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Bilateral Asymmetry in Incisors: Implications for Miocene Hominoid Species Diagnosis

Candace Ann Davis
Southern Illinois University Carbondale, roundapes@yahoo.com

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BILATERAL ASYMMETRY IN INCISORS: IMPLICATIONS FOR MIOCENE HOMINOID SPECIES DIAGNOSIS

By

Candace A. Davis

Bachelor of Arts in Anthropology
University of Illinois, Chicago, 1971

Master of Arts in Anthropology
Southern Illinois University, 2002

A Dissertation
Submitted in Partial Fulfillment of the Requirements for the
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DISSERTATION APPROVAL

BILATERAL ASYMMETRY IN INCISORS:
IMPLICATIONS FOR MIOCENE HOMINOID SPECIES DIAGNOSIS

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A Dissertation in Partial
Fulfillment of the Requirements
for the Degree of
Doctor of Philosophy

Approved by:

Dr. Robert Corruccini, Chair

Dr. Susan Ford

Dr. Ulrich Reichard

Dr. John McCall

Dr. Brenda Benefit

Graduate School
Southern Illinois University
Carbondale, IL
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CANDACE A. DAVIS, for the Doctor of Philosophy Degree in ANTHROPOLOGY, presented on March 31, 2011, at Southern Illinois University at Carbondale.

TITLE: BILATERAL ASYMMETRY IN INCISORS: IMPLICATIONS FOR MIOCENE HOMINOID SPECIES DIAGNOSIS

MAJOR PROFESSOR: Dr. Robert S. Corruccini

The primary purpose of this dissertation is to show how knowledge of variation and asymmetry in incisor antimeric pairs of living great ape genera can be utilized as a “yardstick” for pairwise comparisons of isolated Miocene ape incisors from the two genera *Kenyapithecus* and *Equatorius*. The research was designed to help determine whether these fossil teeth could be reliably sorted into one or more than one genera. Both metric and morphological data for each class of incisor were recorded for *Kenyapithecus* and *Equatorius*, and resampling was performed to determine the significance of variation ($p<.05$) for each of 12 traits. Intraindividual antimeric differences in three genera of extant great apes were compared with interspecimen differences between *Equatorius* and *Kenyapithecus*. Pairwise comparisons using resampling sorted out which traits showed intraindividual significant variation and which could be used to discriminate between the two fossil genera under consideration. Based on these results, one can cautiously conclude the two fossil species within these genera are not different enough to justify placing them in two different genera.

Key words: Miocene; variation; fluctuating asymmetry; incisor morphology; *Kenyapithecus africanus; Equatorius africanus; Kenyapithecus wickeri.*

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CHAPTER ONE

INTRODUCTION

1.1. Incisor Variation Within Species

The purpose of this dissertation is to expand knowledge of the significance of intraspecific and intra-individual variation (especially fluctuating asymmetries) in anterior dentition, determine which traits are useful for interpreting the fossil record with more accuracy, and assess which traits vary too randomly to be useful for deciding to assign fossils to the same or different taxa. The test case for this analysis shall be the distinctness of the genus *Equatorius* from the genus *Kenyapithecus*. The reason for testing *Equatorius* vs. *Kenyapithecus* with this method is that the genus *Equatorius* was defined in part by purportedly distinctive incisor morphology. Therefore, this study examines intraspecific incisor variation between the Middle Miocene hominoids *Equatorius* and *Kenyapithecus*, comparing it with the known amount of demonstrably intraspecific variation (in particular, in intra-individual asymmetry between antimeric pairs) found in extant great-ape specimens.

Fluctuating asymmetry is one of three types of asymmetries that can occur in bilaterally symmetrical organisms. It is the kind of asymmetry with which this dissertation is concerned (page 6). In order to understand the significance of fluctuating asymmetry, it is important to understand dental variation, its causes, and what it can and cannot reveal about hominoid evolution overall.

The concept of intraspecific variation has been one of the cornerstones of evolution since the time of Darwin. Within all populations of sexually reproductive organisms, Darwin (1860) noted “variety” among individuals is observable, and it is these differences upon which natural selection acts. Although Darwin was unclear as to what caused variation (being unfamiliar with Mendel’s work) and by default, returned to the Lamarckian hypothesis of inheritance of acquired characteristics as a possible causative mechanism (Darwin 1860; Scott 2004), his theory was a new way of explaining change through time. Since Darwin’s time, researchers (e.g., Mayr 1963; Gould and Eldredge 1977; Hahlweg 1991; Ridley 1980, 2004; and Futuyma 2005) have contributed knowledge that has refined our understanding of evolution, but Darwin’s basic theory has stood the test of time and has been buttressed by our better understanding of its mechanisms.

While intraspecific variation in individuals within extant species has been observed and described for centuries, variation within (and between) fossil species has always been less clear. Given the vagaries of taphonomic processes that cause organisms either to fossilize or to disintegrate by chance, we are only able to sample a miniscule percentage of individuals (and sometimes only isolated teeth), not populations, comprising fossil species. The human mind naturally classifies the world into discrete categories rather than continua. Therefore, the less information we have about a species, the more likely it becomes that our definitions of that species are typological ones, based on small sample sizes defined by “discrete” traits that may not reflect the full range of variation within that species. Polymorphism within a species can mistakenly convey speciation where there is none. Because morphology and reproductive isolation resulting in speciation are often decoupled in evolution (Tattersall 1986; Masters 1993), recognizing what constitutes a species palaeontologically is always “problematic” (Tattersall 1986). The converse may also be true; i.e., variation interpreted as sexual dimorphism within a putative fossil species may in fact be a genuine discontinuity denoting more than one species (Kelley and Etler 1986; Eldredge 1993; Masters 1993; Kelley *et al*. 1995). Tattersall (1986) and Tattersall and Schwartz (1998) point out that teasing out whether variation is intraspecific or interspecific can be complex. Moreover, Tattersall points out that “inter- and intra-specific variation are often confused” (1986:165) because speciation has sometimes occurred in living species without significant morphological change. Skeletal specimens of *Felis leo* and *Felis tigris,* for example, are indistinguishable without their skins (C. Reed, pers. comm.), and dental and skeletal remains are usually all palaeontologists have of a fossilized specimen. Conversely, fossil specimens may have been incompletely studied, and obscure features such as nasal turbinal anatomy (often poorly preserved) may be overlooked as having potential for significant apomorphies, as in the case of Neanderthal nasal apertures (Schwartz and Tattersall 1996).

Taking a very broad view, Albrecht and Miller (1993) have examined the effects of geographic variation on morphological variation in closely related primate species. They delineate taxa according to a hierarchy of morphological variation: from ontogenetic factors to intrasexual behavior, sexual dimorphism, nterdemic and intersubspecific variation (contained within geographic variation) and finally, interspecific variation. They critique the constraints binomial nomenclature places on the more messy reality of living species. They suggest when it is possible to sample sexual dimorphism in a fossil taxon, it is wise to use specimens at a single locality and in one time frame for comparison. Furthermore, if one is trying to determine if fossils from multiple spots are a single species, one needs ideally to build a set of comparative samples of extant species to represent all levels of variation from intraspecific through interspecific to use as a yardstick with which to compare the fossil population.

Despite disagreements as to definition of what comprises a species (See Mayr 1970; Wheeler and Meier 2000; and Coyne and Orr 2004 for detailed treatments of these debates), researchers agree that species consist of populations of individuals that exhibit variation (Schultz 1963; Cope 1993; Kelley *et al.* 1995; Davis 2002 M.A. Thesis; Groves 2004; and Pilbrow 2006). If researchers were to study variation between two or more populations within the same species, the variation found would be interpopulation and intraspecific. This broad methodological approach is often used in field studies of extant animals. However, the sample size of fossils in a primate species is very much smaller than the number of animals one can find in a living population. Even in extant primate species, obtaining large enough sample sizes of teeth to study becomes challenging because of the finite number of primate skulls stored in each museum. Within that sample of skulls, some have missing teeth. Primates may lose them while they were alive (pre-mortem tooth loss) or the skulls may lose them after they were collected (post-mortem loss). Within the sample of teeth that are left, some are badly worn or broken and thus are of no use to the researcher. What is left to study are the teeth that are only lightly to moderately worn and minimally broken—a much smaller sample size than the total number of teeth of that species within the museum's collection.

A methodological approach somewhat narrower in scope than examining interpopulation variation within a species is therefore needed to study a small sample size. One can examine intraspecific variation, but at the intra-individual level rather than at the population level. If there is enough sexual dimorphism within a known extant species, one could examine dental variation in size or shape within or between sexes. However, fossil teeth are often found as isolated specimens, and without several maxillary or mandibular fragments with many of the teeth *in situ*, it becomes problematic to make intersexual comparisons and assign isolated teeth as being male or female.

One specialized aspect of intraspecific variation that has been overlooked is intra-individual right-left asymmetries (see p. 6). The focus of this dissertation is on incisor variation and asymmetries in great apes, using the data compiled from the right-left incisor antimeric pairs of extant genera from the Cleveland Museum of Natural History and National Museum of Natural History as a keystone (as per Albrecht and Miller [1993]) for interpreting incisor variation in two Miocene genera: *Kenyapithecus* vs. *Equatorius.*

1.2. Intra-individual Variation: Asymmetry

It is important that asymmetry be defined and subdivided correctly. Asymmetry is intra-individual variation between right and left halves of organisms that are ideally bilaterally symmetrical.

1.2.1. Types of Asymmetry

There are three different kinds of asymmetry: (1) directional asymmetry, (2) antisymmetry, and (3) fluctuating asymmetry (Van Valen 1962). Each has a different causal mechanism.

1. Directional asymmetry refers to differential development of organs on either side of the body (Van Valen 1962); e.g., the stomach (left) and the liver (right). In general, it is considered adaptive, is under genetic control, and is developmentally "normal." (It is not the kind of asymmetry with which this dissertation is concerned.)

2. Antisymmetry refers to a variable trait that can be expressed differentially on left and right sides of the body; e.g., handedness. Some individuals (including this author) categorize themselves as "ambidextrous." However, the degree to which they can perform tasks with both hands may develop differently (and on opposite sides) for different tasks. (Again, this kind of asymmetry is not relevant to this study.)

3. Fluctuating asymmetry—deviation from genetically pre-programmed symmetry between sides of the body—is considered to be the result of

“developmental noise” in the environment (Van Valen 1962); e.g., poor nutrition, disease, or parasites. Livshits and Koblyanski (1991) have studied human development and have found a relationship between impaired developmental homeostasis and fluctuating asymmetry. Incisors appear to be affected by fluctuating asymmetry more than molars because molars, being complexly cusped, must overlap perfectly and occlude more closely in order for the organism to process food for digestion. This is not as critical for incisors, which in their initial preparation of food perform a nipping or scissors-like action with flat, blade-like occlusal edges, rather than performing the more complex grinding or slicing performed by the molars. Thus, molar development has been subject to more natural selection constraining morphology and symmetry than incisors (Corruccini and Potter 1981).

1.3. Organization of this Dissertation

This dissertation is divided into seven chapters. In Chapter I, the introductory chapter, I discuss evolution in general and touch upon some factors that can affect intraspecific variation. I discuss fluctuating asymmetry and how it can be useful as a yardstick in sorting genera and species (see above).

A brief history of the genus *Kenyapithecus* (including *Equatorius*) follows in Chapter II. Here I discuss some of the adaptations and relationships of *Kenyapithecus* to some of the other large-bodied Miocene fossil apes in an attempt to give a more holistic “snapshot” of this genus and its relationships with other genera. I discuss in brief the evolution of other catarrhine groups to give this chapter a wider context for the reader. Finally, I discuss the two (perhaps three) species of *Kenyapithecus*, a brief overview of the debates about their relatedness, and the environments in which they lived. A review of the literature follows in Chapter III. I consider the following categories: incisor variation and hypothesis testing, studies on fluctuating asymmetry, evolutionary relationships in Miocene fossils, sexual dimorphism and variation; dental ontogeny, wear, and microanatomy and effects on variation; structural properties of foods and effects on dental wear; palaeoenvironmental reconstruction, and some statistical methods that have been applied to taxonomic problems. In order to gain an in-depth understanding of the variables that can affect incisor morphology (and thus, intraspecific and intra-individual variation), one must have knowledge of the factors, both genetic and environmental, that impact on teeth during development.

Chapter IV describes the materials and methods used to conduct the research for this dissertation, including the definitions (and diagrammatic illustrations) of tooth traits found on lingual surfaces of incisors, the protocols used for measuring, and some illustrations of morphological trait variants observed. In this chapter, I introduce resampling (i.e., bootstrapping), a statistical method that can be useful when sample sizes (e.g., fossils) are small. Illustrations of the traits and their variants can be found in this section.

The results of this study are detailed in Chapter V by tooth: lower central incisors (LI-1s), lower lateral incisors (LI-2s), upper central incisors (UI-1s), and upper lateral incisors (UI-2s), using the known variation within each extant genus as a yardstick against which to compare the pairwise comparisons between the fossil teeth. The reader is referred to several summary tables and photos in the Appendices.

Chapter VI discusses the results of these comparisons and the conclusions the author has made; Chapter VII summarizes and recaps the research presented in this dissertation.

1.4. Why Study Incisor Variation?

Most studies of dental variation have previously focused upon posterior dentition because of more complex cusp topography. The few studies that have investigated variation in anterior dentition (e.g., Pilbrow 2006; Deane 2009) have focused primarily on extant species, only making mention of fossil hominoids, and have not investigated incisor asymmetries, as is proposed for this study. In addition, asymmetry has been primarily studied in modern (and some archaeological) human populations, with the focus being on environmental causative (stress-related) mechanisms and possible correlations between asymmetry and hypoplasias (Corruccini and Potter 1981; Hoover 2001). Deepening the knowledge of dental fluctuating asymmetry as an important source of variation (and the interplay of genetic and environmental factors that cause it) in non-hominid hominoids may aid palaeontologists in decisions regarding lumping fossils into one taxon or splitting them into multiple taxa. In addition, understanding that asymmetries between antimeres occurs intra-individually can increase awareness of this phenomenon as a source of phylogenetic “noise” that may obscure true relationships both within and between species. Further research on intraindividual variation in dental asymmetries might also have broad applications to future bioarchaeological or forensic studies by giving clues as to the overall health of a population (Hoover 2001). More specifically for this dissertation, because the genus *Equatorius* was defined in part by purportedly distinctive incisor morphology (Ward *et al.* 1999; Kelley *et al.* 2002), it is important to examine incisors to determine how much variation in size and morphology occurs within a species—or even within an individual.

This dissertation has two primary purposes. Two research questions on two different levels that will be addressed are as follows:

1. Which of the known extant great-ape genera exhibit more intraspecific and intraindividual incisor variation than others, how widespread is incisor asymmetry across genera, and what are the implications (if any) of this? The null hypothesis is that there will be equal amounts of fluctuating asymmetry in incisor antimeric pairs in the extant great apes and that incisor antimeres will be symmetrical for all morphological traits. The alternative hypothesis is that there will not be equal amounts of fluctuating asymmetry in incisor antimeric pairs in the extant great apes and that incisor antimeres may not be symmetrical for all morphological traits.

2. On a broader level, how can a knowledge of incisor intraspecific variation and intraindividual incisor asymmetries aid researchers in interpreting

the fossil record by a better understanding of which dental traits exhibit genuine discreteness that implies species boundaries, and which vary along too much of a continuum to be useful in demarcations of fossil species?

The directional null hypothesis is that there will be an equal amount of incisor variation in the pairwise comparisons of the fossil incisors than there is intraindividual variation and asymmetry between antimeric pairs in extant genera. The alternative hypothesis will be that the amount of variation in the pairwise comparisons of the fossil incisors will be more than the amount of intraindividual variation and asymmetry between antimeric pairs in the extant genera.

With the purpose and research questions laid out and some basic terminology defined, we turn to our test-case fossil genera: *Kenyapithecus* and *Equatorius* and the world which they inhabited in the Middle Miocene.

CHAPTER TWO

KENYAPITHECUS: ADAPTATIONS AND AFFINITIES

As the test case for this analysis centers around whether or not one can discern from incisor traits that *Equatorius* is distinct enough from *Kenyapithecus* to warrant placement in another genus, it is important to give some background information on the evolution and adaptations of *Kenyapithecus* (encompassing the fossils now placed in *Equatorius* as well as the type species, *K. wickeri*). The following chapter discusses general evolutionary trends and environmental changes in East Africa during the Miocene, a general overview of the adaptive radiation of Miocene apes, and then focuses in on *Kenyapithecus*: its complicated palaeontological and taxonomic history, its adaptations, and its relatedness to other Miocene hominoid species.

2.1. The Miocene: The “Age of Apes”

The fossil record indicates that the Miocene (~23 mya – 5 mya) was a period of time during which catarrhines experienced several adaptive radiations throughout East Africa and Eurasia (Andrews *et al.*, 1996; Fleagle 1999). Some of these catarrhines evolved into pliopithecids, gibbon-sized arboreal catarrhines with very generalized molar cusps, only distantly related to the Miocene apes.

Others evolved into the first “apes of ancient aspect,” with molar cusps very similar to today’s apes, but with body plans that were not yet very ape-like (more on this later.) These proto-apes can be somewhat artificially (not taxonomically) divided into roughly three size classes: small-bodied (~ 3.3 kg – 9 kg; e.g., *Dionysopithecus* [Asia], *Micropithecus* [Africa], and *Dendropithecus* [Africa]), medium-bodied, (~ 10 kg – 27 kg; e.g., *Mabokopithecus* [Africa], *Proconsul africanus* [Africa], *Dryopithecus fontani* [Europe] and *Platydontopithecus* [Asia]), and large-bodied (~. 28 kg – 60 kg and larger; e.g., *Oreopithecus* [Europe], *Griphopithecus* [Eurasia], and *Kenyapithecus* [Africa]) (Fleagle and Simons 1978; McCrossin and Benefit 1994; Fleagle 1999; Begun 2003; Moya-Sola *et al.* 2009; and Kelley *et al.* 2008).

The Miocene has been nicknamed “The Age of Apes” because of the diversity in numbers of these earliest proto-ape species. The early Miocene proto-apes probably evolved from one of the late Oligocene propliopithecids, found in abundance in the Fayum, Egypt (Benefit 1992; Fleagle 1999). Unlike the earliest anthropoids, which had three premolars (also in modern strepsirrhines [prosimians] and retained by platyrrhines [New World monkeys]), propliopithecids had a reduction of one premolar, giving them a dental formula of 2.1.2.3, a derived trait shared with all modern catarrhines. What distinguishes the first incipient apes from earlier, more generalized catarrhines (and from the contemporaneous pliopithecids) is that they share several dental traits in common with modern apes: most notably, the Y-5 cusp pattern arrangement of the lower molars, with mesially shifted buccal cusps (Benefit 1992; Swindler

2002). As for anterior dentition (with which this dissertation is concerned), Miocene ape incisors share in common with modern apes a trend toward higher-crowned, more spatulate upper incisors with increased heterodonty between the central and lateral incisors. The incisors of the earliest proto-apes differ from Middle Miocene (and later) apes in that they are narrower relative to their height. In addition, the lower incisors in many Miocene genera tend to be somewhat taller and narrower than most modern apes. There is even evidence that from the earliest Miocene proto-apes on, sexual dimorphism was present in some genera, based on the variation in size and morphology of the canines (Waddle *et al.* 1995; Fleagle 1999; Schrein 2006).

Although incisor teeth are simple, single-cusped teeth compared with the more complexly cusped premolars and molars, one feature shared by all hominoid incisors, both extinct and extant (with the exception of most modern populations of humans and possibly gibbons) is complex lingual topography. The labial (outside) surface of most incisors is fairly smooth, with little relief. By contrast, the lingual (inside) surfaces of the incisors in apes are sometimes striated with rugose vertical ridges, collared at the cervix with a cingulum, bulged at the cervix with a thick, round basal swelling, thickened at the margins with marginal ridges—or braced in the center with a single central lingual pillar. Some of these features, which appear to buttress and strengthen the spatulate incisor could be adaptations for helping to grasp and process the often coarse plant materials that apes consume in the wild.

Interestingly, the evolution of postcranial morphology lagged behind dental morphology in Miocene apes and appears to have evolved in mosaic fashion (McCrossin 1997). Modern hominoids (including hominins, great apes, and hylobatids) share in common a dorsoventrally flattened, shortened torso (relative to monkeys); suspensory shoulder joint, with circumduction and full rotation, a distal humerus (elbow joint) with an elongated olecranon process and deep groove between the well defined trochlear and capitular articulations with the radius and ulna; longer forelimbs than hind limbs (bipedal hominids being the exception), and lack of a tail. This constellation of traits resulted as adaptation for below-branch suspensory locomotion. Modern apes (and humans) have a mobile shoulder joint, but have more stability in the elbow joint than arboreal quadrupeds (McCrossin 1997). However, most Miocene apes for which we have postcranial remains, with the exception of the Late Miocene ape *Oreopithecus* ("mountain ape") from Tuscany, Italy (Harrison and Rook 1997) and possibly Early Miocene *Morotopithecus* from Uganda (Young and MacLatchy 2004), have long, monkey-like, laterally flattened torsos and shoulder joints with more limited rotation, similar to modern monkeys. This general body plan suggests that arboreal above-branch locomotion (with a combination of above- and below-branch postures, similar to modern platyrrhines) was still the norm (McCrossin 1997).

As mentioned earlier, these first catarrhines with incipient "dental-ape" characters began to emerge in the earliest Early Miocene. By the end of the Early Miocene, proto-apes had adapted to many different niches and spread all over not only East Africa (Figure 1), but across Eurasia as well (Andrews *et al.* 1996). For example, one of the small-bodied apes, *Micropithecus,* can be found abundantly in East African sediments from this time period. A very similar-looking small-bodied ape, *Dionysopithecus*, was discovered in China and other parts of Asia in Early Miocene sediments (Bernor *et al.* 1998). Another Early Miocene proto-ape found in China, this one with striking similarities to East African *Proconsul* (see below) is called *Platydontopithecus* and was described by Gu and Lin (1983). However, Harrison and Yumin (1999) differ in their interpretation of the fossils of *Dionysopithecus* and *Platydontopithecus* and place them with the Pliopithecoidea.

2.2. Early African Miocene Apes

One of the earliest proto-apes to be discovered, most well known of the Early Miocene genera, was a catarrhine with some ape-like dentognathic and postcranial traits, such as squared-off upper molars with a prominent hypocone and lower molars with a ". . . broad talonid basin, surrounded by five prism-like cusps, including a large hypoconulid" (Fleagle 1999:454). This proto-ape was described by Hopwood (1933) and given the genus name "*Proconsul*," after a chimpanzee named "Consul" who lived in the London Zoo in the 1930s. The four other species of *Proconsul* that have since been discovered were of different sizes and occupied different niches. The remains of *Proconsul africanus*, the type species (~18 mya), have been found mostly near Koru, west of Mt. Tinderet

(Figure 2). *Proconsul major*, a very large-bodied species, has been found in sediments that suggest a former rainforest habitat in the Early Miocene. It coexisted with small-bodied apes *Micropithecus* and *Limnopithecus*. Fossils of *Proconsul heseloni* and *Proconsul nyanzae*, medium-bodied apes, have been found plentifully at Rusinga Island (Figure 2) which in the Early Miocene, was a somewhat dry, woodland area. Remains of small-bodied *Dendropithecus* can also be found at this fossil site.

For one species of *Proconsul*, *P. heseloni*, there are a number of cranial parts that have been found and studied. Its auditory region was essentially modern, with a tubular tympanic ear tube, a trait shared by all modern hominoids and Old World monkeys. However, its snout was prognathic, and it had a robust zygomatic bone (Walker *et al.* 1997). An endocast of *P. africanus* exists. Falk (1983) observed that its braincase was small, similar to some cercopithecoids or gibbons, with a more primitive sulcal pattern than is found in modern great apes.

Postcranial remains of *Proconsul* illustrate a mosaic of primitive, monkey-like features mixed with some incipient ape-like traits. The nearly complete skeleton of *P. heseloni* (a juvenile) and some postcranial remains of *P. nyanzae* reveal these dental apes had some primitive traits: a laterally flattened, elongated torso, nearly equal-length limbs (monkey-like), a long olecranon process, and the shoulder joint of a typical arboreal quadruped (C. Ward 1993). However, it also shares some derived traits with modern apes: a robust fibula, widening of the distal humerus (Rose 1988), some similarities in the tarsal bones, and the absence of a tail (C. Ward *et al*. 1991).

A relatively recent proconsulid find, *Proconsul meswae*, has been described from Meswa Bridge in western Kenya by Harrison and Andrews (2009). These authors conclude that due to its greater geologic age and some differences in dental traits (e.g., lower-crowned incisors; broader, more flared, higher-crowned molars with more pronounced cingula), *P. meswae* may be a stem member of the *Proconsul* clade (Harrison and Andrews 2009:479).

Several other Early Miocene proto-apes that share some of the same dentognathic traits were later referred to the extinct Family Proconsulidae. One genus from the Early Miocene that shares some traits with *Kenyapithecus* (*Equatorius*) is large-bodied *Afropithecus turkanensis*, found near Kalodirr, near the western shore of Lake Turkana in northern Kenya (Figure 3). Some of these traits include a low-set, robust zygomatic root, robust, blunt canines, and procumbent, tall incisors foreshadow dental traits found in *Kenyapithecus* (*Equatorius*); it is postcranially most similar to *Proconsul* (Rose 1993).

Turkanapithecus kalakolensis, a medium-bodied species also found at Kalodirr in Early Miocene sediments, has extra-long molars with many accessory cusps, traits probably too derived to be a potential ancestor to *Kenyapithecus*. Although it appears to have been an arboreal quadruped, a feature of its elbow (the olecranon process) is somewhat reduced in size, indicating that perhaps it used below-branch suspensory behavior at least part of the time (Rose 1993).

