near 1.8 to 1.6 Ma as a consequence of the onset and subsequent intensification of high-latitude glacial cycles (ice sheets) respectively. This may in turn have established discrete opportunities for ecological fragmentation and environmental changes that lead to the eventual rise of species adapted to arid conditions.

The changes observed in this study are also timely correlated to other records of African paleoenvironmental change (Vrba, 1985) and to the African fossil record of early hominid evolution (e.g. first occurrence of *Paranthropus aethiopicus* near 2.8 and *Homo erectus* near 1.8 Ma) (Reed, 1997 and Bobe and Behrensmeyer, 2004). And this temporal correlation can be used to examine possible connections between climatic, ecologic, and faunal changes during the Plio-Pleistocene. Thus, the temporal correlation of environmental changes in the Shungura Formation to the East African climatic change suggests that the major Pliocene-Pleistocene evolutionary events may have been climatically mediated. These possible relations between faunal, environmental and climatic change in turn indicates a temporal correlations between terrestrial and marine sequences and also association between the paleoclimatic and paleoanthropological evidences.

5. CONCLUSIONS

Reconstructed dietary adaptations show that except the *Theropithecus* lineage the rest of the cercopithecids are adapted like that of their contemporary lineages, i.e., frugivory in cercopithecines (*Cercopithecus sp*., *Papio*, large papionini, small papionini A and B) and folivory in colobines (*R. turkanaensis, P. mutiwa* and *Colobus sp*.). Remarkably, the *Theropithecus* lineage show different dietary adaptations along their successive temporal scale, i.e., frugivory (most likely soft fruit) in *T. brumpti*, hard food items (most likely seeds or nut-like fruits) in *T. oswaldi* and mostly grass blades in *T. gelada* (modern *Theropithecus*). This hard-food items trophic adaptation together with the coincidence of arid climatic records to the nature of the *T. oswaldi* species, suggest that the species was living in arid open savanna environment, while the rest of the fossil cercopithecids were dwelling at environments with more tree cover or closed habitats (forests to bushlands).

On the basis of the cercopithecids dietary adaptation and habitat preferences, analysis of environmental change shows that the environment at member A and B were closed. However, it became changed to a mosaic of closed and open habitat at member C in 2.85 – 2.52 Ma interval for the first time and open habitat continued as significant component of the ecosystem from member C to member G some 2.33-1.90 Ma. Gradually, open environment gets its dominant or prominent coverage of the ecosystem at member H between 1.90-1.74 Ma. On the other hand, at members J, K and L closed environment again appears to be part of the ecosystem with a lesser degree of coverage than at member C-G intervals. Thus, the Lower Omo environments after member G (1.9 Ma) were markedly more open, and locally arid particularly at member H. In the overall temporal scale, the environment indicates habitats from forest to treeless savanna/grassland or arid land at different stratigraphic members.

Generally, the patterns of relative proportions of cercopithecids with different habitat preference (dietary adaptation) in the Omo reflect a broad ecological shift at members C and H that are consistent with increasing aridity and reduction of closed environments

along with the expansion of open grasslands. The coincidence of this biotic shifts observed in the Shungura Formation to the East African climatic change suggest that

- the deposition of the Shungura Formation recorded the successions of wet-dry cycles that is evident in the marine records and
- the environmental change of the Omo paleo-ecosystem and East African biotic landscape in favor of arid-adapted species or expansion of grassland ecosystems may have been the result of the development of periodically cooler and drier East African climatic conditions near 2.8Ma, and 1.7 $\pm$ 0.1Ma.

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Appendices

Appendix 1. List of fossil cercopithecids that are used in the study as a study materials.

Taxonomic Group	specimen Number	stratigraphic Member	Preserved body element
Cercopithecus sp.	L 621-4a	G 10	mandibular frag with I1-M3
Colobus sp.	P-997-15a	L 2	Rt M1 or M2?
Large Papionini	L 1-95	B 11	Lt M2
Papio sp.	P 996-45	K 3	Lt M2
Papio sp.	L 872-2	E 5	Lt M2
Papio sp.	L 627-246	G 12	Lt M2
Papio sp.	L 398-1303	F 0	Lt M2
Papio sp.	L 338 S-23	E 3	Lt M2?
Papio sp.	Omo 33-346	F	Lt M2
Papio sp.	Omo 58-1248	E 5-F 1	Lt M2
Papio sp.	Omo 149-33	G 3	Lt M2
Papio sp.	Omo 47-2008	G 8	Mandible Rt I1,P3-M3 & Lt I1, C-M3
Papio sp.	Omo 50.F-2327	E 4	Rt Man M1-M3
Paracolobus mutiwa	L-668-37	G-9	Lt
Paracolobus mutiwa	omo-80 C 95	A1	Rt
Paracolobus mutiwa	L-35-59	G 5	Lt mandibular fragment w M3
Paracolobus mutiwa	L-331-40	C 6	Rt mandibular frag.withM1-2
Paracolobus mutiwa	Omo-29-68-14C4	G1-5	Lt mandibular fragment wM2- M3
Paracolobus mutiwa	Omo-56 sup168 2160	C 6-9	Rt mandibular frag.withP4-M3
Paracolobus mutiwa	L390-3 S/CF	?	Lt
Rhinocolobus turkanaensis	Omo -75N-71-35N	C 3	Lt mandibular frag. With M1-M3
Rhinocolobus turkanaensis	Omo-57-4/72-50	E4	Rt mandibular frag. With P4-M3
Rhinocolobus turkanaensis	Omo 57-4-189	E 4	Rt Man with M2-M3
Rhinocolobus turkanaensis	L 627-238	G 12	Rt Man with P3-M2
Rhinocolobus turkanaensis	Omo 75-5-C68	G 6	Rt & Lt Mand but Measuerment is taken on Rt
Rhinocolobus turkanaensis	L-412-1	G 10	Rt & Lt mandible, but meas. On Lt.
Rhinocolobus turkanaensis	P 64-12	A1	Lt
Rhinocolobus turkanaensis	Omo-81-c 96	A3-4	Lt
Rhinocolobus turkanaensis	L1-631	B10	Lt
Small Papionini (A)	L 1-629	B 10	Lt M2
Small Papionini (A)	L 1-628	B 10	Lt M2
Small Papionini (B)	L 1-23c	B 11	Lt M2?
Small Papionini (B)	L 399-31	F 1	Lt M2/M1?
Small Papionini (B)	F 197-23	Er	Rt M2