2.3. Possible Relationships with Eurasian Miocene Apes

As it has been suggested by some researchers that African apes may originally have had a Eurasian ancestor (e.g., Begun and Ward 1997; Moya-Sola *et al.* 2009), it is important not to neglect mentioning the adaptive radiation of ancient apes of the Middle Miocene in Eurasia. Four to five species of a very widespread medium-bodied ape, *Dryopithecus* (“oak ape”) inhabited forests from western Spain to eastern Hungary in Europe (Begun and Kordos 1997). Fossils of another Middle Miocene ape, *Griphopithecus*, have been found in abundance at Pasalar, Turkey (Kelley *et al.* 2008); see Figure 1.

Fossils from Late Miocene sediments reveal another, more recent radiation of ancient apes: *Graecopithecus* and *Ouranopithecus* from the Greek peninsula (Koufos and deBonis 2004), which have been contenders for possible last common ancestor of great apes and humans; the insular and specialized *Oreopithecus* from Tuscany, Italy (Harrison and Rook 1997) that became an evolutionary dead-end; *Ankarapithecus* (=*Sivapithecus*) *meteai* from Sinap, Turkey; three species of *Sivapithecus* from Eastern Europe to northern India and the closely related *Gigantopithecus*, known from the Late Miocene to the Late Pleistocene (Begun 2005); and *Lufengpithecus* in China (Liu and Zheng 2005) . In Africa, fossils of *Samburopithecus* (a very large-bodied ape that may be closely related to the modern gorilla) were found in Late Miocene sediments in the Samburu Hills near Nachola (Figure 3). More recently, fossils of *Nakalipithecus nakayami*, a Late Miocene (~9.9 mya) large-bodied ape have been found near Nakali, Kenya (Kunimatsu *et al.* 2007). These authors state it is " . . . a large hominoid similar in dental size to female gorillas and orangutans" (2007:19220) and may be a contender for a close last common ancestor to great apes and humans, as it purportedly has less specialized characters on its molar teeth than *Samburopithecus*. It is also during the latest Late Miocene that a whole new adaptive radiation occurred: the first bipedal apes, *Sahelanthropus*, *Orrorin*, and others emerged (Brunet *et al.* 2002). As more of them are unearthed, it has become ever more challenging to sort out the relationships between these later emerging apes and their predecessors from the Early and Middle Miocene.

At the pinnacle of the "Age of Apes," we know of over 40 species that occupied forests covering most of Eurasia as well as Africa. Later, as the climate dried and became chilly in the early Pliocene, most of the Miocene apes went extinct. The apes that exist today—the large-bodied chimpanzees (including bonobos), gorillas, orangutans, and the medium-bodied gibbons and siamangs—are relicts of a much more speciose epoch and do not occupy any niches outside the tropics.

2.4. Decline of Miocene Apes and Emergence of Old World Monkeys

On the other hand, modern Old-World monkeys thrive in climates from the arid Kalahari Desert of South Africa to the tropical regions of central Africa. They number many species to this day, can subsist on a wide variety of foods, and survive at high altitudes in the mountain grasslands of Ethiopia and at high latitudes, such as the temperate forests of Japan and northern China. Where did they come from?

Old-World monkeys emerged in another catarrhine adaptive radiation in the Late Miocene, about the time the ancient apes were starting to dwindle. They can be distinguished dentally from ancient apes and pliopithecids in part by their incipient bilophodont, four-cusped molars—so called because of the crests, or lophs that connect the cusps in modern Old World monkeys--and trend toward reduction of and eventual loss of the hypoconulid on LM-1s and LM-2s (McCrossin and Benefit 1994). As the climate grew drier in the Late Miocene to Early Pliocene, forests grew patchier, and fruits, scarcer, these early cercopithecoids took over the niches left behind by declining numbers of species of apes. Behavior and physiology do not leave fossil evidence, of course, but some proto-monkeys may have begun to exploit a brand new niche by biochemical evolution of the ability to digest unripe fruits (McCrossin and Benefit 1994:97). According to this hypothesis, unripe fruits may have been a new addition to their already-eclectic diets, perhaps due to ancestral facultative folivory (Andrews and Aiello 1984). Studies of modern cercopithecoids reveal that many have stomach enzymes that can digest these food items (McCrossin and Benefit 1994:97; Benefit, class notes).

2.5. The Three Species of *Kenyapithecus*

At this time, there are two (or three) recognized species within the genus *Kenyapithecus*. *Kenyapithecus* (= *Equatorius*) *africanus* has been found at Maboko Island (Figure 2) and at Kipsaramon (Figure 3); *K. wickeri* (the type species) has been found at Fort Ternan, Kenya (Figure 2), and most recently, *K. kizili* has been found at Pasalar, Turkey. Each of these *Kenyapithecus* species will be discussed in turn.

2.5.1. *Kenyapithecus* (= *Equatorius*) *africanus*

Kenyapithecus africanus was a large-bodied, ~ 41-kg (Fleagle 1999), Middle Miocene ape (~14.5 mya). Fossil fragments of this species have been found abundantly along the eastern shores of Lake Victoria at Maboko Island.

This fossil species has a complicated and somewhat controversial history. Before 1979, it was believed to have also been found on Rusinga Island. There are a few fossils of this species, found before 1987, the provenience of which is uncertain (Andrews and Molleson 1979). Their field numbers are prefixed “RU” (from Rusinga Island), but the fossils most likely came from Maboko Island instead. Andrews and Molleson (1979) explain how this misinterpretation came about. They state that MacInnes first described the type specimen of *“Sivapithecus*” *africanus* (now *K. africanus*) in 1943, but did not give a specific locality. He had been collecting fossils from both Maboko and Rusinga; however, MacInnes fell seriously ill before he could finish his work. The *K. africanus* fossils (including the type specimen) were possibly mislabeled by someone else as having come from Rusinga. Several decades later, Andrews and Molleson (1979) tested the matrix attached to these fossils of questionable provenience and discovered it matched that of Maboko rather than Rusinga. This revision is important to understanding evolution of Miocene primates in East Africa because the sediments at Rusinga are two million years more ancient than those at Maboko and contain fossils of *Proconsul*, which never occur in the same sediments as *Kenyapithecus* and *Victoriapithecus* (Andrews and Molleson 1979). No other fossils of *Kenyapithecus* have ever been found on Rusinga.

For decades, it was assumed that there had been no findings of lower lateral incisors for *Kenyapithecus africanus* because the description of *K. africanus* mistakenly included some jaws and teeth of *Proconsul nyanzae* and *P. major* from Songhor and Rusinga Island (McCrossin and Benefit 1994). Assumptions were made that *Kenyapithecus* (once lumped as "*Ramapithecus wickeri*") had small incisors (Andrews and Walker 1976) until a nearly complete juvenile mandible was found at Maboko by McCrossin and Benefit (1993b). This mandible, KNM-MB 20573 (Plate 34) preserved several postcanine teeth on both sides and a single lateral incisor on the left. The morphology of that incisor overturned prevailing beliefs about anterior dental morphology of this species, because it was tall, mesiodistally narrow, lacking a distally flared margin, and strongly procumbent (McCrossin and Benefit 1994:108). Benefit (pers. comm.) recalled having seen a few other such incisors; they had been mistakenly classified and stored with fossils of the Family Suidae (pigs). Thus, a new picture of the lower incisor morphology of this species began to emerge.

More fossil fragments of a “new” Miocene ape were described by Ward *et al.* (1999), about 125 km east of Lake Victoria, at Kipsaramon in the Tugen Hills area north of Mt. Tinderet (see Maps 1, 2, and 3). The fossils found in the Tugen Hills in Bed 3, dated at ca. 15.5 mya (Behrensmeyer *et al.* 2002) were named *Equatorius africanus* (Ward *et al*. 1999), and in many traits, they fall within the range of variation of the *Kenyapithecus africanus* fossils found at Maboko and may be congeneric with another species, *K. wickeri* (Benefit and McCrossin 2000; Davis 2002 [M.A. Thesis]). Ward *et al.* (1999) and Kelley *et al.* (2002) prefer to subsume all the previously known *K. africanus* fossils under the genus “*Equatorius*;” *contra* Benefit and McCrossin (2000), who prefer to include the fossils from Kipsaramon under the older name, “*Kenyapithecus africanus*.”

Complicating the picture were dentognathic remains discovered in a fossil site near Nachola (northern Kenya) in 1982 by Ishida and his colleagues (Ishida *et al.* 1984; Nakatsukasa and Kunimatsu 2009). The first of these, a fragment of a large hominoid maxilla found near Camp 22 in the nearby Samburu Hills, later became the type specimen of *Samburopithecus kiptalami.* Later, just outside the village of Nachola in a road cut exposure, a second find—the tooth of another large-bodied ape—was found (Nakatsukasa and Kunimatsu 2009). During the 1982 season, Ishida and colleagues discovered 18 dentognathic remains from this exposure and noted some strong similarities between these new remains and the teeth of *Kenyapithecus africanus*. Initially, they were hesitant to assign the new teeth formally to this species because of the small sample size and its variability, so they tentatively referred to it at first as cf. *K. africanus.* Then, from 1996 – 1998, a partial hominoid skeleton (adult) from another site, a partial infant skeleton, and more teeth from the original site were unearthed. It became apparent that the fossils from Nachola were distinct enough from *Kenyapithecus* (both *K. africanus* and *K. wickeri*) that they needed to be placed in a new genus; thus, Ishida and his colleagues named the Nachola fossils *Nacholapithecus kerioi*.

Ward *et al.* (1999) then published their finds on the new large-bodied ape they had found at Kipsaramon. Based upon their finds, plus the dentognathic remains from Nachola (i.e., the finds initially catalogued as "cf. *Kenyapithecus africanus*"), they erected a new genus, *Equatorius africanus*. These researchers placed all the fossils formerly known as *K. africanus* from Maboko into this new genus, based in part upon some morphological differences in lingual traits on incisors and maxillary fragments between *K. africanus* and *K. wickeri*. Several years later, Kelley *et al.* (2008) stated they removed the *Nacholapithecus* teeth from the hypodigm of *E. africanus* because *Nacholapithecus* is now known to be morphologically (and generically) distinct from *E. africanus*, due to the addition of the new specimens by Ishida and his crew in the late 1990s (Kelley *et al.* 2008; Nakatsukasa and Kunimatsu 2009).

Pilbrow (2006) summarizes the argument of Ward *et al.* (1999) and Kelley *et al.* (2002) as follows: Their hypothesis hinges on some overall similarities in morphology between the incisor of *K. wickeri* and one of two species of Miocene hominoids at Pasalar, Turkey, studied by Alpagut *et al.* (1990). The latter species was recently named "*Kenyapithecus kizili*" by Kelley *et al.* (2008), two years after Pilbrow's article came out (more on this species later). Ward *et al.* (1999) and Kelley *et al.* (2002) have argued that there are derived traits in the upper central incisor of a "shelf-like, lingual tubercle and robust, sharply angled marginal ridges that obliterate the foveae" shared between *Kenyapithecus wickeri* and the lesser known of the (at that time unnamed) species at Pasalar (i.e., *K. kizili*). The corresponding *Equatorius* incisor, in their assessment, has more "primitive" large-hominoid features; i.e., a continuous cingulum and distinct foveae. In addition, they contend, the upper lateral incisor of *Equatorius* has a derived feature not shared by *K. wickeri*: a spiraled cingulum. The presumed synapomorphies between this single known upper central incisor of *K. wickeri* and the incisors of *K. kizili* (Kelley *et al*. 2008) supposedly indicate a phyletic link between the two, so goes their argument, and *K. africanus*, in their opinion, should be put in a new genus, which they designated "*Equatorius*" to avoid having a paraphyletic genus.

The debate as to the generic status of *Equatorius* vs. *Kenyapithecus* is important to this dissertation, and an analysis of the purported distinctiveness in lingual traits on incisors between the two (i.e, whether or not the differences can be encompassed along a gradient of variation that exists between individuals in a species or whether these traits are distributed discretely between the two species) follows in a later chapter.

At the time that *Kenyapithecus africanus* inhabited Maboko, it appears to have been initially a riverine woodland, with thick brush cover (Benefit 1992:170). The fossil proto-monkey *Victoriapithecus* (Family Victoriapithecidae) has also been found in abundance there (Benefit 1992). In addition, fossils of a medium-bodied, Middle Miocene African oreopithecid ape, *Mabokopithecus*, have been found at Maboko as well as many other mammalian species; e.g., a galagid (*Komba*), a shrew-like insectivore (*Amphechinus rusingensis*), several rodent species, a creodont, two hyena species, canine and viverrid (weasel-like) species, three proboscideans (fossil elephants), two kinds of rhinocerotids, a chalichothere, and several artiodactyls, including suids (fossil pigs) and hippopotamus (*Kenyapotamus*) (Retallack *et al.* 2002).

Based on its dental morphology (similar to the Tuscan Late Miocene ape, *Oreopithecus*, with high cusp relief and an odd, extra centroconid cusp on its molars), *Mabokopithecus* was probably primarily folivorous and occupied a different niche than *Kenyapithecus.* Later (at the time Bed 5 was deposited), the climate had changed somewhat, and has been described as a “nyika semi-arid Acacia-Commiphora with grass patches and gallery forest along seasonally flooding streams with nearby swamp and mixed forest patches” (Benefit 1992:170). Retallack *et al.* (2002) discuss the impact of the gradual shift of climate to a more arid, mixed forest/grassland to the somewhat terrestrial adaptations of the proto-monkey, *Victoriapithecus* and of *Kenyapithecus*.

2.5.2. *Kenyapithecus wickeri*

About 100 km northeast of Maboko, another closely related, slightly geologically younger, possibly smaller, ~ 27-kg species (Fleagle 1999) occurs: *Kenyapithecus wickeri* at Fort Ternan. Fossil plants found at Fort Ternan that date back to the Middle Miocene indicate there existed a mosaic of "early successional woodland (on Dhero paleosols), grassy woodland (on Chogo clay eroded . . . paleosols), and wooded grassland (on Chogo and Onuria clay paleosols)" (Retallack 1991:383).

K. wickeri is the type species for the genus *Kenyapithecus* and was first re-described and renamed by L.S.B. Leakey (1961). Prior to his analysis, it had been lumped with the Asian genus "*Ramapithecus*" by Simons and Pilbeam (L. Leakey 1967), but in Leakey's opinion, many of its purported shared traits with "*Ramapithecus*" were based upon reconstructed parts, not all actual fossil material. (The actual fossils of *"Ramapithecus,"* minus the reconstructions, eventually became subsumed under another Asian Miocene genus, "*Sivapithecus*" when it was discovered that their morphology and provenience showed no important differences to warrant placing them in different genera.) In any case, Leakey noted that the new incisors of *Kenyapithecus wickeri*, which he described as "remarkably like that of *Homo*" (1967:3), were distinct from the Early Miocene *Proconsul* (with oval, rather than trihedral roots). In the 1960s, in part because the primate fossil record was still poorly known, palaeontologists were attempting primarily to find the missing links between modern species and fossil ones, with a strong bias toward searching for human ancestors. They would arrange the fossils in anagenetic, ancestor-descendant lineages, as cladistic analysis was in its infancy, and the possibility that the hominoid evolutionary tree might be much more speciose was largely unacknowledged (Benefit and McCrossin 1995). As finding the “missing link” between humans and apes was considered of prime importance during the early-to-middle 20th century, one can understand the elder Leakey’s mistake in the l960s of thinking *K. wickeri* might be directly ancestral to the human line.

Leakey (1961) mentioned differences in characters of the canines and postcanine teeth of “*Sivapithecus”*(= “*Ramapithecus*” *africanus*; now *K. africanus*), found at Rusinga from *K. wickeri*, but, curiously, omitted the differences in characters on the lingual surface of the incisors. However, he also noted some dentognathic traits shared by *K. wickeri* and “*Sivapithecus*” *africanus*: “ . . . a well defined canine fossa; low-crowned molars and premolars; the upper canines are small and set vertically in their sockets” . . . “and the root of the malar (zygomatic) process is set just above the first molar” (L. Leakey 1961:690). From these shared, derived traits, Leakey determined that “*S.*” *africanus* was congeneric with *Kenyapithecus wickeri* and therefore renamed it *Kenyapithecus africanus.* He recommended that the genus “*Sivapithecus*” be reserved for the Asian Miocene hominoid fossils for which this name originated and not include the African fossils (L. Leakey 1961).

Although *Kenyapithecus wickeri* is the type species for the genus *Kenyapithecus*, fewer fossils of it have been found than *K. africanus*. In particular, there are no known lower incisors for this species (McCrossin and Benefit 1994). However, there is a mandibular fragment (KNM-FT 45) containing third and fourth premolars, vacant incisor sockets, and intact mandibular symphysis. McCrossin and Benefit (1994) state that the morphology of the mandibular symphysis is an important key to differentiating Miocene hominoids. After the discovery and examination of a nearly complete juvenile mandible of *Kenyapithecus africanus* at Maboko (KNM-MB 20573), preserving deciduous third premolars and permanent first molars on both sides, left permanent lateral incisor and second molar, vacant incisor and canine sockets, and an undistorted mandibular symphysis, McCrossin and Benefit (1994:108) state that both species of *Kenyapithecus* (i.e., *K. africanus* and *K. wickeri*) share in common with other Middle Miocene apes the following derived features of the mandible: a robust corpus, strong inferior transverse torus, and posteriorly directed genioglossal fossa. Derived traits distinguishing the two species from other Miocene apes are a strongly proclined long axis of the symphysis (ca. 30-40 degrees to the alveolar margins of postcanine teeth) and (comparing the orientation angle of the vacant sockets of *K. wickeri* with the strongly procumbent lower incisors of *K. africanus*), strongly procumbent lower incisors (McCrossin and Benefit 1994:108).

2.5.3. *Kenyapithecus kizili*

If the fossils of *Kenyapithecus kizili* fall within the range of variation of this genus, it would be the only species of *Kenyapithecus* known from the Middle East. A large number of isolated teeth found in the 1980s in Middle Miocene fossil beds in Pasalar, Turkey, were discovered by Alpagut *et al.* (1990). At the time, these teeth had not yet been sorted out to determine how many species they might represent, but Alpagut *et al.* (1990) postulated that they might represent one or two previously undescribed species. Due to the nature of the distribution of these fossils, these authors postulated that this was a catastrophic assemblage; i.e., sudden death of all individuals at the same time in a cataclysmic event, such as a flood or a volcanic eruption, resulting in mass burial beneath sediment or ash (Alpagut *et al*. 1990).

Kelley *et al.* (2008) were able to sort these isolated teeth, plus maxillary fragments, into two “morphs” by first sorting maxillary and mandibular fragments that contained teeth *in situ* and then matching isolated teeth that most closely resembled each in size and morphology: Morph I (eventually named *K. kizili*) and Morph II (*Griphopithecus alpani*). These authors maintain that in the central incisors of Morph I, the lack of a lingual tubercle and extremely thickened marginal ridges one-third of the distance from the incisive edge of the tooth, meeting in a V-shaped cervical margin (derived traits) make it “very similar” to *K. wickeri* from Fort Ternan, Kenya (2008:457). In Fig. 4 of this article (2008:458), the Morph I upper lateral incisor depicted reveals a caniniform incisor with converging shallow crenulations and again, very thickened marginal ridges, with a U-shaped cervical margin, whereas Morph II (representative of *Griphopithecus*) (2008:458) appears more incisiform. In the present author’s opinion (judging from the photos of these teeth), with the exception of similar crenulations, the Morph II lateral incisor more closely resembles the *K. wickeri* upper lateral incisor, which is incisiform (see Plate 32, left) than the Morph I upper lateral incisor, which is caniniform.

At this time, there are no known lower incisors for *K. wickeri*, only a mandibular fragment with vacant incisor alveolae. However, there are many known for *K. africanus* (including two lower lateral incisors and one lower central incisor for *Equatorius* from Kipsaramon) for comparison. The lower central and lower lateral incisors of neither morph from Turkey resemble those of *K. africanus*; both LI-1s and LI-2s of this species have very little lingual relief, whereas those of *K kizili* (Morph I) show a pronounced lingual cingulum with thickened marginal ridges and a slight lingual pillar. In addition, the LI-2s of *K. africanus* from Maboko and Rusinga (and of the *Equatorius africanus* specimen from Kipsaramon) are extremely long and narrow, almost tusk-like in appearance.

There are unfortunately no known mandibular specimens for *K. kizili* at this time. Until these are found someday, there is no way to compare morphology of its mandibular symphysis with the mandibular fragment and vacant incisor alveolae of *K. wickeri* (Kelley *et al.* 2008). However, there are maxillary remains of *Kenyapithecus kizili*. Kelley *et al.* (2008) bolster their argument for the inclusion of the Morph I fossils in the genus *Kenyapithecus* by comparing maxillary morphology between the type specimen of *K. kizili* with the KNM-FT46a maxillary fragment of *K. wickeri*. Both of these fragments are “almost identically preserved” (2008:471) and, according to the authors, share several derived features in common that distinguish them from other Miocene hominoids, including *Equatorius africanus*: “ . . . large separation between the maxillary sinus and canine alveolus . . . (and a) zygomatic process that originates superior to (U)M-1 – (U)M-2 with a root not excavated by the maxillary sinus" (Kelley *et al.* 2008:471).

Because of the geographic separation between these fossils and the fact that the incisors of Morph I from Pasalar may not fall within the range of variation known for *Kenyapithecus* incisors (see Plates 27-32), it is this author's opinion that a future pairwise comparative study of these incisors with those of *K. africanus* and *K. wickeri* might be helpful to determine whether Morph I from Pasalar should be placed in the genus *Kenyapithecus* (or is, in fact, something entirely new), even though the maxillary and canine morphology appear to be similar.

2.6. Overall Morphology of *Kenyapithecus*

Morphology of the known postcranial elements of *Kenyapithecus* suggests it was a semiterrestrial quadruped. The humerus retains a catarrhine-like shoulder joint with limited rotation, but the olecranon process is elongated and retroflexed. Relatively short, straight phalanges with an adducted hallux indicate terrestriality; it could utilize food sources on the ground, such as fallen fruits as well as arboreal fruits (Benefit 1992:170).

Kenyapithecus (and *Equatorius*) have been classified within the Hominoidea (Family Hominidae per Andrews *et al.*1996), either as within the subfamily Dryopithecinae (Tribe Kenyapithecini; Andrews *et al.* 1996) or (more cautiously) simply noted by some authors as Subfamily *Incertae sedis* (Fleagle

1999). *Kenyapithecus africanus* shares several dentognathic traits with *Griphopithecus* from Turkey and with earlier Miocene *Afropithecus*; e.g., a deep mandible, thick-enameled molars, somewhat prognathic incisors, and robust canines, an adaptation also seen today in modern pitheciine platyrrhines that eat fruits with hard sclerocarps and nuts, such as the uakari (Benefit 1992).

As platyrrhines became geologically isolated from catarrhines tens of millions of years earlier, these dentognathic similarities in form and function is one of many examples of parallel evolution in primates. In *K. africanus*, this adaptation is taken to the extreme, with tall, procumbent mandibular incisors (the laterals are narrow and tusk-like) and a very sturdy, proclined mandibular symphysis (Benefit 1992:170). The root of the zygomatic bone is low and placed anteriorly over the first molar. Although feeding behavior is not preserved directly in the fossil record, one could surmise from the known behavior and diet of modern pitheciines and the similarities in dentognathic anatomy of *Kenyapithecus* that *Kenyapithecus* might also have included sclerocarp fruits in its diet.

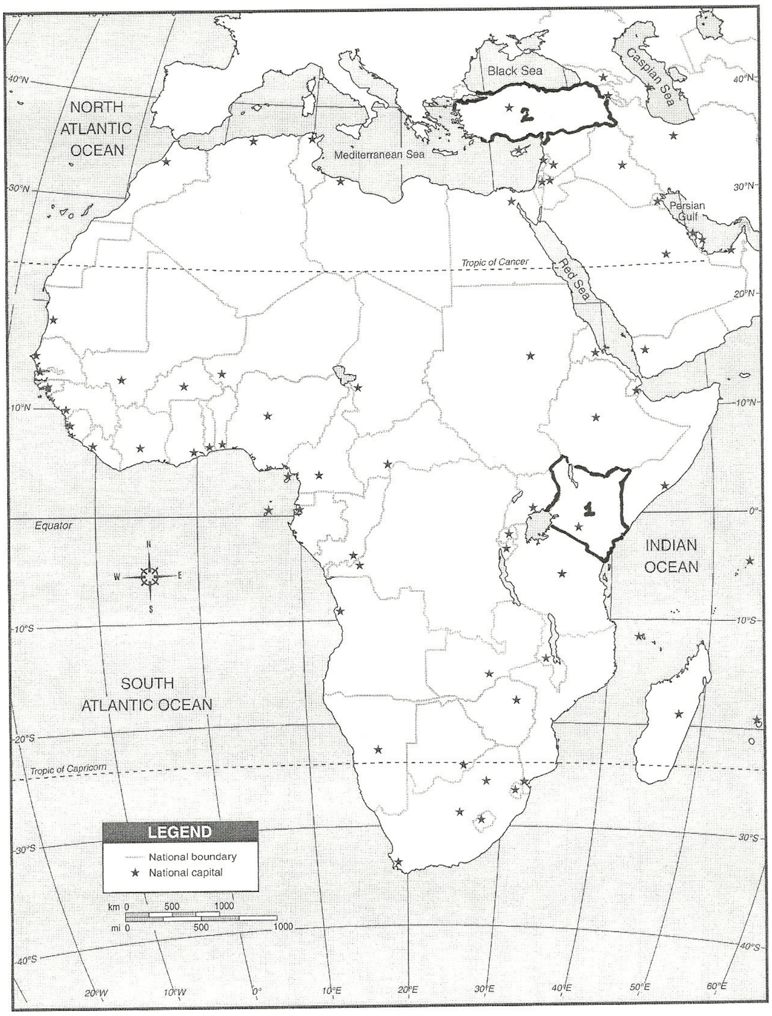

Figure 1. Africa and the Mediterranean. Two countries are outlined in bold: 1 Kenya. 2 Turkey.
(From www.eduplace.com)

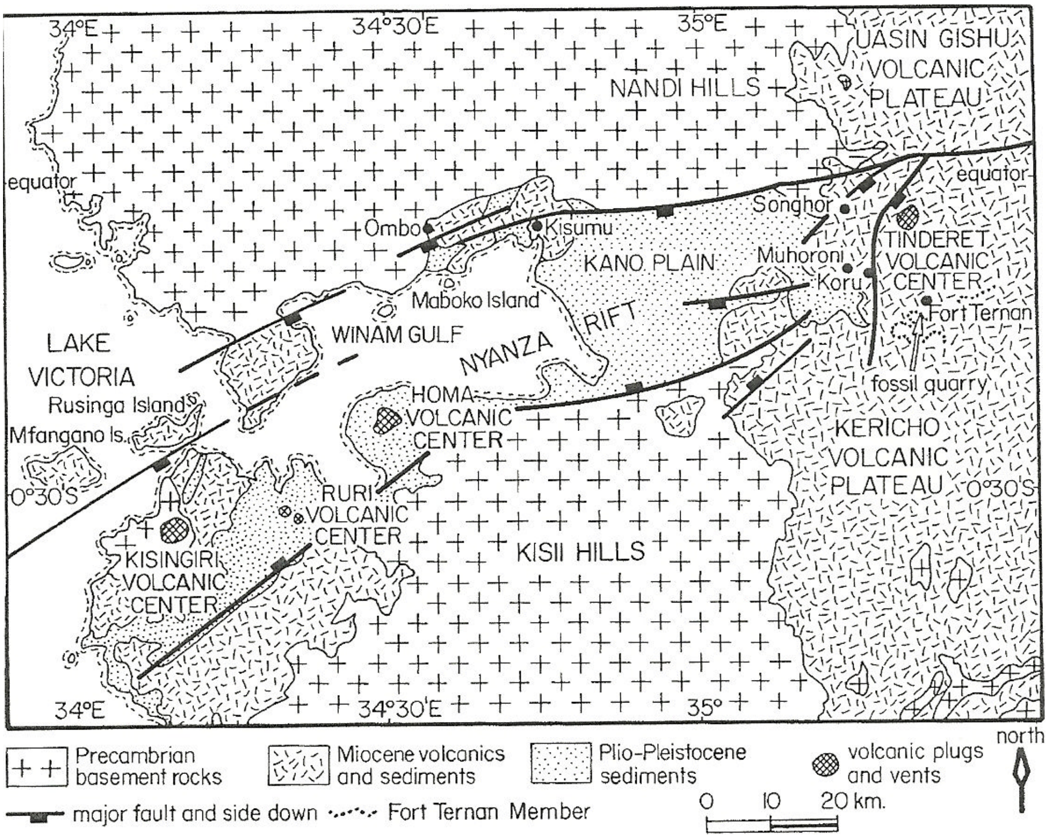

Figure 2. Detail of eastern part of Lake Victoria, showing Rusinga and Maboko Islands and Fort Ternan, Kenya, some sites where Miocene apes have been found. (From Retallack *et al.* 2002.)

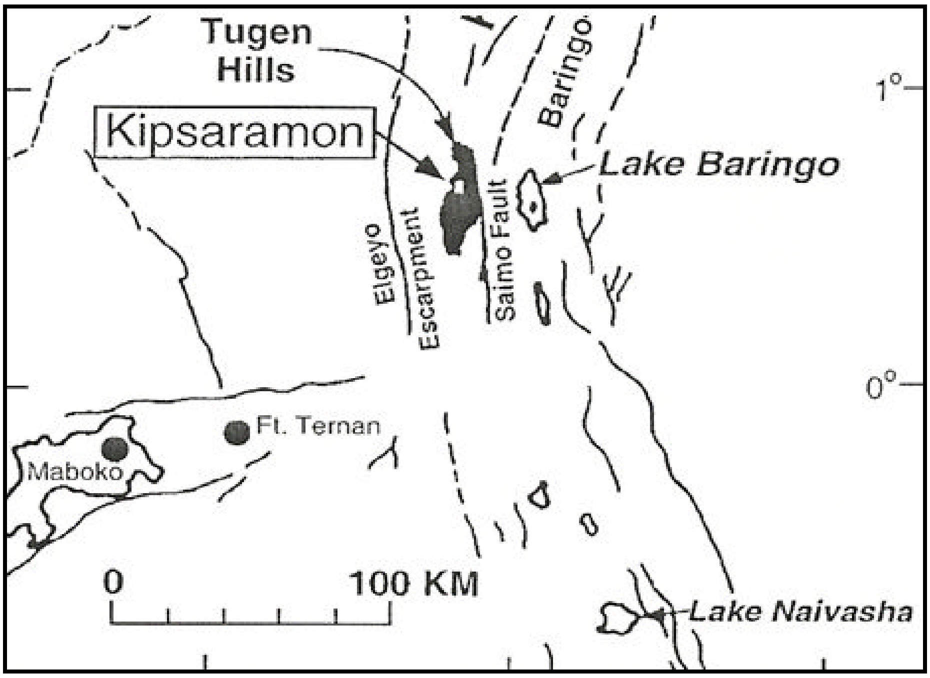

Figure 3. Kipsaramon site, Tugen Hills, Kenya in context of East African Rift system. Other Middle Miocene hominoid-bearing sites are marked with solid circles. (From Behrensmeyer *et al.* 2002.)

CHAPTER THREE

REVIEW OF THE LITERATURE

A review of the literature pertinent to investigating the aforementioned research questions reveals that incisor variation, both in fossil and extant primates, has been observed and investigated for 50 years or more (Weidenreich 1946; Hooijer 1948; and Butler and Mills 1959). Schultz (1963) was aware that hominoids exhibit intraspecific variation and focused on the extreme examples within species. Cope (1993) measured dental variation in sympatric *Cercopithecus* species to determine whether the sample contained one or more species. More recently, Swindler (2002) has come out with a revised reference on non-human primate dentition with both descriptions and metric data as to morphology and size; Whitehead *et al.* (2005) have published a comprehensive photographic atlas on the primate skeleton, with a very detailed section on primate dentition. Pilbrow (2006a) has published a quantitative study on lingual incisor traits in modern hominoids and their significance for assessing fossil hominoid relationships. Pilbrow published another study (2006b) on utilizing molar morphometrics to partition extant species of *Pan* and found that her dental results matched well with molecular studies that had partitioned these same species. Although the hominoid fossil record in the Miocene is lacking in analyzable DNA, Pilbrow's study reveals that there are comparative methods with teeth that can be used to predict whether two samples are from the same or different species. Studies like these provide a starting point for a researcher to observe what size range and morphological traits are “normal” for extant hominoids and later build upon this knowledge with one’s own research.

Other research has focused on testing hypotheses as to what the significance, causes, and function of this variation might be. For example, Gingerich and Schoeninger (1979) performed a comparative study on patterns of tooth-size variability in different primate genera, an important pioneering study that consolidated much of what was known about dental variation and gave an overall perspective on it. Eaglen (1984) compared incisor morphology and incisor row width between platyrrhines and catarrhines. He found that within the two broad categories of anthropoids, similar relative results were obtained, with primarily frugivorous species having broader incisor rows and broader incisors than folivores, whose incisors tended to be smaller and narrower, relative to posterior dentition. However, he also discovered that platyrrhines had absolutely smaller incisors than catarrhines. He concluded that absolute size was constrained in part by genetic factors related to ancestry. Having knowledge about the genetic constraints imposed by ancestry as well as environmental factors driving evolution is important when making decisions about what might be “normal” dental variation for a particular fossil species.

3.1. Evolutionary Relationships in Miocene Fossils

Some studies (e.g. Ruliang *et al.* 2004) have revealed that relationships between fossil and extant forms can sometimes be discerned by comparing amounts of variation in metric traits on primate molars. Can incisor variation likewise be used as a tool for sorting fossil species? Answers to that question have been equivocal over the years. Benefit (1992), McCrossin and Benefit (1993a, b), Benefit and McCrossin (1997),and McCrossin (1997) have attempted to sort out fossil species of Miocene hominoids around Lake Victoria and determine their adaptations by examining dentition, mandibular orientation, and a few rare postcranial fossils. As discussed in more detail in the previous chapter, Ward *et al.* (1999) and Kelley *et al.* (2002), announced the discovery of some Miocene ape fossils at Kipsaramon in the Tugen Hills, Kenya. After describing these fossils, they decided to erect a new genus, "*Equatorius*," and place them (and all fossils previously referred to *Kenyapithecus africanus*) into it. Their decision to make *E. africanus* generically distinct from *K. wickeri* was based upon some assumptions about incisor variation that have been called into question (Benefit and McCrossin 2000; also see Chapter II). Benefit and McCrossin (2000) disagree with the aforementioned assessment. Because of close morphological similarities between the incisors of *Equatorius* and *K. africanus*, these researchers believe that the former is just a new representative from Kipsaramon of the ubiquitous *K. africanus*, found abundantly at Maboko during the same time period. Furthermore, Benefit and McCrossin (2000) believe that *K. africanus* (encompassing *Equatorius*) may not be different enough from *K. wickeri* to justify generic distinction. Benefit and McCrossin (2000:2735a) state "new upper central incisors from Maboko extend the range of variation from the site to encompass the morphology of the Fort Ternan incisor."

To test Benefit and McCrossin's (2000) contention, Davis (2002, M.A. Thesis) examined incisor variation in extant great apes from both the Cleveland Museum of Natural History and the National Museum of Natural History. This author also examined casts of a few incisors of *K. africanus* and *K, wickeri* from Dr. Benefit's collection. Frequency data were taken on all the morphological traits studied. Davis (2002, M.A. Thesis) found a wide range of variation in all incisor classes, even between right and left antimeric pairs on the same individual.

Kelley and Etler (1989), Kelley (1993), and Kelley and Plavcan (1998), have typically acknowledged the importance of intraspecific dental variability. Their studies provide a background for analyzing dental variability in this study.

Less controversially, Scott and Lockwood (2004) found patterns in tooth crown size and shape in hominoids and have discussed how this can aid the researcher in discriminating between fossil species. Ungar and Kay (1995) analyzed Miocene pliopithecids as well as hominoids and compared them with extant hominoid teeth to deduce primate dietary adaptations from shear crest development on the molars. Because there was far greater diversity in Miocene hominoid species than in the relict extant hominoids left today, the range of dietary adaptations would have had to have been wider in the Miocene. They suggested that some of the extreme dietary adaptations might confound phylogenetic analysis, an important consideration when trying to sort fossil species. Moya-Sola *et al.* (2009) have described an intriguing new fossil, which they have named *Anoiapithecus brevirostris*, named for its short, surprisingly orthognathic face (relative to the somewhat prognathic faces of most hominoids). The new fossil, found at the Valles Penedes Basin paleontological site in Spain and dated at ~ 11.9 mya, consists of a partial face and dentition. *Anoiapithecus* shares some derived traits with the early Middle Miocene hominoids, the afropithecins (e.g., *Afropithecus* from East Africa) and the closely related Kenyapithecinae (*Kenyapithecus* [including *Equatorius*] and *Griphopithecus* from Pasalar, Turkey: thick enamel, robust mandible, molars with bunodont (low, rounded) cusps, and a strong inferior mandibular ramus, to mention a few. Unfortunately, the only surviving incisor in this specimen is the left lower central incisor, so its anterior dentition is as yet poorly known. Its exact relationship to these subfamilies may become more apparent as more material is found, but it opens up new questions about East African *vs.* Eurasian origins of hominoids and their relationships to one another.

3.2. Sexual Dimorphism

Sexual differences in anterior dentition have also been studied (Almquist 1974). Kelley and Etler (1989), Kelley (1995a, b), Kelley *et al.* (1995), Kelley and

Plavcan (1998), Scott and Lockwood (2004), and Schrein (2006) have focused much of their research on the phylogenetic significance of incisor heteromorphology in hominoids and/or on factoring in sexual dimorphism within a species when determining whether or not one or more fossil species are present. Sexual dimorphism, like fluctuating asymmetry, is a factor one must consider when attempting to sort out fossil species, because there can be dramatic differences in canine size between males and females that might mistakenly lead a researcher into concluding that there were two species, when, in fact, there is only one.

Greenfield (1996) studied sexual dimorphism in the sectorial, honing lower premolars in baboons. He was curious as to how female baboons (who do not use their canines for defense as do the males) would still have the honing complex. He concluded that because females and males belong to the same species, female dentition is constrained by the same genes that express themselves in male dentition as a functional honing complex, even though sometimes in females, having smaller canines, the honing premolar can be somewhat detrimental in wearing them down. This is a good example of the constraints of development and illustrates the nonpurposeful nature of evolution and adaptation.

Two more examples of sorting species from comparing amounts of dental variation (factoring in possible sexual dimorphism) can be found in studies done by Waddle *et al.* (1995) and Kelley and Alpagut (1999). Each of these teams came up with two different methods of sexing isolated hominoid canines of the middle Miocene specimens from Pasalar, Turkey (and very different conclusions as to whether there were two species or only one). For many years, researchers have used *Gorilla* and *Pongo* as models for how much sexual dimorphism and/or other dental variation may exist within a species. These two extant hominoid genera exhibit a large amount of sexual dimorphism. Researchers then compare dental variation found in a fossil sample with these extant species to predict whether it is possible that the fossils are from one species or multiple species. One hypothesis not often mentioned (and one that would be hard to test) is that there might actually have been more sexual dimorphism in some Miocene apes than in modern apes. This is somewhat related to Ungar and Kay's (1995) study, mentioned earlier, in which they also hypothesized that dental variability in general might have been higher in the Miocene because of greater diversity in kinds of foods the Miocene apes were eating.

3.3. Dental Ontogeny

Still other studies have focused on ontogeny of anterior teeth (Leigh *et al.* 2005; Nargolwalla *et al.* 2005). Schwartz *et al.* 2005 have investigated canine sexual dimorphism from an ontogenetic standpoint. Dean (1989) studied development of anterior dentition and their structure in hominoids. Smith *et al.* (2004) examined dental development in a fossil Miocene species from Europe, *Graecopithecus* (= *Ouranopithecus*). Deciduous teeth, smaller and less commonly found in the fossil record, have also been examined for variation (e.g., Koufos and deBonis 2004) and have sometimes been used to assess relationships between fossil species, based upon shared derived traits that may not be as apparent in the permanent dentition.

It is important to understand dental development in extant hominoids in order to be able to age and sex fossil hominoid teeth and to see how species in the past followed similar or different patterns to those in the present in their development. Understanding how teeth develop is one more aspect of knowledge to inform one more fully about being able to sort isolated teeth into species.

3.4. Dental Wear: Heritable vs. Environmental Factors

In order to understand fully the factors that lead to variation and asymmetries in anterior teeth, one must understand some are heritable; others, environmental (Hoover 2001; Corruccini 2005). Wear is an environmental influence on incisor variation, but it is coupled with enamel microstructure, under genetic control. For example, the rate at which teeth wear is influenced by whether enamel is thick or thin (Molnar and Gantt 1977; Shellis and Hiiemae 1986), and by the underlying microstructure of enamel and loading stresses to it (Maas and Dumont 1999; Macho *et al.* 2003; and Shimizu *et al.* (2005). Wear can be asymmetrical, depending on how the apes pull a food across their incisor row (e.g., favoring left or right hand, pulling up or down or diagonally; P. Walker 1973), thus impacting the symmetry of the antimeric pairs in a way that is not under genetic control.

In a recently published article, Macho and Shimizu (2010) performed computer- simulated testing on dental enamel microstructure, comparing *Australopithecus anamensis* teeth with those of *Pan* and *Gorilla* to test what adaptations to different mechanical stresses each species had and thus reveal more clearly whether the diet of *A. anamensis* might have been more similar to chimpanzees, gorillas, or something very different from either. Most of their testing has been done on molars. Pertinent to this dissertation that focuses on incisors, however, Macho *et al.* 2010:27) surmise that “due to their position away from the fulcrum, i.e., the temporo-mandibular joint or TMJ, anterior teeth are expected to show adaptations towards a greater range of loading angles than posterior teeth.”

Dean and Reid (2001) counted perikymata (periodical structural layering in enamel) and measured its spacing on hominid anterior teeth. Macho *et al.* (2003) used computer simulation to model enamel microstructure in three dimensions. Dumont (1995) studied enamel thickness and dietary adaptations, comparing extant primates with chiropterans (bats). Studies on enamel microstructure in palaeontological specimens have been undertaken on particular Miocene hominoid species such as *Lufengpithecus* and *Afropithecus* by Schwartz *et al.* (2003) and Smith *et al.* (2003). The way teeth wear is influenced by enamel microstructure, making it important to the overall study of incisor fluctuating asymmetry.

Martin *et al.* (2003) studied enamel thickness and microstructure in the New World pitheciines. Their results support the hypothesis that perhaps the

Miocene hominoid *Kenyapithecus* (though not at all closely related to New-World primates) evolved a dentition in parallel that enabled it (like the pitheciines) to be a hard-object feeder.

Wright (2005) also investigated ingestive behavior of *Cebus* (Subfamily Cebinae), more commonly available for laboratory study than the pitheciines, but also a hard-object feeder. He selected different laboratory foods known to be eaten by different primates and tested the biomechanical properties of these foods to determine values for two important properties: toughness and stiffness. Wright suggested that wild primate foods be collected in the field to be later tested in order to understand primate mastication better and how evolution has shaped the form and function of primate jaws, important in understanding also the form and function of the teeth in those jaws. Wherever one's geographic area of specialty is located, it is important to acquire an overall knowledge of dentition and diet of living primates. Studies like those of Martin *et al.* (2003) and Wright (2005) can sometimes unexpectedly provide living analogues from very different parts of the world for fossil species with similar-appearing dental adaptations developed in parallel, such as the adaptations of both New-World pitheciines (and *Cebus*) and Miocene ape *Kenyapithecus* from the Old World.

Conroy *et al.* (1995) have studied enamel thickness and prism packing in *Otavipithecus*, the only Miocene ape known from the south of Africa. Comparing enamel thickness and prism packing between different genera can aid in understanding whether the histology of enamel evolved with primarily phylogenetic constraints (i.e., show relatedness between species) or environmental adaptations (i.e., homoplasies between species that evolved thick or thin enamel to aid in ingesting available foods in their environments).

Most recently, Deane (2009) discovered that when he quantified incisor curvature for seven genera of fossil Miocene catarrhines, his results showed it increases with increased hardness of foods consumed, being most extreme for hard-object frugivores, just as is the case in extant hominoids. However, as per Eaglen (1984), he agreed that phylogenetic constraints may be responsible for the fact that compared to extant hominoids, Miocene fossil incisors overall are smaller, narrower, and have less pronounced curvature. Therefore, one must understand that the incisor curvature rule must be applied in a relative way when comparing fossil species that have a different range of variation than can be found in extant species.

Skinner *et al.* (2009) came up with a method of discriminating between species of extant species and subspecies of *Pan* by using the enamel-dentin junction morphology of the mandibular molars. Because the dentin beneath the enamel cap of the tooth preserves much of the tooth's morphology with regard to shape of the crown (2009:1), one can use microcomputed tomography to image the EDJ and thus be able to compare (without destruction) molars from different individuals. With this tool, one can determine to which species or subspecies they might belong, yet another method in sorting fossil species.

3.5. Structural Properties of Foods and Primate Ingestive Behaviors

Other research has investigated the interaction between incisal structure (genetics) and wear (environment), asking the questions in reverse: What materials do teeth come into contact with, and what behaviors do primates exhibit while processing foods? P. Walker (1973) did a pioneering study on feeding behavior in living great apes and wear patterns caused by pulling different kinds of foods across their incisors.

More than two decades later, Strait (1997) investigated the physical properties of the foods themselves; Ang *et al.* (2006) investigated the angle of occlusion between incisors and how this angle affects biting efficiency, depending upon what food substrate is being processed. Observing what behaviors primates exhibit while processing foods that can cause asymmetrical wear and understanding the physical properties of the foods themselves (and how these properties impact food processing in the mouth) are important to discovering why teeth wear the way they do.

Hylander (1975) studied the relationship between incisor size and diet in anthropoids. He argued that, compared to folivorous catarrhines, frugivores have mesiodistally longer UI-1, UI-2, and LI-1 crowns and that these longer crowns resisted incisor wear better than the shorter ones of folivores. The assumption he made was that frugivores use their incisors more intensively (i.e., to scoop fruit) than folivores, which tend to grasp leaves, but not start processing them

(Hylander 1975). McCollum (2007), recently contested this assumption when, in comparing incisal wear between chimpanzees and gorillas, found that both have comparable amounts when scaled for body size.

Ungar (1996a, b; 1998) undertook several studies to examine the effects different primate diets have on dental microwear. As studies had been done on captive primates and ingestive behavior to assess the effects of diet on dental wear, but not in the wild, Ungar (1994) undertook a study in the Ketambe Research Station, Gunung Leuser National Park, Sumatra, Indonesia on wild primates, catalogued each species' ingestion technique (i.e., how the incisors were used, such as not at all, nipping, or scraping) and how this impacted on the wear patterns that could be found on their teeth—again, important to understanding how environmental factors might affect fluctuating asymmetry.

3.6. Palaeoenvironmental Reconstruction

The aforementioned types of research are important in understanding incisor variation and asymmetries because hominoid teeth do not develop independently of the animals to which they belonged. In order to reveal a broader picture of what these Miocene large-bodied apes were like, one must attempt to understand not only their geological contexts, but be able to reconstruct the palaeoenvironments in which they lived.

Many studies have focused upon the geology of East Africa; a few, more specifically on Maboko Island and Fort Ternan, Kenya, where *Kenyapithecus* *africanus*, (Maboko), *Kenyapithecus wickeri* (Fort Ternan), and the fossils in question, *Equatorius africanus*, have been found. Andrews *et al.* (1981) worked out a geochronology for Maboko Island, and over 20 years later, Behrensmeyer *et al.* (2002) worked out the geochronology of Fort Ternan, where *K. wickeri* was discovered. Thus, we know that these fossils are of middle Miocene age (ca. 14-15.5 mya).

Hominoid primates, extant and extinct, are (or were once) inextricably part of the habitat in which they live(d) (Palmer 2000). Nesbit Evans *et al.* (1981) and later Kappelman (1991) examined the palaeoecology of Miocene sites in western Kenya and found that the plant and animal species that flourished there were adapted to somewhat wetter conditions than today. Palmer, Benefit, McCrossin and Gitau (1998) did a preliminary study on how analysis of dental microwear for the middle Miocene primate fauna of Maboko Island might shed light on the palaeoecology of the area. With these and additional data, Palmer (2000, M.A Thesis) analyzed microwear patterns on fossil hominoid teeth on Maboko Island to reconstruct palaeoecological adaptations, including food sources the animals favored. In order to understand these extinct species as once having been living animals that thrived in a particular habitat, just as extant primates do today, studies such as Palmer *et al.* (1998) give us a richer picture of life long ago. In addition, knowing how teeth wear, one can determine to what extent fluctuating asymmetry is caused by environmental vs. genetic factors.

Thus, questions about variation and asymmetry can be applied broadly to how primates, living and extinct, cope with their environment. More importantly, bilateral fluctuating asymmetry can be used as a minimal measure of how much variation can be expected within a species, as it represents variation within an individual.

3.7. Statistical Methods and Taxonomic Problems

Still other authors have focused on the validity of applying certain statistical methods to taxonomic problems that arise from uncertainties about how much variation is too much (or too little) to justify naming a new species or genus. Corruccini and Potter (1981), Corruccini (1987, 1992), Corruccini *et al.* (2005), Lockwood *et al.* (1996), Cameron (1997), Donnelly and Kramer (1999), Harvati (2003), and Humphrey and Andrews (2008), among others, have revealed different statistical methods, such as exact randomization procedures, CV-based parametric bootstrapping, calculating coefficients of similarity, and principal components analysis, to be useful tools to test for significance in dental, cranial, and postcranial morphological variation.

More specifically, Cameron (1997) discussed the pros and cons of using the coefficient of variation (CV) vs. range-based statistics that are less dependent upon similarly structured sample sizes, sometimes difficult to obtain in fossil taxa. Kelley *et al.* (1998) tested for hominoid species number at Lufeng and concluded that the CV in palaeotaxonomy be used with caution because it “cannot be used to falsify a single-species hypothesis in any meaningful way” (1998:577).

In one of many statistical analyses over the years, Corruccini and Potter (1981) explored the relationship between crown component asymmetry and developmental stress indicators in twins by comparing size, bilateral asymmetries, and occlusal discrepancies in pairs of monozygotic twins. This pioneering study illustrates that even in genetically identical individuals, environmental factors acting differentially on each organism can produce fluctuating asymmetries in antimeric pairs of teeth within an individual. Fluctuating asymmetry in teeth and some of the factors that can cause it was seminal in providing the idea that asymmetry between antimeres in teeth could also be applied in a different way: as a comparative method to assess variation in fossil species.

Patel and Grossman (2006) were curious as to whether there was enough overlap in dental metric traits between the type specimens of *Morotopithecus* and *Afropithecus* to justify them being in different genera. They performed pairwise comparisons in premolar and M3 size between all possible pairs, using the observed amount of variation in extant pairs as a yardstick to assess whether *Morotopithecus* and *Afropithecus* teeth both fell within a common range of variation and found that these type specimens did fall within the observed range of variation in living apes ($p>0.05$). Therefore, they concluded, *Morotopithecus* is not different enough from *Afropithecus* to be in a separate genus. Because they used a similar statistical method (i.e., pairwise comparisons) to assess the dental traits, this illustrates that pairwise comparisons using known amounts of variation in comparable traits in extant apes is a valid method that can be used to sort fossil genera.