Small Papionini (B)	L 1-625	B 10	Rt M2
Small Papionini (B)	L 1-23b	B 11	Rt M2
Theropithecus brumpti	L-773-1	C 8	Lt. mandib frag with M2cusp tips broken
Theropithecus brumpti	L-864-1	G 13	Lt mandibular frag with P3-M3
Theropithecus brumpti	L 576-8	C 9	Rt. & Lt. M1-M3 lacking Rt. ramus
Theropithecus brumpti	L 305-6	C 6	Lt. P3-M3 & Rt.C
Theropithecus brumpti	L 345-4	C 9	Lt. mand. With P3-M3 lacking ramus
Theropithecus brumpti	L 345-25	C 9	Rt. M2-M3
Theropithecus brumpti	L 317-4	C 8	Lt. M1-M3
Theropithecus brumpti	L 331-4	C 6	Rt. M2-M3
Theropithecus brumpti	L 345-31	C 9	Lt.
Theropithecus brumpti	L 199-5	C 7	Rt. P3-M3 with Lt P3-P4
Theropithecus brumpti	L 227-6	D 2	Rt. M1-M3
Theropithecus brumpti	L 47-44	C 8	Lt. M2-M3
Theropithecus brumpti	L 49-1	E 2	Rt & Lt M1-M3, but measurement is taken on Rt
Theropithecus brumpti	Omo 158-343	C 8	Rt Man C-M2 but except M2 the rest are at their cercex
Theropithecus brumpti	Omo 18-371	C 8	Lt M2-M3
Theropithecus brumpti	Omo 28-557	B 10	Rt man M2-M3
Theropithecus brumpti	Omo 75.N-71-C2	G 12-13	Rt & Lt body,symphysis with Lt C-M3,& Rt P3-M3
Theropithecus brumpti	Omo 169-846	E 1	Rt Man P4-M2 with symphysis
Theropithecus brumpti	L 1-249	B 11	Lt M2
Theropithecus brumpti	L 36-17a	D 3	Lt M2-M3
Theropithecus brumpti	L 51-8e	C 9	Rt Man M2-M3
Theropithecus brumpti	L 51-8f	C 9	Lt Man M2
Theropithecus brumpti	L 127-47	E 3	Lt M2
Theropithecus brumpti	L 161-26	D 3	Rt M2
Theropithecus brumpti	L 193-36	C 8	Lt M2
Theropithecus brumpti	P 578-?	C 7	Lt M2
Theropithecus brumpti	L 627-91	G 12	Lt M2
Theropithecus brumpti	L 449-3	C 8	Rt M2
Theropithecus brumpti	L 161-30	D 3	Rt M2
Theropithecus brumpti	L 335-15	C 5	Rt M2
Theropithecus brumpti	L 335-34	C 5	Lt M2
Theropithecus brumpti	L 327-19	C 6	Rt M2
Theropithecus oswaldi	L 40-15b	E 5	Rt M2
Theropithecus oswaldi	Omo 25-5	G 4	Rt M2
Theropithecus oswaldi	Omo 33-3092	F 00	Rt. dM4?, M1?,M2? (subadult specimen

Appendix 2. List of extant frugivorous cercopithecines that are used in allometric scaling of shearing quotient of fossil cercopithecids.

Taxa	Side in which measurment was taken	Status of teeth wear	Body element	Source
Chlorocebus aethiops (M 151)	Lt	Unworn	Skull	ZNHM
Chlorocebus aethiops (M 191)	Lt	Unworn	Skull	ZNHM
C. aethiops(M236)	Lt	Unworn	Skull	ZNHM
C. aethiops(M302)	Rt	Nearly unworn	Skull	ZNHM
Cercopithecus mutice	Rt	Nearly unworn	Skull	Individual
Cercopithecus sp.?	Lt	Nearly unworn	Skull	NME
Cercopithecus sp.? (zoo. Lab.)	Rt	Nearly unworn	Skull	AAUZL
Chlorocebus sp.	Rt	Nearly unworn	Skull	Individual
Papio anubis (M198)	Rt	Unworn	Skull	ZNHM
Papio anubis (M277)	Lt	Nearly unworn	Skull	ZNHM
Papio hamadryas	Rt	Nearly unworn	Skull	NME
Papio hamadryas	Rt	Nearly unworn	Skull	NME