Lee (2005) examined the Dmanisi hominoid crania and performed pairwise comparisons with crania of extant hominoids of known capacity to determine both intrasexual and intraspecific variation and predict whether the fossil crania were of one or multiple species. The null hypothesis was that the variation within the Dmanisi sample was within what was expected for a single species. Lee took the resulting pairwise ratios and bootstrapped them to generate comparative distributions (2005:264) and used a one-tailed t-test to determine whether the variation within the Dmanisi crania could be due to sexual dimorphism. He found that the variation in the Dmanisi crania was comparable to that found in male-female pairs of extant species in the study, but concluded that more study needs to be done due to his small sample size of fossil crania (n=3). Although Lee's (2005) study is on crania rather than teeth, I include it because he utilized a method similar to the one used in this dissertation.

Hlusko *et al.* (2002) compared the efficacy of determining crown areas by computer digital analysis vs. estimated molar crown areas (M-D length x B-L width) in using the results to predict heritability patterns in baboons and found that, contrary to their hypothesis that the computer digital analyses would be more accurate, estimated molar crown areas worked about as well. Their study illustrates that while advanced digital techniques to predict patterns can be useful, old-fashioned measuring can still be an accurate way to collect dental data.

Lockwood *et al.* (1996) have shown that randomization procedures can be an effective tool in analyzing sexual dimorphism in *Australopithecus afarensis*. I include it because the method used in this dissertation is similar, though put to a different use.

Humphrey and Andrews (2008) examined metric variation in hominoid fossil postcanine teeth from the Middle Miocene site of Pasalar, Turkey, where Kelley *et al.* (2008) named "*Kenyapithecus"kizili*. Using coefficients of variation and bootstrapping the data, they concluded that in a sample comprised of two unequally represented species, only where the teeth differ markedly in size could this method reliably sort the two species. Coefficients of variation were used in Davis (2002, M.A. Thesis) to determine the range of variation within modern ape genera. In the present dissertation, bootstrapping the pairwise comparisons of fossil genera with the numbers of asymmetries between antimeres found intraindividually in extant apes (both with metric and morphological data) was the method used.

Schrein (2006) bootstrapped the coefficients of variation found in pairwise comparisons of molar occlusal areas (M-D x B-L) of *Ouranopithecus* (a late Miocene species) with those of living apes. She concluded that perhaps the amount of sexual dimorphism in past species could exceed that in extant species, because the alternative hypothesis, that of two separate monomorphic hominoid species being represented by the individuals killed in this catastrophic assemblage, is less probable. Three years later, some new research by Scott, Schrein, and Kelley (2009) elaborated on this method for evaluating variation and sexual dimorphism in samples of fossil hominoids. They hypothesized that because there are only three extant genera of great apes (compared with many more during the Miocene), perhaps the three extant genera do not exhibit the full range of sexual dimorphism that may have existed during the Miocene, the “Age of Apes.” Scott *et al.* (2009) found that sexual dimorphism in the postcanine dentition of *Lufengpithecus*, a late Miocene hominoid from China, exceeded that of modern *Pongo* and *Gorilla*. Using resampling methods with the modern papionin *Mandrillus* as an outgroup because it exhibits extreme dental sexual dimorphism, these authors evaluated molar dimensions in two genera of Miocene great apes: *Ouranopithecus* from Greece and *Sivapithecus* from India. They found that *Ouranopithecus* exhibited more sexually dimorphic molars than extant taxa, similar to *Lufengpithecus*, and that *Sivapithecus* molars exhibited even more sexual dimorphism than *Lufengpithecus.* The possibility remains that the *Sivapithecus* molars may represent more than one species, so they state their results for *Sivapithecus* as equivocal (Scott *et al.* 2009).

With some previous research projects utilizing resampling (more specifically, bootstrapping the data) as an effective tool to make pairwise comparisons of variation between the better known living hominoids and a less well known fossil species, this method will be used in this dissertation as well (see Chapter IV Materials and Methods).

CHAPTER FOUR

MATERIALS AND METHODS

Four metric and nine morphological traits were compared on all upper and lower incisors (both right and left) of individuals from collections of the craniodental remains of the three genera of extant great apes (*Gorilla*: n=30; *Pan*: n=20; *Pongo*: n=20), housed at the Cleveland Museum of Natural History and the National Museum of Natural History. *Pan* and *Pongo* specimens had been lumped respectively (when curated) into two species: *Pan troglodytes* and *Pongo pygmaeus*. The specimens from Cleveland were captive decedents from the Cleveland Zoo; the specimens from the National Museum were primarily wild-shot, “collected” specimens. Specimens of *Gorilla* were from two different subspecies: *G. gorilla gorilla* (the lowland gorilla; deceased captive individuals from the Cleveland Zoo, housed at CMNH) and *G. gorilla berengei* (the mountain gorilla; wild-shot individuals housed at NMNH). Sex was already noted at time of curation for each individual. In the *Gorilla* sample, there were 14 females and 16 males; in the *Pan* sample, 10 females and nine males; and in the *Pongo* sample, 10 females and 10 males. Juveniles (*Gorilla*: n=6; *Pan*: n=2; *Pongo*: n=0) were eliminated from this study due to incompletely erupted permanent incisors, but subadults (i.e., individuals with all permanent dentition, except unerupted third molars) were included. This study was not designed to compare intraspecific differences between the sexes (isolated fossil incisors are hard to identify as male or female), but instead one of intraindividual variation between antimeric pairs of incisors (minimal variation) as a yardstick against which to test pairwise comparisons of the fossils. Therefore, the sexes of the known extant individual apes were pooled for this study. Likewise, gorilla subspecies were lumped, as it was not intersubspecific variation, but intraindividual variation being compared.

The same traits were compared on mostly isolated Miocene fossil upper and lower incisors (where available) of *Kenyapithecus africanus* (n=46), *Equatorius africanus* (n=5), and *K. wickeri* (n=2), housed at the Kenya Museum of Natural History. Comparisons were made intra-individually between antimeres for fluctuating asymmetries in the incisors of extant hominoid genera *Gorilla*, *Pan*, and *Pongo*. The data on fluctuating asymmetry were used as a “yardstick” for the minimal amount of variation that is demonstrably “intraspecific.”

Trait selection was based upon specific traits referred to by McCrossin and Benefit (1997), Ward *et al.* (1999), Benefit and McCrossin (2000), and Kelley *et al.* (2002) in their debate over whether *Kenyapithecus africanus* and *K. wickeri* should be congeneric (McCrossin *et al.* 1997; Benefit *et al.* 2000) or reassigned to separate genera; i.e., *Equatorius africanus* for all material found at Maboko Island and Kipsaramon, with the genus *Kenyapithecus* being retained only for the maxillary fragments, isolated teeth, and postcranial fossils found at Fort Ternan; i.e., *K. wickeri* (Ward *et al.* 2000). Both metric and non-metric traits were chosen in order to assess within-species variation in both size and shape.

4.1. Data

Metric data were divided into those features that either could be affected by crown wear, such as crown height, mamelon height, and cingulum (cingulid) height, or those less affected by wear; e.g., crown length, because incisors wear from the occlusal surfaces down, not from side to side.

Like metric data, non-metric data can also be divided into features potentially affected by wear and those less susceptible to it. Margin shape, presence or absence of a cingulum (cingulid), presence or absence of vertical ridges, presence or absence of mamelons, and presence or absence of lingual pillars could be affected by severe wear or never have been present in the first place. Conversely, skew, spiraling, root implant angles and shape, and whether or not maxillary lateral incisors are caniniform or spatulate are traits of overall shape or orientation on which wear might play little, if any role.

4.1.1. Metric Data

Measurements were taken for four traits on each of eight incisors in each specimen. Each tooth trait was measured three times to improve accuracy; the recorded measurement was the mean of the three. Measurements on both left and right antimeres were taken in order to discern asymmetries between them and to determine which extant species have higher frequencies of asymmetries than others. The following measurements were taken to the nearest 0.01 mm:

1. Maximum lingual crown height—taken as a cord from the center of the lingual crown base (at the CEJ) to the highest point on the occlusal surface, the

crown apex. Measured on the lingual surface, as most features examined on incisors were found lingually.

2. Maximum crown length—taken mesiodistally at the widest point on the incisor.

3. Mamelon height—where present, taken from the base of the mamelon to the highest point on the apex of the occlusal surface.

4. Marginal cingulum (cingulid) height—measured from the lowest point on the lingual surface of the crown base to the central point of the lingual surface of the incisor where the cingulum abuts against the tubercle.

Intraspecific incisor variation for metric traits in the study sample of extant apes was determined by calculating the absolute differences (d = |n1 – n2|) between left and right antimeres for each incisor class (mandibular central and lateral incisors; maxillary central and lateral incisors) for each individual in the sample and averaging these differences (mean = |n1-n2| + |n3-n4| + ... |nn – no| . . . = sum/#|diffs|). Next, as the fossil incisors were more often isolated than found in antimeric pairs, absolute pairwise differences between the incisors for each *Kenyapithecus* and *Equatorius* were calculated. These absolute differences were then compared with those in the extant sample and resampled for significance (p=.05, with confidence limits of 95%). The hypothesis to be tested is that the degree of asymmetry between right and left antimeres in extant great-ape species can be sampled from the same statistical universe as the corresponding pairwise differences in *Kenyapithecus africanus* and *Equatorius africanus* specimens.

4.1.2. Non-metric (Morphological) Data

To obtain a more complete picture of incisor morphology, several non-metric traits were examined for the lingual surface of each tooth:

1. Mamelon number—the number of small, rounded projections found most commonly on newly erupted incisors. Scored as 0 (absent), or 1-4.

2. Cingulum (maxillary teeth) or cingulid (mandibular teeth) —a thickened area that forms a “collar” around the cervix of a tooth; in this study, around the lingual part of the cervix. Scored as present (1) or absent (0). (Fig. 4).

3. Vertical ridges—nearly parallel multiple ridges extending from the cingular margin to the apex of the tooth. Scored as present (1) or absent (0). (Fig. 5.)

4. Margin shape—the shape of the juncture between cingulum (cingulid) and the rest of the crown. Scored as 4 (discontinuous), 5 (U-shaped), 6 (V-shaped), or 7 (W-shaped). (Fig. 6).

5. Skew—the angle at which the incisor crowns deviate from vertical in the mesiodistal plane. Scored as 0 (absent), 1 (slight), or 2 (moderate).

6. Spiraling—diagonally twisted marginal ridge merging into a cingulum (cingulid) that is thin and high mesially and becomes thicker and lower distally. Scored as 0 (absent), 1 (slight), or 2 (moderate). (Fig. 7).

7. Lingual pillar—a vertical enamel abutment rising from the base of the lingual cingulum (cingulid) of the incisor (or arising from the cervix if the cingulum is absent), generally tapering slightly and terminating close to the apex. Scored as present (1) or absent (0). (Fig. 8).

8. Enamel curling—enamel on the mesial- or distal-most vertical ridge of the incisor that curls in on itself, forming a small scroll or fold. Scored as 0 (absent), 1 (slight), or 2 (moderate). (Fig. 9).

9. Caniniform lateral incisor—pointed or conical-shaped, rather than spatulate-shaped upper lateral incisor. Scored as either “no” (0) or “yes” (1). (Fig. 10).

Two conditions had to be present for statistical comparisons to be performed on non-metric (morphological) data: (1) In extant apes, there had to *be* asymmetry for the trait to be resampled, and (2) in *Kenyapithecus vs. Equatorius*, there had to be at least some *individual* variation, because there is no point to computing statistics of dispersion when there is no variation.

One limitation with comparing asymmetries in extant genera with variation in teeth in fossil genera is that there is sometimes within-genus symmetrical morphological variation in traits, and that variation cannot be revealed by the aforementioned method of pairwise comparisons. Let us use the example of incisor spiraling. Spiraling (if it occurs at all) can be found most commonly on upper lateral incisors (UI-2s) of most hominoid genera, though it is occasionally found on other anterior teeth. An examination of incisor spiraling for UI-1s in *Gorilla* by this author revealed that most upper central incisors (UI-1s) did not exhibit spiraling. However, in three individuals, spiraling occurred, but it was symmetrical and therefore intraspecific variation, rather than antimeric. Regular sorts of intraindividual variation are not asymmetrical; therefore, they do not show up when this method is applied.

4.2. Data Recording

For each hominoid specimen, both extant and extinct, the following data were recorded: museum, origin, date collected and collector, wild or captive, genus, species and subspecies (if known), catalogue number, age range (adult, subadult, juvenile), eruption of molars, sex, and amount of tooth wear (slight, moderate, worn). Descriptions with sketches of unusual variations were noted (Davis 2002, M.A. Thesis).

Specimens at the National Museum of Natural History that had incisors with variant morphology were tagged for photography and molding. Each tagged specimen was placed on a copy stand, and full-skull and specimen-tag photos were taken to ensure ease of identification. For the fossil specimens examined at the Kenya National Museum, this process was repeated. Molds made from President's Coltene compound were taken of certain incisors for later casting and examination.

All data were recorded by hand and later transferred to Microsoft Excel files; data on extant great apes are available in Davis (2002, MA Thesis). Data on great apes were initially collected by sex, genus, antimere, and tooth class in extant genera. However, there is no way at present to discern differences between incisors of males and females of fossil genera, so sexes were consolidated in each extant genus, and all worn teeth (i.e., teeth with heavy dentin exposure, breakage, significant crown height loss and obliteration of much of the lingual morphology), fragmentary teeth, and deciduous teeth of juveniles were eliminated from the samples. Statistics completed for metric traits were means, standard deviations (STD), and coefficients of variation (CV). For non-metric traits, frequency of occurrence of degree of traits that had continuous variation (0 = none, 1 = slight, 2 = moderate), different morphologies (i.e., margin shape, scored as 4, 5, 6, or 7 denoting discontinuous, U-shaped, V-shaped or W-shaped), and of presence (1) or absence (0) of traits that had discrete variation were noted. Missing data (e.g., for teeth that were absent, excessively worn, or with broken crowns or lack of roots) were put in the category “unknown.” Variation and frequency of occurrence and presence/absence were then quantitatively compared on each tooth (LI-1, LI-2, UI-1, and UI-2) between genera and intra-individually between antimeres by converting the frequency counts to percentages of the total number of apes and comparing these percentages. In this dissertation, the presence or absence of asymmetry is paramount in importance.

4.3. Data Analysis

Data collected for this dissertation were analyzed by bootstrapping to determine whether there was significantly more variation between taxa or between intra-individual asymmetrical antimeres of the same tooth. Specifically, the absolute value of each right-left sample of quantitative difference for each trait was resampled (random regeneration “with replacement” to the same sample size, n) 10,000 times to establish 95% “exact randomization” confidence limits for the asymmetry in the upper (larger) direction. This range was then applied to the alleged inter-taxon variation within specimens of the large hominoid fossils in question; i.e., *Kenyapithecus* vs. *Equatorius,* to assess whether diagnosed fossil taxa are more variable one from another than are the antimeric pairs in samples of extant taxa (see Table 1).

Summary tables were compiled for both metric and non-metric traits, comparing *Kenyapithecus vs. Equatorius* to each of the extant hominoid genera: *Gorilla*, *Pan*, and *Pongo*. For metric traits, mean asymmetries and probabilities were summarized for each genus (see Tables 2-5). For non-metric traits, frequency data and numbers of discordances for each trait between the *Kenyapithecus* specimens and *Equatorius* were summarized, with corresponding frequency data and numbers of antimeric asymmetries for each extant genus to be compared (see Tables 6-9). Finally, significant vs. nonsignificant results were tallied and added up for each extant hominoid species for both metric and non-metric traits for each class of incisor. The grand total numbers of significant vs. nonsignificant results for all extant hominoids were then summarized for each: metric and non-metric traits (see Tables 9-19). This procedure was repeated when the author compared *K.* (including *E.*) *africanus* vs. *K. wickeri* with each extant ape genus (see Tables 21-35).

This procedure compares many different traits using partly redundant sampling (as regards individual specimens). Furthermore, there is frequently one specimen of *Equatorius* compared repeatedly to multiple *Kenyapithecus* specimens. This raises the spectre of redundant sampling and excessive Type I statistical error. Since there are frequently multiple *Kenyapithecus* to compare to one *Equatorius*, a comparison repeated after multiple traits, it is reasonable in theory, indeed, conservative, to consider also a “Bonferroni” protected probability of .001 as the critical, or alpha p for confident rejection of the null hypothesis. By dividing .05 by the number of univariate tests performed, the Bonferroni principle can help guard against Type I errors.

The resampling procedure is used throughout in the interest of consistency. This method hypothetically is powerful and independent of distributional assumptions and can be applied to all kinds of data: nominal, ordinal, continuous, or even normally distributed, and might be more exact when a critical probability for the null hypothesis approaches the “magical” arbitrary level of p=.05 (Bruce, Simon and Oswald 1997). Nevertheless, in the interest of breadth of treatment, a few selected tests will be repeated at the end of the Results chapter, using classical and more familiar techniques: chi square for one example of a test of present/absent data where p is close to .05, Fisher Exact Theorem (p. 111), and a one-directional t-test applied to an example of the data for a continuous trait.

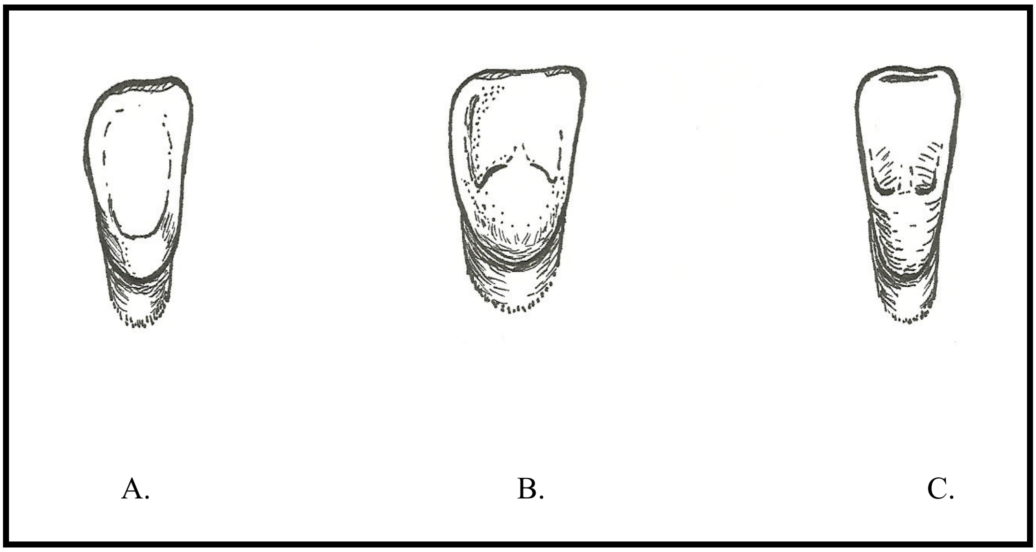

Figure 4. Incisor marginal lingual cingulum variants. A. Collar-like (common on all incisor types). B. Bulbous (basal swelling). More common on UI-1s, especially *Gorilla.* C. Tall, thin (common on *Pongo* LI-2s and LI-2s).

Figure 5. Vertical ridges. A. Vertical ridges present. B. Vertical ridges absent.

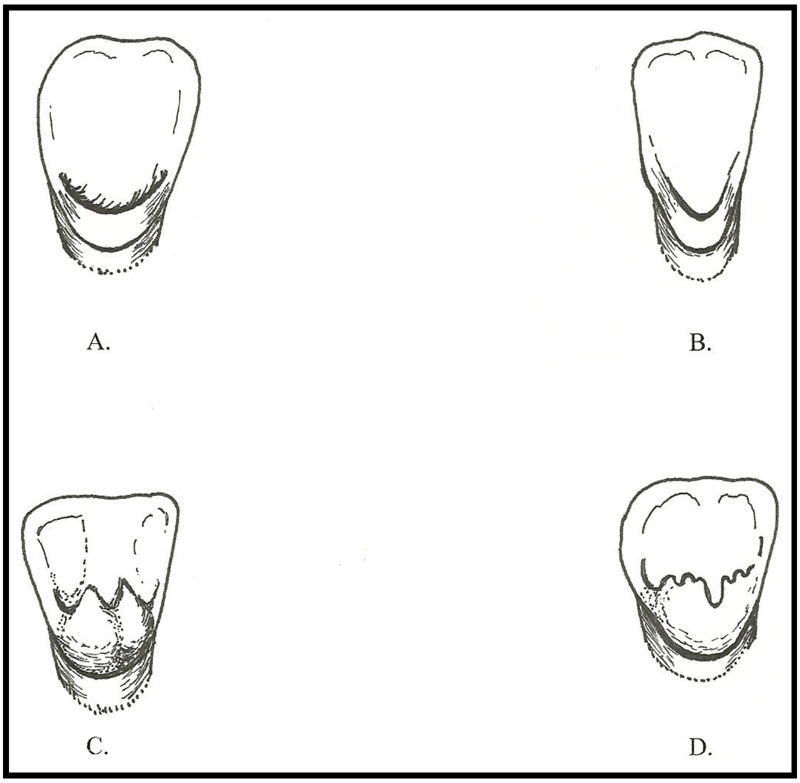

Figure 6. Cingulum margin shape variants. A. U-shaped. B. V-shaped. C. W-shaped (rare). D. Discontinuous margin shape.

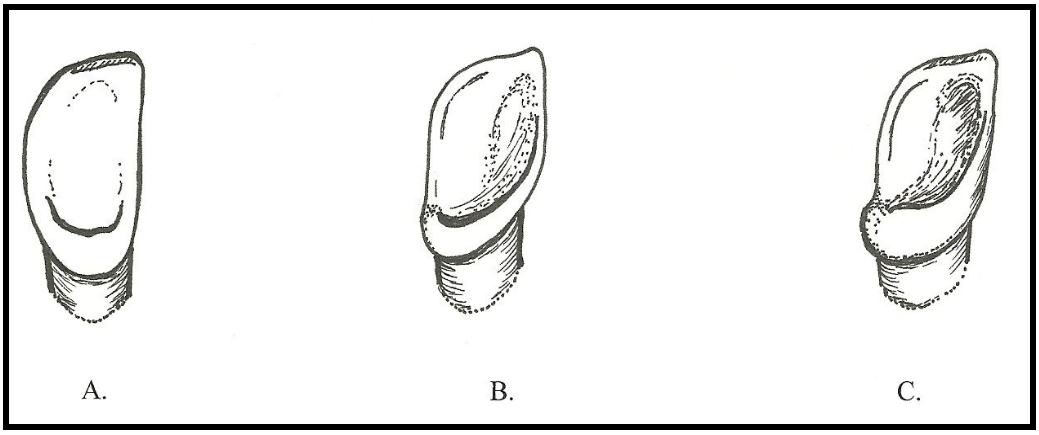

Figure 7. Incisor spiraling variants. A. No spiraling present. B. Slight spiraling. C. Moderate spiraling.

Figure 8. Lingual pillar. A. Lingual pillar present. B. Lingual pillar absent.

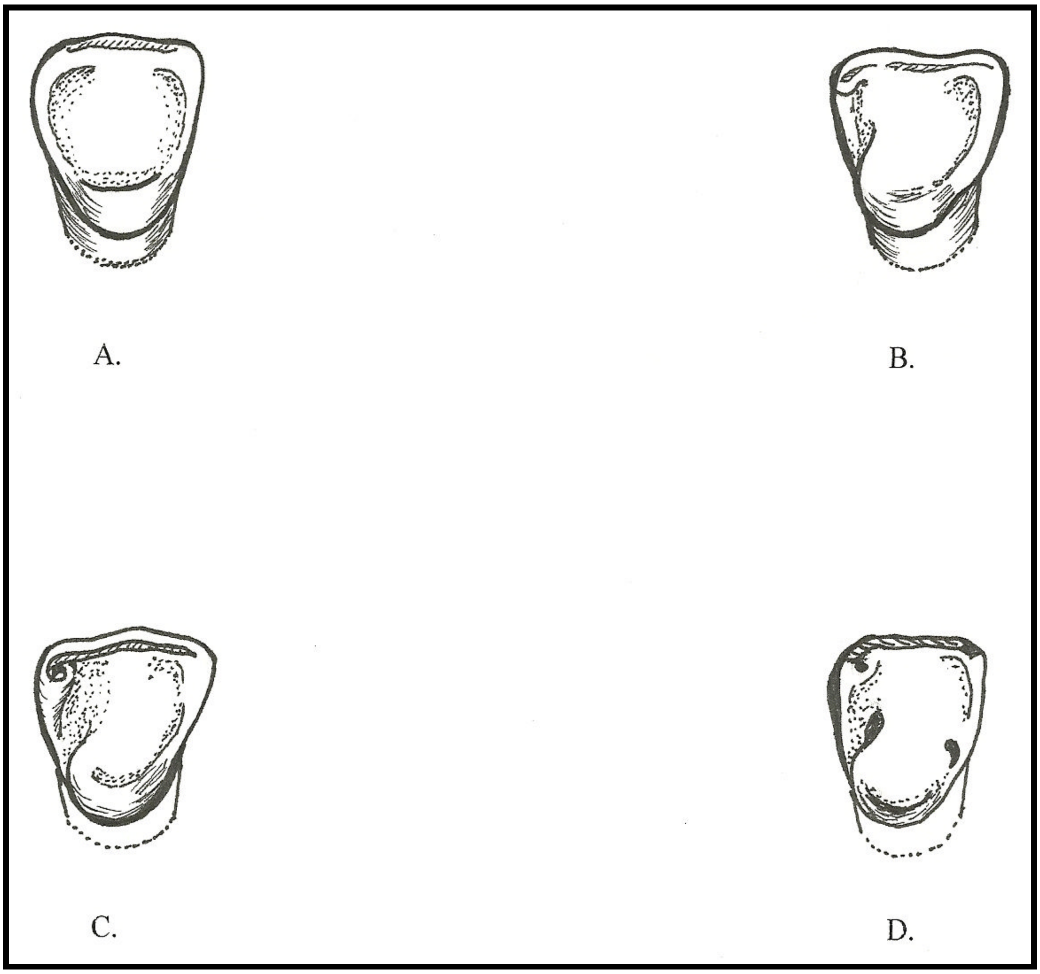

Figure 9. Enamel curling variants. A. No curling. B. Slight curling. C. Moderate curling. D. Curling on worn tooth.

Figure 10. Upper lateral incisor shape. A. Incisiform (spatulate). B. Caniniform.

CHAPTER FIVE

RESULTS

5.1. *Kenyapithecus africanus vs. Equatorius africanus*

As examination of inter- and intraspecific dental variation is one tool we have to discriminate between one or more species, it is important to continue to refine our techniques for solving problems of taxonomic assignment in the most parsimonious way. In that way, we can understand more clearly the phylogenetic history and adaptations of the hominoid superfamily.

Results comparing mean pairwise variation in incisors of *Kenyapithecus africanus* (found abundantly at Maboko Island) *vs.* "*Equatorius*" *africanus* (found at Kipsaramon, Tugen Hills) with fluctuating asymmetry of extant genera (*Gorilla, Pan*, and *Pongo*) are listed by tooth and follow below as a test of the method:

5.1.1. Metric Traits

5.1.1.1. Lower central incisors. Variation in mean crown height difference in *Kenyapithecus vs*. *Equatorius* specimens (2.13mm) was around four times higher than average antimeric asymmetry within any extant genus sample (*Gorilla* and *Pan each* = .40mm; *Pongo* = .46mm; p = 0 for the null hypothesis for all three.) Variation in mean crown length (far less variable at .96mm for *Kenyapithecus vs. Equatorius* incisors) compared with antimeric asymmetry in the incisors of *Gorilla*

(.43mm), *Pan* (.28mm), and *Pongo* (.29mm) revealed that the probability of difference was significant for gorillas (p=.0352) and highly significant for chimpanzees (p=.0039 and orangutans (p=.0032). (See Table 2.)

Neither mamelon nor cingulid heights could be obtained for any of the LI-1s in the fossil sample (LI-1s appear either to lack cingulids, or wear obliterated them); therefore, they could not be resampled.

5.1.1.2. Lower lateral incisors. Variation in mean crown height in *Kenyapithecus vs. Equatorius* (1.40mm) showed a similar result to mean crown *length* in LI-1s, with probability being nonsignificant for *Gorilla* (p=.1658), significant for *Pan* (p=.0204) and highly significant for *Pongo* (p=.0094); see Table 3. Perhaps crown heights in LI-2s of the fossil species vary less than in LI-1s because of the more indirect positioning in which these teeth contact the foods consumed by the animals (P. Walker 1972; Palmer 2000;). Mean variation in crown length was far greater in all three extant genera (*Gorilla* = 0.44mm; *Pan* = 0.67mm; *Pongo* = 0.55mm) than for *Kenyapithecus vs. Equatorius* (0.16mm). Thus, this trait showed a nonsignificant result of p>.50 when compared across all three genera (p=.9993, p=.8186, and p=.9985, respectively; see Table 3), with no discrimination between the African and Asian apes and the fossils.

Mamelon heights and cingulid heights could be measured on some of the *Kenyapithecus vs. Equatorius* LI-2s. There was far more antimeric variation in mamelon height within each extant genus than within the fossils (*Gorilla* = 0.56mm, *Pan* = 0.30mm, and *Pongo* = 0.26mm; *Kenyapithecus vs. Equatorius* = 0.08mm), with automatically nonsignificant probabilities of p>.50 (p=1, p=.9996, and p=.9985, respectively); see Table 3. In cingulid height, however, there was more variation within the fossil genera than within each extant genus (*Kenyapithecus vs. Equatorius* = 1.14mm; *Gorilla* = 0.38mm, *Pan* = 0.27mm, and *Pongo* = 0.42mm), with p = 0 for each (Table 3).

5.1.1.3. Upper central incisors. Variation in crown height in UI-1s for *Kenyapithecus vs*. *Equatorius* (1.41mm) was about twice that of the antimeric differences in extant genera (*Gorilla* = 0.55mm, *Pan* = 0.54mm, and *Pongo* = 0.66mm). Thus, these results were highly significant (p=.0018, p=.0005, and p=.0137, respectively). For crown length in UI-1s, *Kenyapithecus vs. Equatorius* had almost twice as much variation as antimeric asymmetry in the extant African genera (1.04mm), but a nonsignificant amount of variation, compared to the Asian genus (0.92mm). This gives significant results for the African genera (*Gorilla*: p=.0352, *Pan*: p=.0368) and a nonsignificant result for the Asian genus (*Pongo*: p=.3846); see Table 4.

Mamelon heights could be measured for some of the UI-1s in all four samples. There was a slightly lesser amount of antimeric difference in mamelon height in *Gorilla* (0.33mm) as between *Kenyapithecus vs. Equatorius* (0.45mm) and less variation between antimeres in *Pan* (0.29mm) than between the two fossil genera. In Pongo, the antimeric difference was much smaller (=0.12mm). he differences were marginally nonsignificant for *Gorilla* (p=.0609) significant for *Pan* (p=.0368), and highly significant for *Pongo* (p=0). Variation in cingulum height for UI-1s between *Kenyapithecus vs. Equatorius* (0.64mm) was less than asymmetry between antimeres in *Gorilla* (1.74mm), but exceeded that in *Pan*

(0.44mm), and *Pongo* (0.52mm), with nonsignificant results: *Gorilla* (p=.5775), *Pan* (p=.1043), and *Pongo* (p=.2674); see Table 4.

5.1.1.4. Upper lateral incisors. Variation in interindividual crown height in UI-2s between *Kenyapithecus vs. Equatorius* (1.56mm) was more than twice as much as the antimeric differences in height for *Gorilla* (0.61mm), more than three times as much as for *Pan* (0.47mm), and slightly more than twice as much for *Pongo* (0.74mm), giving significant results for all three (*Gorilla* and *Pan*: p=0; *Pongo*: p=.0023). Variation in crown length for UI-2s, on the other hand, showed very little significance between any samples of extant hominoid genera and *Kenyapithecus vs. Equatorius*. For the fossils, crown lengths in UI-2s between *Kenyapithecus vs. Equatorius* varied by 0.88mm. There was slightly less variation in antimeric differences in length for *Gorilla* and *Pan* (0.75mm and 0.69mm, respectively) and half as much variation for *Pongo* (0.48mm) than in the fossil genera, yielding nonsignificant results (*Gorilla*: p=.3031; *Pan*: p=.2111, but a significant result for *Pongo* (p=.0096); see Table 5.

Variation between the interindividual differences between the fossils and antimeric differences in extant apes for mamelon height once again could not be resampled due to the lack of measurable mamelon height on the fossil UI-2s, though there was variation in antimeric asymmetry in mamelon height for all three extant genera. Cingulum height varied almost three times as much in *Kenyapithecus vs. Equatorius* (2.11mm) as in *Gorilla* (0.75mm), more than five times as much as in *Pan* (0.35mm), and about four times as much as in *Pongo*, with highly significant results (p=0 for all three extant genera); see Table 5.

5.1.2. Traits Not Resampled

Below are the non-metric (morphological) traits for each tooth type that did *not* meet criteria for resampling:

5.1.2.1. Lower central incisors. No antimeric asymmetries could be discerned in the following traits on LI-1s:

Pan:

cingulid

vertical ridges

Gorilla:

mamelon number

cingulid

Pongo:

vertical ridges

margin shape

cingulid

spiraling

lingual pillar

There were no data for the fossil sample for the following traits on lower central incisors:

Kenyapithecus vs. Equatorius:

mamelon number in *Equatorius*

Thus, no resampling tests were run on the aforementioned traits on lower central incisors.

5.1.2.2. Lower lateral incisors. No antimeric asymmetries could be resampled (for they did not exist) for the following traits on lower lateral incisors:

Pan:
- margin shape
- lingual pillar
- mamelon number
- enamel curling

Gorilla:
- mamelon number
- enamel curling

Pongo:
- margin shape
- cingulid
- spiraling
- lingual pillar

Kenyapithecus vs. Equatorius:
- margin shape
- mamelon number
- spiraling
- enamel curling

Because no mamelons were present on the fossil LI-2s, there was no way to compare mamelon number with chimpanzee or orangutan samples.

5.1.2.3. Upper central incisors. No antimeric asymmetries could be resampled for the following traits on upper central incisors:

- *Pan*:
  - margin shape
  - cingulum
  - vertical ridges
- *Gorilla*: N/A
- *Pongo*:
  - mamelon number
  - margin shape
  - cingulum
  - vertical ridges
  - lingual pillar
  - spiraling
- *Kenyapithecus vs. Equatorius:*
  - mamelon number
  - cingulum
  - vertical ridges

5.1.2.4. Upper lateral incisors. No antimeric asymmetries could be resampled for the following traits on upper lateral incisors:

- *Pan:*
  - cingulum
- *Gorilla:*

lingual pillar

Pongo:

mamelon number

enamel curling

incisor shape

Kenyapithecus vs. Equatorius:

mamelon number

cingulum

enamel curling

lingual pillar

Although these traits could not be resampled because of symmetry, there is nevertheless important information that can be gleaned from these data. For example, if there is zero variation in a trait between *Kenyapithecus* and *Equatorius* and some variation in antimeric asymmetry within *Gorilla* for that trait, it means that it is a trait that does not support generic differences between the extinct individuals.

5.1.3. Non-metric Traits

The following morphological traits met the criteria for resampling of having both some asymmetry in extant hominids and some intrageneric individual variation in the fossil hominids. (Please note that apparent number of incisors sampled sometimes varied, because where wear or chemical erosion obliterated a trait, data for it was lacking, and therefore that particular tooth or teeth had to be excluded from the sample for that trait.)

5.1.3.1. Lower central incisors. Lower central incisors in all hominoids tend to be small and rather spatulate in morphology, with distinct mesial and distal corners. As these teeth are the first to erupt and are the smallest of the permanent incisors, they tend to have less distinct features on the lingual surfaces than other incisors at the beginning. In addition, the reduced relief on them may be because they are subjected to wear for longer than the other teeth. Lingual pillars, when present, are little more than a thin vertical marking, demarcating very shallow mesial and distal foveae. Unless an LI-1 has just recently erupted (especially in thin-enameled genera; e.g., *Gorilla* or *Pan*), mamelons are rarely present because they have already been worn away. Below are the results for the following traits that were resampled:

5.1.3.1.1. Margin shape. Margin shape can be coded into four categories: discontinuous (an irregular margin—coded as 4), U-shaped (coded as 5), V-shaped (coded as 6), and a rare W-shape (coded as 7) that occasionally accompanies the equally rare twinned lingual pillars. In LI-1s, the smallest incisors, the most common margin shapes in all hominoid species studied appeared to be either the U or V shapes.

Gorilla had the most variation in margin shapes: discontinuous (R=1/15;=2/18). U-shaped (R=5/15; L=4/18); V-shaped (R=9/15; L=11/18), with a single W-shaped margin on one tooth (R=0; L=1/18), with three asymmetries between antimeric pairs. In *Pan*, the lower central incisors were wider and larger, relative to the more folivorous *Gorilla.* Two variants in morphology were observed in *Pan*: discontinuous (R=2/18; L=3/18) and U-shaped (R=16/18;

L=15/18), with one asymmetry in antimeric pairs. Finally, in *Pongo*, there were also two variants: discontinuous (R=3/19; L=4/19) and U-shaped (R=16/19; L=15/19), with one asymmetry in antimeric pairs.

There were 19 LI-1s of *Kenyapithecus*. Of these, 12/19 were concordant with the *Equatorius* LI-1 in having a U-shaped margin. There were 7/19 discordances, with one being discontinuous, one being V-shaped, and five being W-shaped. Results of resampling with *Gorilla* revealed a nonsignificant result (p=.1755), but with *Pan* and *Pongo*, highly significant results (p=.0097; p=.0066 respectively); see Table 6.

<u>5.1.3.1.2. Enamel curling</u>. This incisor trait, enamel curling, observed on an isolated UI-1, according to Ward *et al*. (1999), is supposed to be diagnostic of the species *Kenyapithecus wickeri*, found at Fort Ternan, and to distinguish it from *K.* (= *Equatorius*) *africanus.* However, several other extant hominoid species also infrequently have been observed by this author to display this trait not only on UI-1s, but on other incisors as well (Davis 2002, M.A. Thesis).

Interestingly, the sample size for LI-1s for *Kenyapithecus vs. Equatorius* is larger than the corresponding sample sizes of relatively unworn LI-1s obtained for extant hominoids. None of the three extant hominids had high frequencies of enamel curling on LI-1s, but on the few teeth where it did occur, all three genera exhibited moderate amounts of asymmetry between antimeric pairs, with left teeth favoring more enamel curling. Surprisingly *Gorilla* (which in general has higher frequencies of both asymmetry and lingual dental relief of various kinds) exhibited a lower frequency of enamel curling on LI-1s than either Pan or *Pongo*

(R=2/15; L=1/16), with two asymmetrical antimeric pairs. In *Pan*, there was a slightly higher frequency of enamel curling (R=6/17; L=5/18 with three asymmetrical antimeric pairs. *Pongo* had the highest frequency of enamel curling (R=/18; L=0) and the highest amount of asymmetry, with four asymmetrical antimeric pairs. The one LI-1 of *Equatorius* had no enamel curling. There were 23 LI-1s of *Kenyapithecus africanus* that one could examine for enamel curling*.* Comparing *K. africanus* with *Equatorius*, 20 of 23 were concordant with *Equatorius* with no enamel curling, but 3 of 23 were discordant with *Equatorius*, exhibiting slight enamel curling, supposedly only found in *K. wickeri* (Ward *et al.* 1999). Resampling these data revealed nonsignificant results between the fossils and *Gorilla* (p=.5457), *Pan* (p=.6533), and *Pongo* (p=.7681); see Table 6.

5.1.3.1.3. Skew. Skew, the mesiodistal deviation from vertical of an incisor crown relative to its root (or its position in its socket), can be found to varying degrees across primate genera, from extant platyrrhines to catarrhines (Davis 2002 M.A. Thesis) and across Miocene hominoid genera as well, including small-bodied, medium-sized, and large-bodied hominoids (Davis 2002 M.A. Thesis). Some LI-1s of *Gorilla* (R=10/15; L=12/17) exhibited no skew; others (R=5/15; L=4/17) exhibited slight skew, but only one (a right antimere) exhibited moderate skew. The sample of *Gorilla* LI-1s overall exhibited both the most variation and asymmetry within extant apes, with three asymmetrical antimeric pairs. In *Pan*, many more LI-1s exhibited slight skew (R=11/18; L=9/18), with three asymmetries between antimeric pairs. In *Pongo*, a moderate number of LI-1s exhibited slight skew (R=8/19; L=6/19), with two asymmetries between antimeric pairs.

The one LI-1 of *Equatorius* exhibited no skew. Of the 24 LI-1s of *K. africanus*, 21/24 pairwise comparisons revealed concordance with *Equatorius,* with no skew. Three of 24 comparisons were discordant, exhibiting slight skew. Resampling these data revealed nonsignificant results for *Gorilla*: (p=.7584), *Pan* (p=.6607) and *Pongo* (p=.4263); see Table 6.

5.1.3.1.4. Vertical ridges. Vertical ridges are frequently found upon the lingual surfaces of most non-human hominoid incisors, both extant and extinct. In *Gorilla*, vertical ridges were observed in a majority of LI-1s (R=13/15; L=12/16), with one asymmetrical antimeric pair. In *Pan* (R=16/18; L=16/18), vertical ridges occurred frequently, but symmetrically, with no asymmetrical antimeric pairs. In *Pongo* (R=11/18; L=12/17), vertical ridges also occurred frequently, with no asymmetrical antimeric pairs.

The LI-1 of *Equatorius* exhibited no vertical ridges. Of the 24 LI-1s of *Kenyapithecus africanus* that could be examined for this trait, there were six for which the presence or absence of vertical ridges could not be determined due to wear or erosion of the fossils. Of the remaining eighteen, pairwise comparisons revealed that 16/18 were concordant with *Equatorius*, exhibiting no vertical ridges, and 2/18 were discordant, exhibiting slight vertical ridges. Resampling these data revealed nonsignificant results between the fossils and *Gorilla* (p=.3933); see Table 6.

5.1.3.1.5. Lingual pillars. Lingual pillars are commonly found on non-hominin hominoid incisors. For LI-1s, *Gorilla* exhibited high frequencies of lingual pillars (R=11/17; L=11/19), with four asymmetries in antimeric pairs. In *Pan* (R=10/18; L=11/18), lingual pillars were also common, but with only one asymmetry between antimeric pairs. In *Pongo* (R=13/17; L=13/17), all but three antimeric pairs exhibited lingual pillars, and none of the pairs was asymmetrical. Therefore, *Pongo* could not be resampled with the fossils.

The LI-1 of *Equatorius* exhibited no lingual pillar. There were 23 LI-1s of *Kenyapithecus africanus* that could be examined for this trait. Of the 23 observed, 7/23 were concordant with *Equatorius,* lacking lingual pillars; 16/23 LI-1s were discordant with *Equatorius* and exhibited slight lingual pillars. *Kenyapithecus vs. Equatorius* data were resampled with *Gorilla* and *Pan,* yielding highly significant results (p=.0017; p=0 respectively); see Table 6.

5.1.3.1.6. Incisor spiraling. Incisor spiraling on upper lateral incisors, a trait supposedly "unique" to and part of the diagnosis of the genus *Equatorius* (Ward *et al.* 1999; Kelley *et al.* 2002) does, in fact, occur in many genera of anthropoids (Davis, unpublished data) and on all four incisors, though it is found most frequently on UI-2s. Slight incisor spiraling was found in several LI-1s in *Gorilla* (R=5/15; L=7/17), with two asymmetries between antimeric pairs. Likewise, a few LI-1s of *Pan* (R=3/18; L=6/18) exhibited slight incisor spiraling, with three asymmetries between antimeric pairs. In *Pongo* (R=1/18; L=1/18), there were no asymmetries between antimeres; therefore, resampling could not be performed.

On the one LI-1 of *Equatorius*, there is no incisor spiraling. All 25 LI-1s of *Kenyapithecus africanus* were examined for presence or absence of this trait. Pairwise comparisons between each *K. africanus* LI-1 and the LI-1 of *Equatorius* revealed concordance with *Equatorius* for 22/25 LI-1s. However, there were 3/25 LI-1s of *K. africanus* that were discordant with the *Equatorius* incisor, exhibiting slight spiraling. *Kenyapithecus vs. Equatorius* was resampled with *Gorilla* and *Pan*. The pairwise comparison yielded nonsignificant results for *Gorilla* (p=.6785) and *Pan* (p=.6735); see Table 6.

5.1.3.2. Lower lateral incisors. There are some important differences in morphology between lower lateral incisors in the two fossil Miocene hominoids in this study and in extant apes. In *Kenyapithecus africanus* from Maboko (and "*Equatorius*" from Kipsaramon), the lower lateral incisors are elongated, somewhat procumbent, and extremely narrow, with a rounded crown apical edge and no distinct mesial or distal "corners" to them. As a matter of fact, for several decades, no known LI-2s existed, or so primate palaeontologists believed until a mandibular fragment with incisors in position revealed their surprising morphology (Benefit, pers. comm.).

5.1.3.2.1. Cingulid. The cingulid (referred to as "cingulum" on maxillary teeth) is a thickened enamel collar that, in hominoids (including some early fossil hominids), sometimes rings the base of the incisor crown. In *Gorilla*, cingulids were present in the majority of LI-2s (R=12/15; L=17/19; five were missing), with one antimeric asymmetry . In *Pan*, cingulids were also present in the majority of LI-2s (R=17/17; L=16/17), with one antimeric asymmetry. In *Pongo* (R=16/19;

L=16/19 for cingulid presence), the cingulids were distinctively tall and thin. Cingulids in *Pongo* exhibited complete symmetry between antimeres. Three specimens lacked cingulids.

There are two known LI-2s of *Equatorius*. Of these, the right one exhibited a slight cingulid; the left one lacked a cingulid. There are three known LI-2s of *Kenyapithecus africanus.* Of these, 2/3 were concordant with the right LI-2 of *Equatorius* in possessing cingulids; 1/3 was concordant with the left LI-2 of *Equatorius* in lacking a cingulid. Comparing the fossil LI-2s to *Gorilla* revealed a nonsignificant result (p=.2946); to *Pan*, also a nonsignificant result (p=.2977); see Table 7.

5.1.3.2.2. Vertical ridges. Vertical ridges have been described above. On LI-2s, they were found far more frequently in the extant hominoid samples than in *Kenyapithecus vs. Equatorius*. Lower lateral incisors in modern hominoids are much more spatulate in shape than the narrow, tusk-like LI-2s in the fossil sample. As such, there is more lingual area upon which vertical ridges could be prominent.

Comparison with extant hominoids reveals that in *Gorilla*, vertical ridges were absent on some teeth (R=2/15, 5 missing; L=4/16, 4 missing), but overwhelmingly present in most (R=13/15; L=12/16), with one asymmetry between antimeric pairs. In *Pan*, vertical ridges were absent on some teeth (R=3/17; L=4/17;), but present on most (R=14/17; L=13/17), with one asymmetry between antimeric pairs. In *Pongo*, vertical ridges were absent on some teeth

(R=6/19; L=5/18, with one missing) and present on most (R=13/19; L=13/18;), with one asymmetry between antimeres.

In *Equatorius*, both LI-2s lacked vertical ridges. Of the three LI-2s of *K. africanus*, two were concordant with *Equatorius* in lacking vertical ridges, and one (MB20573) was discordant with *Equatorius*, possessing slight vertical ridges. Resampling the fossils with the extant apes revealed nonsignificant results in *Gorilla* (p=.2971); *Pan* (p=.2961); and *Pongo* (p=.3006); see Table 7.

5.1.3.2.3. Skew. Skew has been described above. In LI-2s, the majority of LI-2s in *Gorilla* and Pongo were unskewed, but in *Pan*, skew was more prevalent. In addition, asymmetry in skew was somewhat variable in extant hominoids. In *Gorilla*, some of the LI-2s exhibited skew (R=5/15; L=4/17, with five missing right teeth and three missing left teeth), and there were three asymmetries between antimeric pairs. In *Pan* (R=14/17; L=8/17), there were five asymmetries between antimeric pairs. LI-2s of *Pongo* exhibited some skew (R=5/19; L=4/19), with two asymmetries between antimeric pairs.

The LI-2 of *Equatorius* exhibited slight skew. When making pairwise comparisons of each of the seven LI-2s of *Kenyapithecus africanus* with the LI-2 of *Equatorius*, one was discordant with *Equatorius*, exhibiting no skew; the other three were discordant due to moderate skew (4/7 discordance). Results were nonsignificant when compared with *Gorilla* (p=.0736), *Pan* (p=.1330), and significant for *Pongo* (p=.0109) see Table 7.

5.1.3.2.4. Lingual pillars. Lingual pillars are a more prominent feature on LI-2s than on LI-1s. Their presence or absence *and* amount of asymmetry was highly variable in *Gorilla* (R=11/17; L=11/19), with two missing teeth), with four asymmetries between antimeric pairs. In *Pan*, lingual pillars could be found on all LI-2s (17/17), with no asymmetries between antimeric pairs. In *Pongo*, lingual pillars were entirely absent from all 19 pairs of LI-2s; thus, there were (of course) no antimeric asymmetries.

The LI-2 of *Equatorius* lacked a lingual pillar. Of the three LI-2s of *Kenyapithecus africanus*, one was concordant with *Equatorius* in lacking a lingual pillar, but two were discordant with *Equatorius*, exhibiting lingual pillars. Results of this comparison between the fossils and *Gorilla* were nonsignificant (p=.0815); see Table 7.

5.1.3.3. Upper central incisors. Upper central incisors (UI-1s) in most hominoids are very similar, being fairly large, spatulate anterior teeth relative to the smaller upper lateral incisors. The mesial corners at the crown apex are sharply defined; the distal corners are gently rounded. In many non-hominin hominoids, the lingual surface of these incisors closely resembles those of extant apes, with a lingual pillar dividing the tooth into mesial and distal foveae, a cingulum at the crown base, and in some genera, a prominent basal swelling at the crown base. In hominoids exhibiting a more “modern” basal swelling, the lingual pillar, instead of being a separate feature, rises out of the basal swelling as a lingual tuberculum (Pilbrow 2006).

The following are traits that were resampled for UI-1s:

5.1.3.3.1. Lingual pillars. Lingual pillars have been described above. In *Gorilla*, UI-1s exhibited the most variation of the three genera of living great apes, exhibiting asymmetries between eight of the antimeric pairs. In addition, *Gorilla* exhibited a rare variation of lingual pillars, with twinned pillars on three of the UI-1s (*Gorilla*: R=11/19; L=12/19) for lingual pillar presence, including the twinned ones. Twinning in lingual pillars was not observed in either *Pan* or *Pongo*, nor did this trait occur in any of the UI-1s in the fossil sample. In *Pan* (R=10/16; L=11/16), there was one asymmetrical antimeric pair. Although 13 UI-1 pairs in *Pongo* had lingual pillars and four lacked them, there were no antimeric asymmetries and could not be resampled.

There is one UI-1 known for *Equatorius*. It is a relatively unworn tooth and lacks a lingual pillar. Of 13 known UI-1s for *Kenyapithecus africanus*, 10 were usable teeth for examining this trait. In comparing each of these with the *Equatorius* UI-1, 8/9 were concordant with *Equatorius* in lacking lingual pillars, and 1/9 (MB32330) was discordant, exhibiting a slight lingual pillar. Interestingly, *K. wickeri* also lacks a lingual pillar on its one known UI-1, so presence or absence of lingual pillars failed to discriminate between *K. wickeri* and *Equatorius* as well.

Resampling this trait revealed nonsignificant results for *Gorilla* (p=.9655) and *Pan* (p=.4471); see Table 8.

5.1.3.3.2. Margin shape. Margin shape refers to the shape of the juncture between cingulum (cingulid) and the rest of the incisor crown. It can be quite variable in hominoids. A prior study (Davis, Master's Thesis 2002) revealed four different variants that can occur: discontinuous, a ragged and irregular margin; U-shaped margin (the most common shape found on upper incisors for all hominoids, fossil and extant), V-shaped margin (more commonly found on lower incisors), and the somewhat rare W-shaped margin (found typically on incisors with lingual-pillar twinning).

Of these variants in margin shape, three could be found in *Kenyapithecus africanus*: discontinuous, U-shaped, and W-shaped. The one UI-1 of *Equatorius* has a U-shaped margin. In *K.* africanus, all 13 UI-1s had visible margin shapes: either discontinuous, U-shaped, or (rarely), W-shaped. Eight of 13 UI-1s of *K. africanus* were concordant with *Equatorius*; 5/13 were discordant. *K. wickeri* is also concordant with *Equatorius* in this trait.

In *Gorilla*, all four margin shape variants were found: discontinuous (R=1/15, with five missing; L=2/18, with two missing), U-shaped (R=5/15; L=4/18), V-shaped (R=9/15; L=11/18;), and W-shaped (R=0/15; L=1/18). Of these UI-1s in *Gorilla*, there was asymmetry between three antimeric pairs.

In *Pan*, two margin-shape variants were found: discontinuous (R=2/16; L=3/16) and U-shaped (R=14/16; L=13/16). There was one asymmetry between antimeric pairs. In *Pongo*, two margin shapes were found: discontinuous (R=3/19; L=4/19) and U-shaped (R=16/19; L= 15/19), with one asymmetrical antimeric pair.

Comparing the *Kenyapithecus vs. Equatorius* sample, three of the four variants of margin shape were found in the following frequencies: discontinuous (3/13), U-shaped (8/13), and W-shaped (an astonishing 2/13), with eight concordant and five discordant with *Equatorius*. Resampling these data revealed nonsignificant results in morphological difference for *Gorilla* (p=.1477), but significant results for *Pan* (p=.0122), and *Pongo* (p=.0090); see Table 8.

5.1.3.3.3. Skew. Incisor skew has been described above. In upper central incisors in extant hominid species, skew was graded as absent (0), slight (1) or moderate (2). In the UI-1s of *Gorilla* (R=9/19; L=10/19), about one fourth of the sample exhibited slight skew, and two individuals exhibited moderate skew on just one side (R=2/19; L=0). Of these UI-1s, five of the antimeric pairs were asymmetrical. In *Pan* (R=11/16; L=9/16 for skew presence), only slight skew (or absence of skew) was observed, with two asymmetries between antimeric pairs. In *Pongo*, some UI-1s exhibited slight skew (R=8/19; L=6/19)), with two antimeric asymmetries.

The UI-1 of *Equatorius* exhibited no skew. Presence or absence of skew could be determined for 11/11 of the UI-ls of *Kenyapithecus africanus.* Eight of the 11 were concordant with *Equatorius*; 3/11 were discordant. Thus, results were nonsignificant for *Gorilla* (p=.4854), *Pan* (p=.1902) and *Pongo* (p=.1385); see Table 8.

5.1.3.3.4. Enamel curling. Enamel curling has been described above. Once thought to be unique to upper central incisors of *Kenyapithecus wickeri* (Ward *et al.* 1999; Kelley *et al.* 2002), this trait has also been found to occur in *K. africanus* and occasionally in extant hominoids. In UI-1s of *Gorilla*, (R=1/17; L=3/19) that exhibited enamel curling, four antimeric pairs were asymmetrical. In UI-1s of *Pan* (R=6/15; L=5/16), there were three asymmetrical pairs of antimeres; for *Pongo* (R=4/18; L=2/18), there was asymmetry between four antimeric pairs.

Comparing the *Kenyapithecus vs. Equatorius* sample with the extant hominoids, 9/12 UI-1s exhibited no enamel curling (one was *Equatorius*), and 3/12 UI-1s (MB104, MB20728, MB24768, and MB32331) exhibited slight enamel curling. Incidentally, one UI-1 observed in *K wickeri* (FT49) exhibited moderate enamel curling. As mentioned, the UI-1 of *Equatorius* has no enamel curling. Concordant with this result were 9/12 UI-1s of *Kenyapithecus africanus*; 3/12 were discordant, as was *K. wickeri*, initially identified as "distinct" from the curled enamel flange on its UI-1. Results were nonsignificant for *Gorilla* (p=.4102), *Pan* (p=.4079), and *Pongo* (p=.4735); see Table 8.

5.1.3.3.5. Spiraling. Incisor spiraling has been described above. Once thought to be diagnostic of the genus "*Equatorius*," and occurring only on UI-2s, this trait has also been found to occur on other incisors and in other genera (Davis M.A. Thesis 2002) . In *Gorilla* (R=5/12; L=7/16), there was slight spiraling on a little less than half the UI-1s, with two asymmetrical antimeric pairs. In *Pan* (R=3/16; L=6/16), three antimeric pairs exhibited asymmetry. In *Pongo*, incisor spiraling occurred on one pair of antimeres (R=1/18; L=1/18), with no asymmetries between antimeric pairs. Because no asymmetries were observed in *Pongo*, spiraling in UI-1s could not be resampled for this genus.

The single UI-1 of *Equatorius* exhibited no spiraling. In *Kenyapithecus africanus*, 12/13 UI-1s were concordant with *Equatorius* for lack of spiraling (as was the UI-1 of *K. wickeri*); only 1/13 was discordant, exhibiting a slight spiral. Resampling the resultant data revealed nonsignificant results for *Gorilla* (p=.8349) and *Pan* (p=.8079); see Table 8.

5.1.3.4. Upper lateral incisors. Upper lateral incisors in hominoids come in two basic shapes: caniniform and incisiform. Caniniform UI-2s occur most frequently in non-hominin hominoids, both extant and in the *Kenyapithecus/Equatorius* sample and derive their name from their superficially canine-like morphology. Caniniform UI-2 crowns are shaped like a “bishop’s hat,” with an incisal surface that comes to a point similar to that of a canine tooth. They are sometimes divided into very small mesial and distal foveae by a lingual pillar; at other times, these features are hard to discern. Conversely, incisiform UI-2s, as their name suggests, are shaped more like smaller versions of the UI-1s, with a spatulate shape, slightly sharp mesial corner, and gently curved, sloping distal corner at the incisal surface.

5.1.3.4.1. Incisor shape. In *Gorilla*, incisiform UI-2s occurred more frequently (R=11/18; L=10/18) than caniniform UI-2s (R=8/19; L=9/19), with only one asymmetry between antimeric pairs. In *Pan*, caniniform UI-2s occurred in approximately half the specimens (R=9/16; L=7/15, with one missing tooth), also with one antimeric asymmetry. In *Pongo*, caniniform UI-2s occurred slightly more frequently than incisiform UI-2s (R=10/18; L=10/18), with no asymmetrical antimeric pairs; thus, incisor shape in *Pongo* could not be resampled.

There is one known UI-2 for *Equatorius*. It exhibits the caniniform morphology. Comparing the UI-2 of *Equatorius* with the seven known UI-2s of *Kenyapithecus africanus*, 7/8 are concordant in morphology, with 1/8 discordance. Resampling this data revealed nonsignificant results for *Gorilla* (p=.3712) and *Pan* (p=.3399); see Table 9.

5.1.3.4.2. Vertical ridges. Vertical ridges have been described above. In *Gorilla* and *Pongo*, vertical ridges on UI-2s occur far less frequently than in *Pan.* In *Gorilla* (R=6/18; L=3/18 for vertical ridges), there were three asymmetrical antimeric pairs. In *Pan*, with much higher frequencies of vertical ridges than *Gorilla* or *Pongo* (R=13/16; L=10/15 with one tooth missing), there were two asymmetrical antimeric pairs. In *Pongo* (R=6/18; L=4/18), there were two asymmetrical antimeric pairs.

Vertical ridges are present on the single UI-2 known for *Equatorius*. There are seven UI-2s known for *Kenyapithecus africanus*; of these, four are concordant with *Equatorius*, and three are discordant, lacking vertical ridges (MB19899, MB28637, and MB32345). Interestingly, the single UI-2 known for *K. wickeri* (not resampled) is also concordant with *Equatorius* for vertical ridges. Resampling revealed nonsignificant results for *Gorilla* (p=.0985) and significant results for *Pan* (p=.0187) and *Pongo* (p=.0173); see Table 9.

5.1.3.4.3. Margin shape. Margin shape has been described above. In UI-2s of *Gorilla*, all four margin shapes were found: discontinuous (R=5/18 [one missing tooth]; L=4/19), U-shaped (R=7/18; L=10/19), V-shaped (R=6/18; L=4/19), and W-shaped (R=0; L=1/19). Of these, four antimeric pairs were asymmetrical. In *Pan*, three out of four margin shapes were found: discontinuous (R= 3/16; L= 3/15 [one tooth missing]). U-shaped (R=10/16; L=9/15), and V-shaped R=3/16; L=3/15). No W-shaped margins were found. Of these, one antimeric pair was asymmetrical. In *Pongo*, all four margin shapes were found: discontinuous (R=4/17; L=3/17), U-shaped (R=11/17; L=10/17), V-shaped (R=1/17; L=3/17) and W-shaped (R=1/17; L=1/17). Of these, four antimeric pairs were asymmetrical.

The margin shape of the single UI-2 known for *Equatorius* is U-shaped. Concordant in morphology with the *Equatorius* incisor were three of the seven UI-2s of *Kenyapithecus africanus*; 4/7 were discordant and W-shaped (as was the UI-2 of *K. wickeri*). Therefore, the two variants occurred in roughly similar frequencies.

Comparing the *Kenyapithecus/Equatorius* sample with the extant hominoid samples, two margin shape variants were found: U-shaped (3/7) and W-shaped (4/7). Each of these variants occurred in roughly equal numbers in *K. africanus*. The number of W-shaped margins in this fossil sample (small, of course, relative to extant samples) was surprising, as the W-shaped margin is found much less frequently in extant hominoids.

Resampling revealed marginally significant differences for *Gorilla* (p=.0480) and *Pongo* (p=.0471), and significant differences for *Pan* (p=.0210); see Table 9.

The following three traits, skew, enamel curling, and spiraling (like margin shape) could be said to lack polarity because there are degrees of skewness, enamel curling, and spiraling. Therefore, as mentioned in Chapter IV, Methods and Materials, they were initially arbitrarily scored as 0 (absent), 1 (slight), and 2 (moderate). However, because these are morphological traits and no computer 3-D mapping programs were used to analyze these incisors, this scoring system was admittedly subjective. Because “slight” and “moderate” are merely degrees of presence of a trait (and in nature, would exist on a continuum, given a large enough sample size), one could argue that “slight” and “moderate” could each be viewed as more “different” from “absent” than they are from one another and could hypothetically be lumped together. Therefore, for UI-2s (a few of which exhibited moderate spiraling in addition to the ones that were slightly spiraled), this author chose to resample skew and spiraling two different ways, in the first trial discriminating between “absent, slight, and moderate” and in the second, lumping “slight/moderate” as “present” (as opposed to “absent”) to determine whether the results would be similar or different for both methods. Because enamel curling in UI-2s was lacking on the fossils (it is characteristic of *Kenyapithecus wickeri*, which was not included in the sample), it could not be resampled in *K. africanus vs. E. africanus* and compared with the extant samples. However, enamel curling was later resampled in this study when the author performed a second set of tests, making pairwise comparisons between *K.* (*E.*) *africanus* and *K. wickeri.* The results of these resamplings of skew and spiraling of *K. africanus vs. E. africanus* follow below:

5.1.3.4.4. Skew (discriminating between degrees of discordance by scoring). Skew has been described above. Skew in UI-2s was found to vary widely in degree, from completely vertical UI-2s to severely skewed ones. In *Gorilla*, the following results were found: Some UI-2s had no skew (R=8/18; L= 6/19), with one tooth missing. Other UI-2s had slight skew (R=7/18; L=9/19). Still others had moderate skew (R=2/18; L=3/19). Finally, a small number of UI-2s were severely skewed (R=1/18; L=1/19). Of these, there were three asymmetrical antimeric pairs in *Gorilla.* In *Pan*, some UI-2s had no skew (R=6/16; L=4/15 [one missing]). Other UI-2s had slight skew (R=8/16; L=10/15). Still others had moderate skew (R=2/16; L=1/15). Of these, there were two asymmetrical antimeric pairs in *Pan.* In *Pongo*, some UI-2s had no skew (R=6/18; L=5/18). Many were slightly skewed (R=11/18; L=13/18). Only one was moderately skewed. Of these UI-2s in *Pongo*, there were four asymmetrical antimeric pairs.

In *Equatorius*, the one known UI-2 is slightly skewed (as is the *Kenyapithecus wickeri* UI-2). Of the seven known UI-2s of *K. africanus*, three were concordant with *Equatorius*. Of the discordant UI-2s, one was discordant compared to *Equatorius* in that it exhibited no skew; three were discordant because they exhibited moderate skew. Resampling revealed a significant result for *Gorilla* (p=.0354), significant result for *Pan* (p=.0156), and a nonsignificant result for *Pongo* (p=.0509); see Table 9.

5.1.3.4.5. Skew (lumping degrees into one category). The frequencies and asymmetries for skew in UI-2s for *Gorilla*, *Pan*, and *Pongo* and the pairwise comparisons between *Kenyapithecus vs. Equatorius* have been described above, and resampling skew when it is split into no skew vs. degrees of skew give the results shown in the above paragraph. If one takes those same pairwise comparisons, but lumps all the UI-2s that are skewed into a category simply called “present” (as opposed to “absent”), the results are very different. In the fossil UI-2s, the UI-2 of *Equatorius* has spiraling present, and (lumping the *K. africanus* UI-2s that exhibit different degrees of skew as simply “present”), six out of the seven are then concordant with *Equatorius*, and only one (which lacks skew) is discordant. Resampling then reveals nonsignificant results for all three extant apes: *Gorilla* (p=.6201), *Pan* (p=.4727), and *Pongo* (p=.6960); see "SkewA" in Table 9.

5.1.3.4.6. Spiraling (discriminating between degrees of discordance). Spiraling (and the controversy surrounding it) has been described above. Spiraling in UI-2s was found to vary widely in *Gorilla* and in the fossil genera and less so in *Pan* and *Pongo*. In *Gorilla*, a few UI-2s exhibited no spiraling (R=5/19; L=6/19). About twice as many exhibited slight spiraling (R=12/19; L=10/19). In addition, a few UI-2s exhibited moderate spiraling (R=2/19; L=3/19). Of the UI-2s in *Gorilla*, there were four asymmetrical antimeric pairs. In *Pan*, there were more UI-2s that exhibited no spiraling (R=13/16; L=9/15, with one missing tooth) and none that exhibited moderate spiraling. Slight spiraling could be found on some UI-2s (R=3/16; L=6/15). Of the UI-2s in *Pan*, there were five asymmetrical antimeric pairs. In *Pongo*, most UI-2s did not exhibit spiraling (R=16/18; L=14/17, with one missing tooth). A very few UI-2s exhibited slight spiraling (R=2/18; L=3/17). None exhibited moderate spiraling. Of the UI-2s in *Pongo*, there were three asymmetrical antimeric pairs.

The known UI-2 of *Equatorius* exhibits moderate spiraling. Of the seven known UI-2s of *Kenyapithecus africanus*, three are concordant for moderate spiraling; three are barely concordant with slight spiraling, and one (MB32344) is discordant, lacking spiraling. Resampling results (if one discriminates between slight spiraling as being discordant with moderate spiraling) reveal marginally significant results for *Gorilla* (p=.0463), nonsignificant results for *Pan* (p=.1425), and marginally significant results for *Pongo* (p=.0335); see Table 9.

5.1.3.4.7. Spiraling (lumping degrees into one category). Depending upon if one lumps “slight” and “moderate” spiraling together as concordant (i.e., more alike than non-spiraling is to slight spiraling), the results are altered in favor of nonsignificance. Lumping the slight and moderate spiraling together as one category, “spiraling present,” means there is then only one discordance between *Equatorius* and *Kenyapithecus* and six concordances. This changes the resampling results: nonsignificant for *Gorilla* (p=.6954), *Pan* (p=.8357), and *Pongo* (p=.6146); see Table 9.

5.2. *Kenyapithecus* (including *Equatorius*) *africanus vs. Kenyapithecus wickeri*

Whether the Miocene ape fossils found at Maboko Island and Kipsaramon are ultimately placed in the new genus, *Equatorius* (as per Ward *et al.* 1999; Kelley *et al.* 2002) or retained in the genus *Kenyapithecus* (i.e., congeneric with *Kenyapithecus wickeri* as per Benefit and McCrossin 2000), there is a close relationship between the two species. Therefore, it became important to make a second set of pairwise comparisons of *K. wickeri* with *K.* (including *E.*) *africanus* to compare with the extant apes. If more variation were found within the fossil incisor sample than intraindividual asymmetries within the extant “yardstick” incisor sample, it would mean that there would be a significant probability that the two species should be placed in different genera. On the other hand, if less variation were found within the fossil incisors than within the extant ones, it could indicate that perhaps they were not different enough to justify being placed in a new genus.

As the lower incisors for *Kenyapithecus wickeri* are unknown at this time, only pairwise comparisons between the upper incisors (UI-1s and UI-2s) of *K.* (*E.*) *africanus vs. K. wickeri* were performed, again using known amounts of variation and asymmetry in extant ape genera as a yardstick. The results follow below:

5.2.1. Metric Traits

5.2.1.1. Upper central incisors. Variation in crown height in UI-1s for *Kenyapithecus* (*Equatorius*) *africanus* vs. *K. wickeri* (1.93mm) was about twice that of the absolute antimeric differences in height in extant genera (*Gorilla* = 0.55mm, *Pan* = 0.54mm, and *Pongo* = 0.66mm). Thus, the results for the African apes were highly significant (p=.0043, p=.0010) and for *Pongo*, slightly significant (p=.0311). For crown length in UI-1s, the two fossil species had slightly more variation (0.88mm) as antimeric asymmetry in the extant African genera (*Gorilla* = 0.54mm, *Pan*= 0.67mm), with closer results to *Pongo* (0.92mm). The results were nonsignificant, however, for all three extant genera (*Gorilla*: p=.1219, *Pan*: p=.2186, and *Pongo*: p=.5312). Variation in mamelon height in UI-1s for *K.* (*E.*) *africanus* vs. *K. wickeri* was 0.98mm, more than three times the amount of antimeric asymmetry found in *Gorilla* (0.33mm) and *Pan* (0.29mm) and almost nine times the amount found in *Pongo* (0.12mm), with nonsignificant results for all three (*Gorilla*: p=.9979, *Pan*: p=.8808, and *Pongo*: p=.2169). Variation in cingulum height in UI-1s for *K.* (*E.*) *africanus* vs. *K. wickeri* was 0.67mm, compared with antimeric asymmetry in *Gorilla* (1.74mm), *Pan* (0.44), and *Pongo* (0.52), with nonsignificant results for all three (*Gorilla*: p=.4960, *Pan*: p=.6285, and *Pongo*: p=.2221; see Table 21.

5.2.1.2. Upper lateral incisors. Variation in crown height in UI-2s for *Kenyapithecus* (*E.*) *africanus* vs. *K. wickeri* (0.79mm) was roughly comparable to the absolute antimeric differences in height in *Gorilla* (0.61mm) and *Pongo* (0.74mm), but more than in *Pan* (0.47mm,). The results with all extant apes were nonsignificant (*Gorilla*=.2016, *Pan*=.5904, and *Pongo*=.3691). For crown length in UI-2s, the two fossil species had a comparable amount of variation in crown height (0.63mm) as antimeric asymmetry in the extant African genera (*Gorilla* = 0.75mm, *Pan*= 0.69mm), with slightly more variation than *Pongo* (0.48mm). The results were nonsignificant, however, for all three extant genera (*Gorilla*: p=.6740, *Pan*: p=.5841, and *Pongo*: p=.1678. Variation in cingulum height in UI-2s for *K.* (*E.*) *africanus* vs. *K. wickeri* was 0.87mm, compared with antimeric asymmetry in *Gorilla* (.75mm), *Pan* (0.35), and *Pongo* (0.48), with nonsignificant results for *Gorilla* (p=.3028), highly significant results for *Pan* (p=.0052), and significant results for *Pongo*: p=.0259); see Table 22.

5.2.2. Non-metric Traits

5.2.2.1. Upper central incisors.

5.2.2.1.1. Lingual pillars. Lingual pillars have been described above. In *Gorilla*, UI-1s exhibited the most variation of the three genera of living great apes, exhibiting asymmetries between eight of the antimeric pairs. In addition, *Gorilla* exhibited a rare variation of lingual pillars, with twinned pillars on three of the UI-1s (*Gorilla*: R=11/19; L=12/19) for lingual pillar presence, including the twinned ones. Twinning in lingual pillars was not observed in either *Pan* or *Pongo*, nor did this trait occur in any of the UI-1s in the fossil sample. In *Pan* (R=10/16; L=11/16), there was one asymmetrical antimeric pair. Although 13 UI-1 pairs in *Pongo* had lingual pillars and four lacked them, there were no antimeric asymmetries and could not be resampled.

There is one UI-1 known for *Kenyapithecus wickeri*. It has almost no wear on it and lacks a lingual pillar. Of 13 known UI-1s for *Kenyapithecus africanus* (from Maboko and Rusinga), 10 were usable teeth for examining this trait. In comparing each of these with the *K. wickeri* UI-1, 8/9 were concordant with *Equatorius africanus* (from Kipsaramon) in lacking lingual pillars, and 1/9 (MB32330) was discordant, exhibiting a slight lingual pillar. Interestingly, the UI-1 of *E. africanus* also lacks a lingual pillar on its one known UI-1, so presence or absence of lingual pillars failed to discriminate between *K. wickeri* and *E. africanus* as well.

Resampling this trait revealed nonsignificant results for *Gorilla* (p=.9846), but significant results for *Pan* (p=.0028); see Table 23.

5.2.2.1.2. Margin shape. In *Gorilla*, all four margin shape variants were found: discontinuous (R=1/14, with two missing; L=2/14, with two missing), U-shaped (R=5/14; L=3/14), V-shaped (R=9/14; L=11/14;), and W-shaped (R=0/14; L=1/14). Of these UI-1s in *Gorilla*, there was asymmetry between three antimeric pairs.

In *Pan*, two margin-shape variants were found: discontinuous (R=2/16; L=3/16) and U-shaped (R=14/16; L=13/16). There was one asymmetry between antimeric pairs. In *Pongo*, two margin shapes were found: discontinuous (R=3/19; L=4/19) and U-shaped (R=16/19; L= 15/19), with one asymmetrical antimeric pair.

Comparing the *Kenyapithecus* (*E.*) *africanus* vs. *K. wickeri* sample with *Gorilla*, three of the four variants of margin shape were found in the following frequencies: discontinuous (3/14), U-shaped (9/14), and W-shaped (an astonishing 2/14), with nine concordant and five discordant with *K. wickeri*. Resampling these data revealed nonsignificant results in morphological difference for *Gorilla* (p=.2610), *Pan* (p=.3825), and *Pongo* (p=.1003); see Table 23.

<u>5.2.2.1.3. Skew</u>. Incisor skew has been described above. In the UI-1s of *Gorilla* (R=9/19; L=10/19), about one fourth of the sample exhibited slight skew, and two individuals exhibited moderate skew on just one side (R=2/19; L=0). Of these UI-1s, five of the antimeric pairs were asymmetrical. In *Pan* (R=11/16; L=9/16 for skew presence), only slight skew (or absence of skew) was observed, with two asymmetries between antimeric pairs. In *Pongo*, some UI-1s exhibited slight skew (R=8/19; L=6/19)), with two antimeric asymmetries.

The UI-1 of *Kenyapithecus wickeri* exhibited no skew. Presence or absence of skew could be determined for 13/13 of the UI-Is of *K.* (*E.*) *africanus.* Nine of the 13 were concordant with *K. africanus*; 3/13 were discordant. Results were nonsignificant for *Gorilla* (p=.6037), *Pan* (p=.2179) and *Pongo* (p=.1460); see Table 23.

5.2.2.1.4. Enamel curling. Enamel curling has been described above. Once thought to be unique to upper central incisors of *Kenyapithecus wickeri* (Ward *et al.* 1999; Kelley *et al.* 2002), this trait has also been found to occur in *K. africanus* and occasionally in extant hominoids. In UI-1s of *Gorilla*, (R=1/19; L=3/19) that exhibited enamel curling, four antimeric pairs were asymmetrical. In UI-1s of *Pan* (R=6/15; L=5/16), there were three asymmetrical pairs of antimeres; for *Pongo* (R=4/18; L=2/18), there was asymmetry between four antimeric pairs.

Comparing the *Kenyapithecus africanus* vs. *K. wickeri* sample with the extant hominoids, 9/12 UI-1s exhibited no enamel curling (one was *Equatorius africanus*), and 3/12 UI-1s (MB104, MB20728, MB24768, and MB32331) exhibited slight enamel curling. *K wickeri* (FT49) exhibited moderate enamel curling. As mentioned, the UI-1 of *E. africanus* has no enamel curling. Concordant with this result were 3/12 UI-1s of *K. africanus*; 9/12 were discordant. Results were highly significant for *Gorilla* (p=.0007), *Pan* (p=0), and *Pongo* (p=.0001); see Table 23.

5.2.2.1.5. Spiraling. Incisor spiraling has been described above. In *Gorilla* (R=5/12; L=7/16), there was slight spiraling on a little less than half the UI-1s, with two asymmetrical antimeric pairs. In *Pan* (R=3/16; L=6/16), three antimeric pairs exhibited asymmetry. In *Pongo*, incisor spiraling occurred on one pair of antimeres (R=1/18; L=1/18), with no asymmetries between antimeric pairs.

Because no asymmetries were observed in *Pongo*, spiraling in UI-1s could not be resampled for this genus.

The single UI-1 of *Kenyapithecus wickeri* exhibited no spiraling. In *K.* (*E.*) *africanus*, 12/13 UI-1s were concordant with *K. wickeri* for lack of spiraling; only 1/13 was discordant, exhibiting a slight spiral. Resampling the resultant data revealed nonsignificant results for *Gorilla* (p=.9337) and *Pan* (p=.9367); see Table 23.

5.2.2.2. Upper lateral incisors.

5.2.2.2.1. Incisor shape. In *Gorilla*, incisiform UI-2s occurred more frequently (R=11/18; L=10/18) than caniniform UI-2s (R=7/18; L=8/18), with only one asymmetry between antimeric pairs. In *Pan*, caniniform UI-2s occurred in approximately half the specimens (R=9/16; L=7/15, with one missing tooth), also with one antimeric asymmetry. In *Pongo*, caniniform UI-2s occurred slightly more frequently than incisiform UI-2s (R=10/18; L=10/18), with no asymmetrical antimeric pairs; thus, incisor shape in *Pongo* could not be resampled.

There is one known UI-2 for *Kenyapithecus wickeri*. It exhibits the incisiform morphology. Comparing the UI-2 of *K. wickeri* with the seven known UI-2s of *K.* (*E.*) *africanus*, 1/9 are concordant in morphology, with 8/9 discordance. Resampling this data revealed highly significant results for *Gorilla* (p=0) and *Pan* (p=0); see Table 24.

5.2.2.2.2. Vertical ridges. Vertical ridges have been described above. In *Gorilla* and *Pongo*, vertical ridges on UI-2s occur far less frequently than in *Pan.* In *Gorilla* (R=6/18; L=3/18 for vertical ridges), there were three asymmetrical antimeric pairs. In *Pan*, with much higher frequencies of vertical ridges than *Gorilla* or *Pongo* (R=13/16; L=10/15 with one tooth missing), there were two asymmetrical antimeric pairs. In *Pongo* (R=6/18; L=4/18), there were also two asymmetrical antimeric pairs.

Vertical ridges are present on the single UI-2 known for *Kenyapithecus wickeri*. There are nine UI-2s known for *K.* (*E.*) *africanus*; of these, six are concordant with *K. africanus*, and three are discordant, lacking vertical ridges (MB19899, MB28637, and MB32345). Resampling revealed nonsignificant results for *Gorilla* (p=.2221),*Pan* (p=.1264), and *Pongo* (p=.0686); see Table 24.

5.2.2.2.3. Margin shape. Margin shape has been described above. In UI-2s of *Gorilla*, all four margin shapes were found: discontinuous (R=5/18 [one missing tooth]; L=4/19), U-shaped (R=7/18; L=10/19), V-shaped (R=6/18; L=4/19), and W-shaped (R=0; L=1/19). Of these, four antimeric pairs were asymmetrical. In *Pan*, three out of four margin shapes were found: discontinuous (R= 3/16; L= 3/15 [one tooth missing]). U-shaped (R=10/16; L=9/15), and V-shaped R=3/16; L=3/15). No W-shaped margins were found. Of these, one antimeric pair was asymmetrical. In *Pongo*, all four margin shapes were found: discontinuous (R=4/17; L=3/17), U-shaped (R=11/17; L=10/17), V-shaped (R=1/17; L=3/17) and W-shaped (R=1/17; L=1/17). Of these, four antimeric pairs were asymmetrical.

The margin shape of the single UI-2 known for *Kenyapithecus wickeri* is W-shaped. Concordant in morphology with the *K. wickeri* incisor were five of the nine UI-2s of *Kenyapithecus* (*E.*) *africanus*; 4/9 were discordant and U-shaped. Therefore, the two variants occurred in roughly similar frequencies.

Resampling revealed nonsignificant differences for *Gorilla* (p=.1530) and *Pongo* (p=.1096), and significant differences for *Pan* (p=.0125); see Table 24.

5.2.2.2.4. Skew (discriminating between degrees of discordance). Skew has been described above. Skew in UI-2s was found to vary widely in degree, from completely vertical UI-2s to severely skewed ones. In *Gorilla*, the following results were found: Some UI-2s had no skew (R=8/18; L= 6/19), with one tooth missing. Other UI-2s had slight skew (R=7/18; L=9/19). Still others had moderate skew (R=2/18; L=3/19). Finally, a small number of UI-2s were severely skewed (R=1/18; L=1/19). Of these, there were three asymmetrical antimeric pairs in *Gorilla.* In *Pan*, some UI-2s had no skew (R=6/16; L=4/15 [one missing]). Other UI-2s had slight skew (R=8/16; L=10/15). Still others had moderate skew (R=2/16; L=1/15). Of these, there were two asymmetrical antimeric pairs in *Pan.* In *Pongo*, some UI-2s had no skew (R=6/18; L=5/18). Many were slightly skewed (R=11/18; L=13/18). Only one was moderately skewed. Of these UI-2s in *Pongo*, there were four asymmetrical antimeric pairs.

In *Kenyapithecus wickeri*, the one known UI-2 is slightly skewed (as is the *Equatorius africanus* UI-2 from Kipsaramon). Of the nine known UI-2s of *K.* (*E.*) *africanus*, four were concordant with *K. wickeri*. Of the discordant UI-2s, one was discordant compared to *K. wickeri* in that it exhibited no skew; three were discordant because they exhibited moderate skew. Resampling revealed a nonsignificant result for *Gorilla* (p=.0930), a barely significant result for *Pan* (p=.0365), and a nonsignificant result for *Pongo* (p=.0928); see Table 24.

5.2.2.2.5. Skew (lumping degrees into one category). In the fossil UI-2s, the UI-2 of *Kenyapithecus wickeri* is slightly skewed (as mentioned above), and (lumping the *K.* (*E.*) *africanus* UI-2s that exhibit different degrees of skew as simply "present"), eight out of the nine are then concordant with *K. africanus*, and only one (which lacks skew) is discordant. Resampling then reveals nonsignificant results for all three extant apes: *Gorilla* (p=.7368), *Pan* (p=.6044), and *Pongo* (p=.7369); see "SkewA" in Table 24.

5.2.2.2.6. Spiraling. Spiraling (and the controversy surrounding it) has been described above. Spiraling in UI-2s was found to vary widely in *Gorilla* and in the fossil genera and less so in *Pan* and *Pongo*. In *Gorilla*, a few UI-2s exhibited no spiraling (R=5/19; L=6/19). About twice as many exhibited slight spiraling (R=12/19; L=10/19). In addition, a few UI-2s exhibited moderate spiraling (R=2/19; L=3/19). Of the UI-2s in *Gorilla*, there were four asymmetrical antimeric pairs. In *Pan*, there were more UI-2s that exhibited no spiraling (R=13/16; L=9/15, with one missing tooth) and none that exhibited moderate spiraling. Slight spiraling could be found on some UI-2s (R=3/16; L=6/15). Of the UI-2s in *Pan*, there were five asymmetrical antimeric pairs. In *Pongo*, most UI-2s did not exhibit spiraling (R=16/18; L=14/17, with one missing tooth). A very few UI-2s exhibited slight spiraling (R=2/18; L=3/17). None exhibited moderate spiraling. Of the UI-2s in *Pongo*, there were three asymmetrical antimeric pairs.

The known UI-2 of *Kenyapithecus wickeri* exhibits no spiraling. Of the seven known UI-2s of *Kenyapithecus* (*Equatorius*) *africanus*, two are concordant for lack of spiraling, three are discordant, having slight spiraling, and four are discordant, having moderate spiraling. Resampling results (if one discriminates between slight spiraling as being discordant with moderate spiraling) reveal nonsignificant results for *Gorilla* (p=.5772) and highly significant results for *Pan* (p=.0023) and *Pongo* (p=.0001); see Table 24.

5.3. Classical Statistics to Cross-Check Validity of Resampling Results

5.3.1. Non-metric examples

In some cases where there were no asymmetries between antimeric pairs in certain traits for extant apes, the variation could not be resampled. Take, for example, UI1 spiraling in *Pongo* (see Table 8). Out of 18 teeth, 17/18 antimeric pairs exhibited no spiraling, but one out of the 17 pairs did exhibit spiraling. Intraspecific symmetrical variation cannot be resampled, because there is zero variation between any two antimeres, even if some specimens exhibit different variants of a trait. However, methods other than resampling can in these cases give some idea of the p for the null hypothesis, based on statistical (binomial) theory. The Fisher Exact Theorem, for example, yields p=.4194 for spiraling in UI-1s of *Pongo*, a decidedly nonsignificant result.

The same test suggests that for incisor shape in UI-2s of *Pongo* (where the choices are incisiform or caniniform), p=.2800. This is borne out by binomial theory. Because the combined extant great-ape (bilateral) and fossil (inter-specimen) discordance frequency is 1/25 and concordance is 24/25, the pooled concordance would be 24/25. In a random sample of seven fossil pairs, the odds of uniform sameness would be .96 to the seventh power; i.e., .75. Therefore, the exact probability of the observed difference (1/7 discordance in the fossil pairs; 0/18 discordance bilaterally in *Pongo* is 1-.75 = .25, a probability not even close to significance (see Table 9).

Let us now use some examples where resampling was possible, but use a more conventional statistical method for comparison. For example, comparing the margin shape of the UI-2s of *Gorilla* with the fossils can be done using a chi square test with a 2 x 2 contingency table. Doing so yields chi square = 3.127, with a one-tailed p=.0385. With Yates' correction, chi square = 1.66 and p=.0988. That the rather outdated Yates correction in fact overcorrects is shown by the resampling p=.0479. Results for this trait, therefore, show fair consistency in significance between chi square and resampling.

5.3.2. Metric examples

For a metric trait, crown length of UI-1 comparison between the fossils and *Pan* was re-done, using a one-tailed t test. For samples of 10 and 17 pairs, respectively, t=1.936, with 25 df (degrees of freedom), the one-tailed p=.032 yields a comparably slightly significant result to the resampling result of p=.0352. Interestingly (and worthy of some future consideration), the variances are quite heterogeneous, being 0.94 for fossil pairs, but only 0.121 for extant asymmetry. This could make directional sense, as levels of bilateral asymmetry in well sampled contemporary apes might be expected to be more constant than differences between possibly non-contemporaneous pairs of fossils that may or may not be different species. F = 7.77, a variance ratio that with 9 and 16 df yields $p<.001$ for the null hypothesis (of equal variability). T tests that adjust for variance “heteroscedasticity” are obviously more appropriate for this study than accepting an assumption of homogeneous variance. This is another reason (in theory) to favor the resampling approach.

CHAPTER SIX

DISCUSSION AND CONCLUSIONS

6.1. Incisor Variation and Fluctuating Asymmetry

Preliminary research (Davis 2002, M.A. Thesis) showed a trend that hinted at a significant amount of incisor variation across genera, species, and sexes in the three extant great apes. While doing research at the Kenya Museum of Natural History, this author discovered by examining other fossil Miocene apes (in addition to *Kenyapithecus* and *Equatorius*) that some incisor traits, declared to be diagnostic by Ward *et al.* (1999) of one fossil species (e.g., incisor spiraling on upper lateral incisors in *Equatorius africanus* from Kipsaramon; enamel curling on central incisors in *Kenyapithecus wickeri*) can actually be observed in specimens of many other genera of anthropoids, both living and extinct (pers. obs.). Spiraling and/or enamel curling are traits that can be either present or absent in some individual fossil incisors of Early Miocene apes of widely different sizes: *Proconsul* and *Afropithecus* (enamel curling, but no spiraling); *Limnopithecus*, *Simiolus*, and *Micropithecus* (both spiraling and enamel curling); and *Dendropithecus* and *Kalepithecus* (spiraling, but no enamel curling). Some incisors of the medium-bodied, Middle-Miocene genus *Mabokopithecus*, a folivorous oreopithecid ape occupying a different niche from

Kenyapithecus, also exhibit either spiraling or enamel curling. And spiraling and enamel curling are not even unique to apes. This author's examination of small samples of platyrrhine and catarrhine monkeys in the collection at Southern Illinois University's Department of Anthropology revealed that spiraling (including reverse spiraling on some platyrrhine incisors) occur on some incisors. Thus, at least these two traits are very old, indeed.

Furthermore, some of these supposedly diagnostic traits are not discrete, but vary along a continuum. If these traits still occur on extant ape incisors, one can hypothesize that they must have been widespread among Miocene apes, including the ones that eventually became ancestral to the relict great ape species of today, or these traits would have disappeared with the extinction of the genera *Kenyapithecus* and *Equatorius*.

In this dissertation, pairwise comparisons of the fossil incisors of *Kenyapithecus africanus* from Maboko were made with the incisors from Kipsaramon (i.e., those of *Equatorius africanus*). In addition, pairwise comparisons were made between the combined samples of *Kenyapithecus* (including *Equatorius*) *africanus* and the incisors of *K. wickeri* from Fort Ternan. A different method of comparing them; i.e., applying the quantitative method of bootstrapping the results through resampling was employed in order to build upon the earlier method used in Davis 2002 (M.A. Thesis), which involved taking means, standard deviations, and coefficients of variations for metric data and taking frequency data for non-metric data. The method used in this dissertation of comparing the fossil incisors with the asymmetrical antimeres of extant great-ape incisors utilized intraindividual variation as a yardstick, but was not able to use intraspecific (but symmetrical) variation within a species. For example, within all three extant species, there were instances where some specimens had slight incisor spiraling on UI-1s and others in their species in the sample had none (intraspecific variation), but because it was not asymmetrical between antimeres, that trait could not be resampled between the fossils and *Gorilla* or the fossils and *Pongo.*

Nevertheless, a surprising amount of fluctuating asymmetry between antimeres in many specimens in all species sampled was found (e.g., spiraling on a left maxillary lateral incisor, but not on the right one; lingual pillar twinning on a right maxillary central incisor and a single lingual pillar on the left one). To review asymmetry: Van Valen (1962) defined three types of asymmetries found in nature: directional (genetically mandated by the normal development of the body plan; e.g., the stomach develops on the left, and the liver develops on the right), antisymmetry (e.g., handedness), and fluctuating (those small asymmetries between antimeres resulting from environmental “noise” during development) (see p. 5). Some of the fluctuating asymmetry (e.g., in incisor crown height or in presence or absence of vertical ridges) occurs due to differential wear across the incisor row, depending on individual idiosyncrasy in pulling tough foods across the incisors and the toughness of the foods consumed (P. Walker 1973; Strait 1997). Other asymmetry between antimeres occurs because of slight developmental variation, not as critical to proper occlusion in incisors as it would be in more complexly cusped, distal teeth (Corruccini and Potter 1981).

6.2. Discussion of Results

6.2.1. *Kenyapithecus africanus vs. Equatorius africanus*

More specifically, results in this study revealed that the amount of variation present between the incisors of *Kenyapithecus africanus* from Maboko and Rusinga and *Equatorius africanus* from Kipsaramon, as compared with asymmetry in antimeres within living hominoid species, differed in kind and significance, depending upon relative sample size and which tooth and which trait was being examined. For an example of the former, there are 25 known fossil LI-1s of *Kenyapithecus africanus*, but only four known LI-2s with which to compare the extant samples. For some traits on some teeth, the asymmetrical range of variation was wider in living species than discordances between *Kenyapithecus africanus* and *Equatorius africanus*; however, complicating matters was the fact that sometimes results were unexpectedly significant between fossil and extant traits for one genus, but not another (see Tables 20 and 35). For example, in non-metric traits (e.g., margin shape in UI-1s), comparison of *K. africanus* vs. *E. africanus* with *Pan* and *Pongo* yielded significant results, whereas comparisons with *Gorilla* yielded nonsignificant results. On the other hand, for most metric traits, comparisons of the fossils with the extants revealed more significant results than nonsignificant ones with all three extant genera. With crown height for LI-1s (to use another example), there was less antimeric variation within *Gorilla*, *Pan*, or *Pongo* than there was between *K. africanus* and *E. africanus*, yielding significant probabilities, but in LI-2s, there was more variation within *Gorilla* than between *K. africanus* and *E. africanus*, yielding a nonsignificant probability for *Gorilla*, but significant probabilities for *Pan* and *Pongo*.. In UI-1s and UI-2s, there was significantly more variation in crown height between *K. africanus* and *E. africanus* than for any of the extant apes, yielding highly significant probabilities, but for crown length in both UI-1s and UI-2s, there was less variation in crown length between *Kenyapithecus* and *Equatorius*, yielding nonsignificant probabilities. For a more complete breakdown of significant and nonsignificant probabilities found, making pairwise comparisons in metric and non-metric traits, please refer to Tables 2-9. (Tables 10-20 contain comparative summaries of the results.)

In non-metric (morphological) traits, extant great apes exhibited varying degrees of fluctuating asymmetries, with *Gorilla* by far exhibiting more asymmetrical antimeric pairs in all incisor categories (and in most traits) than either *Pan* or *Pongo*, with a high of eight asymmetries in lingual pillars in UI-1s. By contrast, antimeric pairs of incisors in *Pongo* were the most symmetrical for the three genera, with a high of eight traits which varied between individuals in the sample. However, these traits could not be resampled because the antimeric pairs were all symmetrical. *Pan*, with just two traits that were symmetrical for all antimeric pairs and asymmetries never exceeding five, was intermediate in asymmetries. (For a complete breakdown of these results, see Tables 6-9.)

When significant vs. nonsignificant results across teeth were summarized and tallied within the categories of metric vs. non-metric traits, the following pattern becomes clear: For metric traits, probabilities for 25 were significant, and 14 were nonsignificant, giving significant results an edge over non-significant ones (see Table 16). For non-metric traits, the opposite held strongly true: probabilities for 15 were significant, and 41 were nonsignificant (see Table 17).

When significant vs. nonsignificant results across teeth and combined metric and non-metric traits for each extant species were summarized and tallied, the resulting totals reveal that for only a minority of traits were probabilities for smaller antimeric variation for the extant African apes than for fossil “taxonomic” variation significant (*Gorilla*: 11; *Pan*: 15), with a majority, nonsignificant (*Gorilla*: 24; *Pan*: 18). On the other hand, *Pongo*, the only Asian ape in the samples, had a slight majority of significant over nonsignificant results (*Pongo*: 14 significant vs. 13 nonsignificant). When significant vs. nonsignificant results for all three species were tallied, there were 40 that were significant and 55 that were nonsignificant, with 19 traits on various teeth that could not be resampled due to symmetry between antimeres. In other words, overall, the total amount of variation in asymmetry in the yardstick species exceeded the amount of variation between the incisors of *Kenyapithecus africanus* and *Equatorius africanus* (see Tables 10-17).

6.2.2. *Kenyapithecus* (including *Equatorius*) *africanus vs. K. wickeri*

There are unfortunately at this time far fewer dental remains of *Kenyapithecus wickeri* than there are of the more abundant ones of *K. africanus.*

For example, as mentioned earlier, there are no known lower incisors of *K. wickeri*, so only upper central and upper lateral incisors could be used for pairwise comparisons with the extant ape- asymmetry yardstick. Thus, UI-1s and UI-2s were resampled, using the same method as was used in discriminating between *K. africanus vs. E. africanus* (the former sample).

Some differences between the two sets of results were found. For example, comparing *K.* (*E.*) *africanus vs. K. wickeri* (the latter sample) against the variation in extant apes, there was a higher number of metric traits (e.g., crown length and mamelon height for both UI-1s and UI-2s) that showed nonsignificant probabilities than for the *K. africanus vs. E. africanus* sample, in which those traits had mostly significant probabilities (Tables 4 and 21; Tables 5 and 22).

For non-metric traits, comparing enamel curling on UI-1s with all three extant apes yielded highly significant results, unlike the results of *K. africanus vs. E. africanus* with the extants, where the probabilities were all nonsignificant. An unexpected, highly significant result occurred while comparing presence/absence of lingual pillars of *Kenyapithecus* (*Equatorius*) *africanus vs. K. wickeri* with *Pan*, whereas comparisons of *K. africanus vs. E. africanus* with both *Gorilla* and *Pan* had nonsignificant probabilities (Tables 8 and 23).

For non-metric traits on UI-2s, incisor shape separated *K. wickeri* from *K.* (*E.*) *africanus.* It was the only one of the fossil UI-2s that was incisiform; the *K. africanus* and *E. africanus* UI-2s were all caniniform. The result (p=0 for both African apes) was highly significant, with *Pongo* having no asymmetries between antimeres. The one caveat here is that there is only one known UI-2 that has been described for *K. wickeri*. In extant apes, occasionally one UI-2 antimere is caniniform; the other, incisiform, so it is possible that in some not-yet found incisors of *K. wickeri*, this could also be the case. Until other upper lateral incisors of this species are found, however, the assumption is that the UI-2s of this Miocene species were incisiform. Vertical ridges had different results, too, with significant probabilities between *K.* (*E.*) *africanus vs. K. wickeri* only compared with *Pan*, whereas in the former sample, there were barely significant probabilities compared with all three extant apes. The UI-2 of *K. wickeri* exhibited no spiraling. So while the spiraling trait (discriminating between degrees of spiraling) yielded barely significant results compared with *Gorilla* and *Pongo* and nonsignificant results compared with *Pan* in the former sample, it yielded highly significant results compared with *Pan* and *Pongo* in the latter sample (Tables 9 and 24).

Tallying up the metric results by significance for all three extant ape genera revealed that there were more than twice as many nonsignificant results as there were significant ones (significant: 8; nonsignificant: 18; no asymmetries: 3). This result for *Kenyapithecus* (*Equatorius*) *africanus* vs. *Kenyapithecus wickeri* contradicts what was found for *Kenyapithecus africanus vs. Equatorius africanus*, where there were more significant than nonsignficant results. (See Tables 13 and 28 to compare the two.) By contrast, tallying up the non-metric results by significance showed a similar pattern in the *K.*(*E.*) *africanus* vs.

K. wickeri sample to the *K. africanus vs. E. africanus* sample (significant: 12; nonsignificant: 21; no asymmetries: 3). (See Tables 17 and 28 for comparison.)

When significant vs. nonsignificant results across teeth and combined metric and non-metric traits for each extant ape genus were summarized and tallied, the resulting totals for *Kenyapithecus* (*Equatorius*) *africanus vs. K. wickeri* were somewhat different than for *K. africanus vs. E. africanus.* For example, comparing them with *Pan* yielded more significant than nonsignificant results (12 and 10, respectively), while comparing them with *Gorilla* and *Pongo* yielded results more consistent with the results for *K. africanus vs. E. africanus*; i.e., more nonsignificant than significant results (*Gorilla* =17; *Pongo*=12) (see Tables 18 and 33).

The grand totals of results of *K.* (*E.*) *africanus vs. K. wickeri* compared with all three extant apes (combining metric and non-metric results) are lower than for the grand totals for *K. africanus vs. E. africanus.* The reason is that the sample size of *K. wickeri* incisors, in the absence of lower incisors with which to make pairwise comparisons with *K.* (*E.*) *africanus,* is so much smaller. Still, the grand totals of results for all three genera combined (20 significant; 39 nonsignificant, 6 with no asymmetries) indicate a larger overall proportion of nonsignificant results, which is the same as in the former comparison (see Table 35).

6.3. Checking Some Resampling Examples with Classical Statistical Methods

Simply adding numbers of traits undergoing statistical testing is admittedly crude, but as seen above, there are some trends. In addition, there is considerable redundancy in using the same samples of animals for testing multiple traits, and in often using just one "*Equatorius*" (or *Kenyapithecus wickeri*) in multiple comparisons against a series of *K. africanus* specimens. If alpha probabilities are considerably narrowed according to the Bonferroni method, "protecting" probabilities against Type I error, an alpha of .001 is not at all too harsh and might even be rather generous. A standard alpha of .05, tested repeatedly against the redundancy factor of 10 for *Equatorius* comparisons and 5 for repeat traits measured on the same great-ape specimens (to be conservative), would suggest using alpha = .05/50 or .001 to be certain of significance. With this "protected" critical probability, the null hypothesis is rejected only for 13 of 39 metric traits and for 13 of 60 total traits.

This demonstrates a significant overall degree of difference in "taxonomic" morphological discord exceeding antimeric asymmetry. Whether the consistency of rejecting this null hypothesis (low in metric and very low in non-metric) suffices to justify generic separation in the fossils becomes problematic.

All three extant species (*Gorilla* most noticeably) show equal or greater antimeric variation than *Equatorius*-to-*Kenyapithecus* variation in some of these traits, which is of critical importance to the hypothesized genus level of separation. For example, the highest number of asymmetries in antimeric pairs

(8/19 pairs) can be found for lingual pillars on the UI-1s of *Gorilla* in the following specimens:

USMNH 174697 (subadult female)
CMNH B1997 (adult female)
USMNH 396936 (subadult female)
USMNH 545027 (adult female)
USMNH 239883 (adult male)
USMNH 395636 (adult male)
USMNH 397351 (adult male)
USMNH 545028 (adult male)

Asymmetries in antimeric pairs could be found across sexes and age classes. By contrast, of the nine pairwise comparisons made between *Equatorius africanus* and *Kenyapithecus africanus* for lingual pillars, 8/9 (KMNH MB11831, MB104, MB29026, MB24768, MB32331, MB32341, RU1681, and MJ9734) were concordant with the *Equatorius africanus* UI-1, with only one discordance (MB32330). In addition, it becomes obvious that there is far less variation between *E. africanus* and *K. africanus* in presence/absence of lingual pillars than in the yardstick species against which it was measured (see Table 8). In the ten pairwise comparisons made between the combined *Kenyapithecus* (*Equatorius*) *africanus vs. Kenyapithecus wickeri* sample and the extant apes, the *K. wickeri* incisor was also concordant with the majority of the *K. africanus* incisors in lacking a lingual pillar, thus having less variation within its sample than its extant counterpart, *Gorilla*, but slightly more variation than in *Pan.*

As mentioned earlier in this study, incisor spiraling in UI-2s, a trait considered by Ward *et al.* (1999) and Kelley (2002) to be one of the traits diagnostic of the genus *Equatorius*, can be used as another example. An earlier study (Davis 2002 M.A. Thesis) revealed the presence of spiraling on incisors not only on the *Equatorius* UI-2 fossil, but on 6/7 of the UI-2s of *Kenyapithecus africanus.* In addition, though found less frequently on other incisors, its occasional presence was noted on all three extant genera as well. It is a good trait to use as an example of equal or greater antimeric variation, for moderate levels of asymmetry in antimeric pairs can be found on all three extant genera:

Gorilla (4/18 pairs):

    USMNH 174697 (subadult female)
    CMNH B1945 (adult female)
    USMNH 545027 (adult female)
    USMNH 545032 (adult female)

Pan (5/15 pairs):

    CMNH B2002 (adult female)
    CMNH B2748 (adult female)
    USMNH 176226 (adult female)
    USMNH 176236 (subadult male)
    CMNH B1882 (adult male)

Pongo (3/17 pairs):

    USMNH 143597 (adult female)
    USMNH 143561 (subadult male)

USMNH 143588 (adult male)

All three extant genera exceeded the amount of variation between *Equatorius africanus* and *Kenyapithecus africanus* (6/7 concordances), with nonsignificant results when the degrees of spiraling were lumped as “present.” Comparing *K.* (*E.*) *africanus* with *K. wickeri* with the extant genera, there were 7/9 concordances (just one more than in the former sample), with *K. wickeri* being one of the two discordant specimens, with nonsignificant results when the degrees of spiraling were lumped as “present.”

The final example is enamel curling. This trait, defined in Davis (2002 M.A. Thesis) as “enamel on the mesial- or distal-most vertical ridge of the incisor that curls in on itself, forming a small scroll or fold” has been used to distinguish the UI-1 of *Kenyapithecus wickeri* (FT49) from *Equatorius africanus* or *Kenyapithecus africanus.* In fact, this author also observed slight enamel curling on the UI-1s of three specimens of *K. africanus* (MB20728, MB24768, and MB32331), though most of the *K. africanus* specimens (like *E. africanus*, TH28860) lack enamel curling. Furthermore, enamel curling can be found occasionally on the UI-1s (and other tooth classes) of extant great-ape genera. Like lingual pillars and spiraling, the enamel curling trait sometimes exhibited asymmetry in antimeric pairs. Because enamel curling is found on the UI-1 of *K. wickeri*, this example will use asymmetries in antimeric pairs on the UI-1s of extant hominoids:

Gorilla:

USMNH 174698 (adult female)

CMNH B1795 (adult male)
USMNH 239883 (adult male)
USMNH 545028 (adult male)

Pan:

USMNH 220064 (adult female)
CMNH B2001 (adult male)
CMNH B1882 (adult male)

Pongo:

USMNH 143169 (adult female)
USMNH 143598 (adult female)
USMNH 143601 (adult female)
USMNH 143558 (adult male)

Once again, all three extant genera exceeded the amount of variation between *Equatorius africanus* and *Kenyapithecus africanus*, with nonsignificant results. Tables 6-9 illustrate other examples where the "yardstick" genera exceed the variation between the fossil genera. This could be seen as devastating to the hypothesis of generic distinctness between *Equatorius* and *Kenyapithecus*.

When adding metric and non-metric results together, slightly more asymmetry and variation in incisor measurements and morphology was found within the extant species than there was between the incisors of actual *Kenyapithecus* specimens (minus the *Nacholapithecus* incisors that were formerly misattributed to *Kenyapithecus*) and the incisors of the putative genus

"*Equatorius*." It is therefore this author's cautious assessment that the *Equatorius* incisors found at Kipsaramon could fit within the range of variation found in the genus *Kenyapithecus* (including both *K. africanus* and *K. wickeri*) and could be part of that genus.

The metric traits more consistently show *Equatorius africanus* to be outside the estimated sampling limits of *Kenyapithecus africanus* teeth when those limits are based upon extant hominoid bilateral asymmetry. In addition, the four specimens of *E. africanus* sampled are consistently larger than *K. africanus*, especially in height. One hypothesis could be that the individual teeth studied making up part of the hypodigm of *E. africanus* were unusually large, or disproportionately male, as compared to the *Kenyapithecus* remains. An alternate hypothesis could be that the remains of *E. africanus* could be a distinct, larger species of *K. africanus* with otherwise similar morphology that might be attributed to a distinct new species, but not justifying generic distinction.

As the sample size of incisors in extant genera in the preliminary research was small, one prediction is that by compiling larger samples with more species in them and performing more sophisticated statistical analyses on them, it will become more apparent that the null hypothesis (i.e., that there will be equal amounts of incisor variation in the pairwise comparisons of the fossil incisors and intraindividual variation and asymmetry between antimeric pairs in extant genera) can be more consistently falsified.

CHAPTER SEVEN

SUMMARY

This dissertation explored variation and intra-individual asymmetry in hominoid incisors as one means to inform us about assignment of fossils to the same or different genera by asking two research questions at different hierarchical levels: (1) Which species exhibit the most intra-individual variation; i.e., asymmetries in incisor antimeres, and what does this imply? and (2) How can a broad-based understanding of these relationships aid in making interpretations about variation in fossil species? Examining incisors of the three genera of extant great apes: *Gorilla*, *Pan*, and *Pongo* from the Cleveland Museum of Natural History and the National Museum of Natural History for absolute differences (metric) and numbers of asymmetrical antimeric pairs (non-metric), a “yardstick” of what is normal antimeric variation in living genera was constructed and used to compare with the mostly isolated fossil incisors of *Kenyapithecus africanus* and *Equatorius africanus* from the Kenya Museum of Natural History as a test case. Afterwards, resampling was also performed on the very much smaller sample size of fossil incisors of *K. wickeri*, comparing them with the *K.* (*E.*) *africanus* sample. This antimeric asymmetry was postulated as a quite minimal criterion of intraspecific variation in extant species. Pairwise comparisons between each incisor of *Kenyapithecus* against the incisors of *Equatorius* were performed, and these asymmetries and pairs were resampled in order to determine whether each trait in the fossils fell within the normal range of variation in living genera or fell outside it. Significance was set at p=.05, with 95% confidence limits. Results of resampling indicated that for metric traits overall, more than half the results were significant (25 vs. 14, with 9 unknown; see Table 12), and for non-metric traits overall, less than half the results were significant (15 vs. 41, with 10 with no asymmetries); see Table 16), with 19 traits (combining metric plus non-metric) that showed complete symmetry and were therefore not resampled (see Table 17). Therefore, it is this author's opinion that the null hypothesis cannot consistently be falsified. Almost every trait showed nonsignificantly differing fossil differences to at least one of the three extant samples (see Tables 20 and 35). The results of this study indicate that the incisors of *Equatorius africanus* are not different enough from those of *Kenyapithecus africanus* (or *K. wickeri*, for that matter) to use as justification for placing *E. africanus* in a separate genus.

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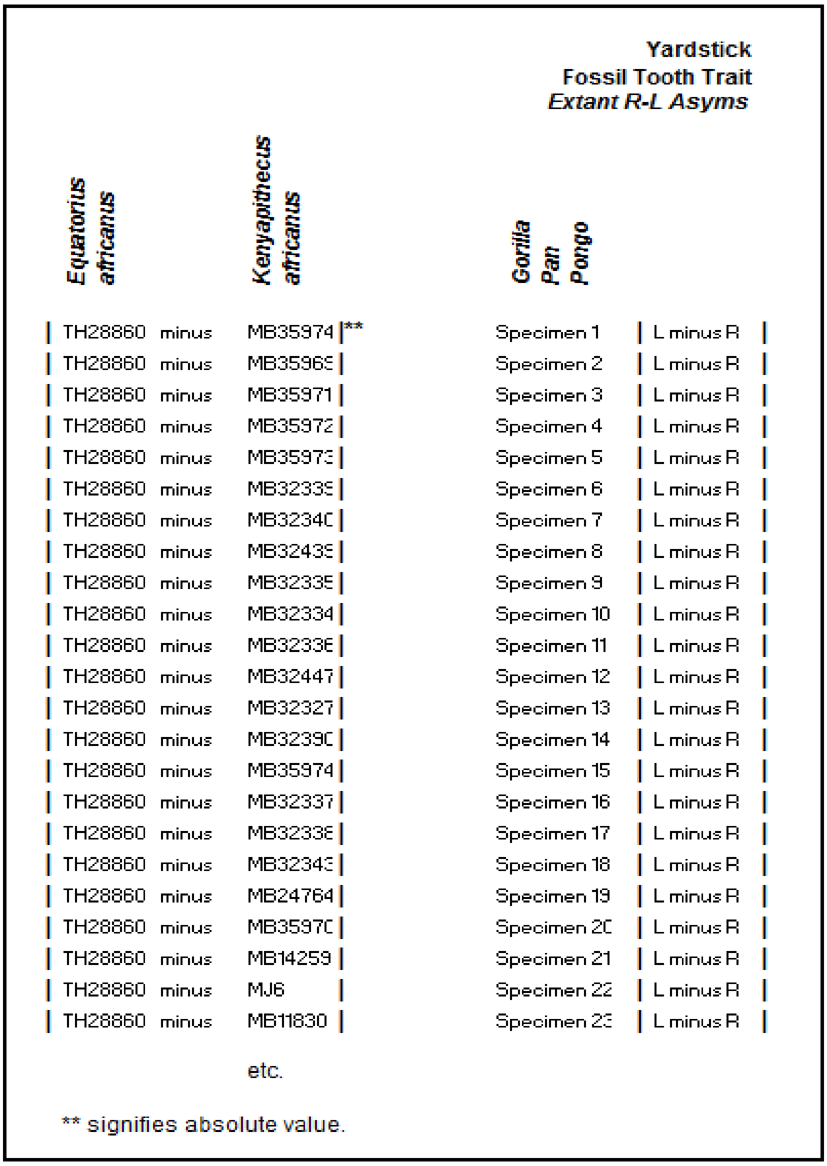
APPENDICES

APPENDIX A

TABLES 1-35

Table 1. Template showing pairwise comparison method used.



Yardstick
Fossil Tooth Trait
Extant R-L Asyms

<table>
<tr><th></th><th><i>Equatorius africanus</i></th><th></th><th><i>Kenyapithecus africanus</i></th><th></th><th><i>Gorilla
Pan
Pongo</i></th><th></th><th></th></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB35974</td><td>|**</td><td>Specimen 1</td><td>| L minus R</td><td>|</td></tr>
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<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB35973</td><td>|</td><td>Specimen 5</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32339</td><td>|</td><td>Specimen 6</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32340</td><td>|</td><td>Specimen 7</td><td>| L minus R</td><td>|</td></tr>
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<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32336</td><td>|</td><td>Specimen 11</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32447</td><td>|</td><td>Specimen 12</td><td>| L minus R</td><td>|</td></tr>
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<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32390</td><td>|</td><td>Specimen 14</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB35974</td><td>|</td><td>Specimen 15</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32337</td><td>|</td><td>Specimen 16</td><td>| L minus R</td><td>|</td></tr>
<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB32338</td><td>|</td><td>Specimen 17</td><td>| L minus R</td><td>|</td></tr>
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<tr><td>|</td><td>TH28860</td><td>minus</td><td>MB11830</td><td>|</td><td>Specimen 23</td><td>| L minus R</td><td>|</td></tr>
</table>

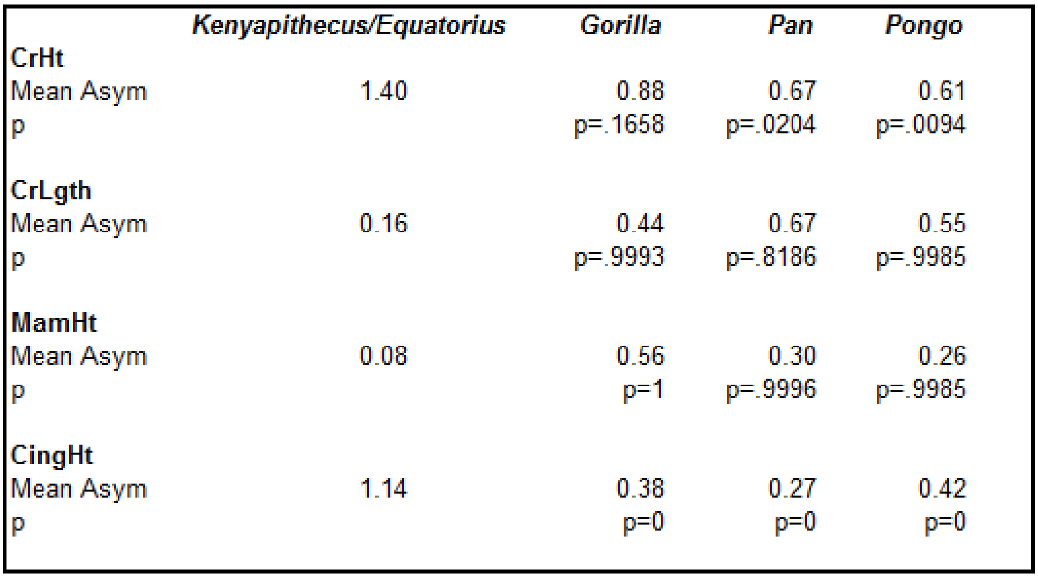
etc.

** signifies absolute value.

Table 2. Lower Central Incisor Asymmetry: Metric.
(*K. africanus/E. africanus* with Extant Apes)

	Kenyapithecus/Equatorius	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	2.13	0.40	0.40	0.46
p		p=0	p=0	p=0
CrLgth				
Mean Asym	0.96	0.43	0.28	0.29
p		p=.0352	p=.0039	p=.0032
MamHt				
Mean Asym	Unknown	0.59	0.22	0.23
p				
CingHt				
Mean Asym	Unknown	0.60	0.52	0.52
p				

Table 3. Lower Lateral Incisor Asymmetry: Metric.
(*K. africanus/E. africanus* with Extant Apes)

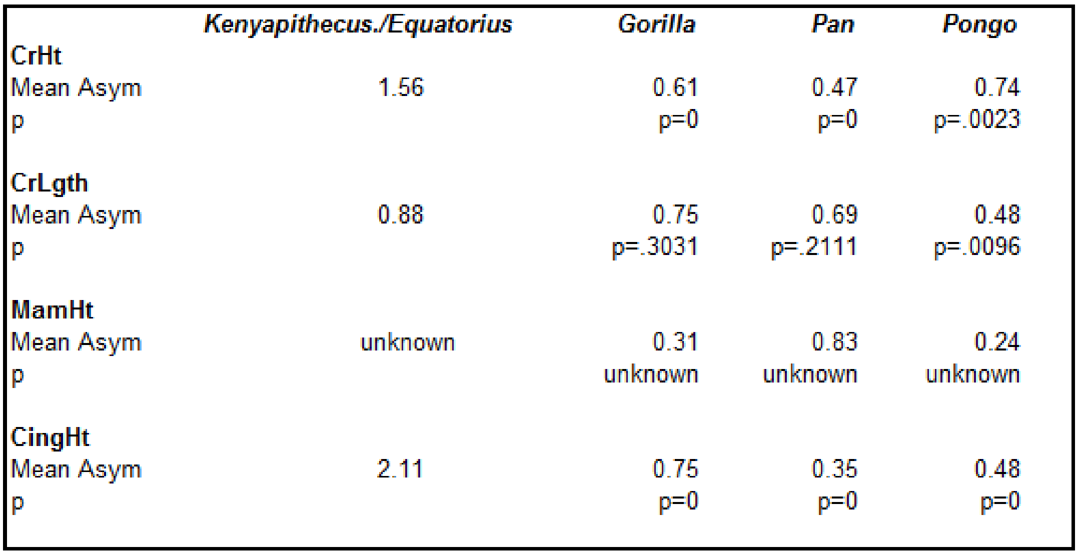


	Kenyapithecus/Equatorius	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	1.40	0.88	0.67	0.61
p		p=.1658	p=.0204	p=.0094
CrLgth				
Mean Asym	0.16	0.44	0.67	0.55
p		p=.9993	p=.8186	p=.9985
MamHt				
Mean Asym	0.08	0.56	0.30	0.26
p		p=1	p=.9996	p=.9985
CingHt				
Mean Asym	1.14	0.38	0.27	0.42
p		p=0	p=0	p=0

Table 4. Upper Central Incisor Asymmetry: Metric.
(*K. africanus/E. africanus* with Extant Apes)

	Kenyapithecus/Equatorius	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	1.41	0.55	0.54	0.66
p		p=.0018	p=.0005	p=.0137
CrLgth				
Mean Asym	1.04	0.54	0.67	0.92
p		p=.0352	p=.0368	p=.3846
MamHt				
Mean Asym	0.45	0.33	0.29	0.12
p		p=.0609	p=.0368	p=0
CingHt				
Mean Asym	0.64	1.74	0.44	0.52
p		p=.5775	p=.1043	p=.2674

Table 5. Upper Lateral Incisor Asymmetry: Metric.
(*K. africanus/E. africanus* with Extant Apes)



	Kenyapithecus./Equatorius	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	1.56	0.61	0.47	0.74
p		p=0	p=0	p=.0023
CrLgth				
Mean Asym	0.88	0.75	0.69	0.48
p		p=.3031	p=.2111	p=.0096
MamHt				
Mean Asym	unknown	0.31	0.83	0.24
p		unknown	unknown	unknown
CingHt				
Mean Asym	2.11	0.75	0.35	0.48
p		p=0	p=0	p=0

Table 6. Lower Central Incisor Asymmetry: Non-metric. (*K. africanus/E. africanus* with Extant Apes)

		Fossils		*Gorilla*			*Pan*			*Pongo*		
			Discord	R	L	Asyms	R	L	Asyms	R	L	Asyms
MargShp	4	1/19		1/15	2/18		2/18	3/18		3/19	4/19	
	5	1/19		5/15	4/18		16/18	15/18		16/19	15/19	
	6	12/19		9/15	11/18		0	0		0	0	
	7	5/19		0	1		0	0		0	0	
			7/19	p=.1755		**3/14**	p=.0097		**1/18**	p=.0066		**1/19**
EnamCrl	0	20/23		13/15	15/16		11/17	13/18		14/18	18/18	
	1	3/23		2/15	1/16		6/17	5/18		4/18	0	
	2	0		0	0		0	0		0	0	
			3/23	p=.5457		**2/12**	p=.6533		**3/17**	p=.7681		**4/18**
Skew	0	21/24		10/15	12/17		7/18	9/18		11/19	13/19	
	1	3/24		5/15	4/17		11/18	9/18		8/19	6/19	
	2	0		0	1/17		0	0		0	0	
			3/24	p=.7584		**3/13**	p=.6607		**3/18**	p=.4263		**2/19**
VertRidge	0	16/18		2/15	4/16		2/18	2/18		7/18	6/17	
	1	2/18		13/15	12/16		16/18	16/18		11/18	12/17	
	2	0		0	0		0	0		0	0	
			2/18	p=.3933		**1/13**	----		**0/18**	----		**0/17**
LingPill	0	7/23		6/17	8/19		8/18	7/18		4/17	4/17	
	1	16/23		11/17	11/19		10/18	11/18		13/17	13/17	
	2	0		0	0		0	0		0	0	
			16/23	p=.0014		**4/16**	p=0		**1/18**	----		**0/17**
Sprl	0	22/25		10/15	10/17		15/18	12/18		17/18	17/18	
	1	3/25		5/15	7/17		3/18	6/18		1/18	1/18	
	2	0		0	0		0	0		0	0	
			3/25	p=.6785		**2/13**	p=.6735		**3/18**	----		**0/17**

* (----) Signifies that resampling cannot be meaningfully performed, as there are no asyms against with to make pairwise comparisons.

Table 7. Lower Lateral Incisor Asymmetry: Non-metric. (*K. africanus/E. africanus* with Extant Apes)

		Kenyapithecus/Equatorius		*Gorilla*			*Pan*			*Pongo*		
			Discord	R	L	Asyms	R	L	Asyms	R	L	Asyms
Cing	**0**	2/3		3/15	2/19		0	1/17		3/19	3/19	
	1	1/3		12/15	17/19		17/17	16/17		16/19	16/19	
			1/3	p=.2946		**1/15**	p=.2977		**1/16**	----		**0/19**
VertRidge	**0**	2/3		2/15	4/16		3/17	4/17		6/19	5/18	
	1	1/3		13/15	12/16		14/17	13/17		13/19	13/18	
			1/3	p=.2971		**1/13**	p=.2961		**1/16**	p=.3006		**1/18**
Skew	**0**	1/7		10/15	12/17		3/17	8/17		13/19	15/19	
	1	3/7		5/15	4/17		14/17	8/17		5/19	4/19	
	2	3/7		0	1/17		0	1/17		1/19	0	
			4/7	p=.0736		**3/13**	p=.1330		**5/16**	p=.0109		**2/19**
LingPill	**0**	1/3		6/17	8/19		17/17	17/17		19/19	19/19	
	1	2/3		11/17	11/19		0	0		0	0	
			2/3	p=.0817		**4/16**	----		**0/16**	----		**0/19**

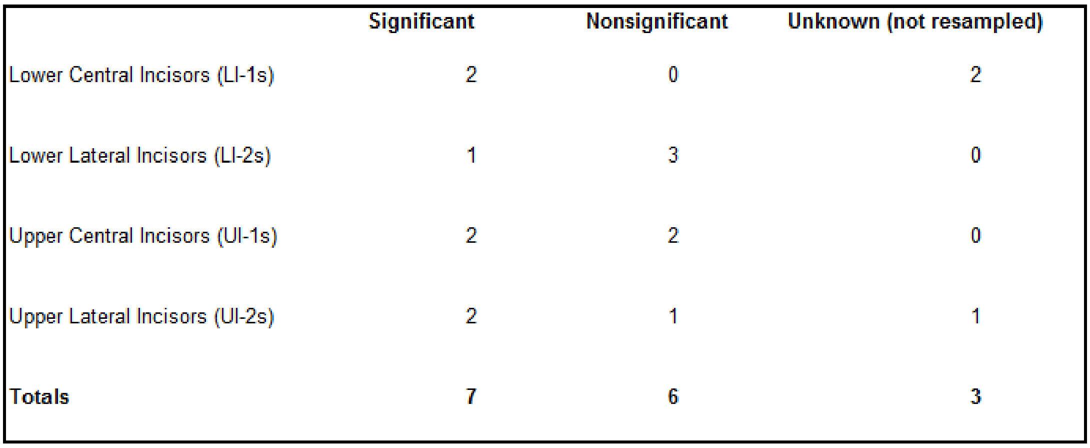
Table 8. Upper Central Incisor Asymmetry: Non-metric. (*K. africanus/E. africanus* with Extant Apes

		Kenyapithecus/Equatorius		*Gorilla*			*Pan*			*Pongo*		
			Discord	R	L	**Asym**	R	L	**Asym**	R	L	**Asym**
LingPill	**0**	8/9		8/19	6/19		6/16	5/16		4/17	4/17	
	1	1/9		10/19	11/19		10/16	11/16		13/17	13/17	
	2	0		0	0		0	0		0	0	
	22 (twinned)	0		1/19	2/19		0	0		0	0	
			1/9	p=.9655		**8/19**	p=.4471		**1/16**	----		**0**
MargShp	**4** (discont.)	3/13		1/14	2/14		2/16	3/16		3/19	4/19	
	5 (U-shaped)	8/13		5/14	3/14		14/16	13/16		16/19	15/19	
	6 (V-shaped)	0		9/14	11/14		0	0		0	0	
	7 (W-shaped)	2/13		0/14	1/14		0	0		0	0	
			5/13	p=.1477		**3/14**	p=.0122		**1/16**	p=.0090		**1/19**
Skew	**0**	8/11		8/19	9/19		5/16	7/16		11/19	13/19	
	1	3/11		9//19	10/19		11/16	9/16		8/19	6/19	
	2	0		2/19	0		0	0		0	0	
			3/11	p=.4854		**5/19**	p=.1902		**2/16**	p=.1385		**2/19**
EnamCrl	**0**	9/12		18/19	16/19		9/15	11/16		14/18	18/18	
	1	3/12		1/19	3/19		6/15	5/16		4/18	0	
	2	0		0	0		0	0		0	0	
			3/12	p=.4102		**4/19**	p=.4079		**3/15**	p=.4735		**4/18**
Sprl	**0**	12/13		8/12	9/16		13/16	10/16		17/18	17/18	
	1	1/13		5/12	7/16		3/16	6/16		1/18	1/18	
	2	0		0	0		0	0		0	0	
			1/13	p=.8349		**2/12**	p=.8079		**3/16**	----		**0**

Table 9. Upper Lateral Incisor Asymmetry: Non-metric. (*K. africanus/E. africanus* with Extant Apes)

		Kenyapithecus/Equatorius		*Gorilla*			*Pan*			*Pongo*		
			Discord	**R**	**L**	**Asym**	**R**	**L**	**Asym**	**R**	**L**	**Asym**
IncisShp	0	1/7		11/18	10/18		7/16	8/15		8/18	8/18	
	1	6/7		7/18	8/18		9/16	7/15		10/18	10/18	
			1/7	p=.3712		**1/18**	p=.3399		**1/15**	----		**0**
VertRidge	0	3/7		12/18	15/18		3/16	5/15		12/18	14/18	
	1	4/7		6/18	3/18		13/16	10/15		6/18	4/18	
	2	0		0/18	0/18		0/16	0/15		0/18	0/18	
			3/7	p=.0985		**3/18**	p=.0187		**2/15**	p=.0173		**2/18**
MargShp	4	0		5/18	4/19		3/16	3/15		4/17	3/17	
	5	3/7		7/18	10/19		10/16	9/15		11/17	10/17	
	6	0		6/18	4/19		3/16	3/15		1/17	3/17	
	7	4/7		0/18	1/19		0/16	0/15		1/17	1/17	
			4/7	p=.0479		**4/19**	p=.0410		**1/15**	p=.0471		**4/17**
Skew	0	1/7		8/18	6/19		6/16	4/15		6/18	5/18	
	1	3/7		7/18	9/19		8/16	10/15		11/18	13/18	
	2	3/7		2/18	3/19		2/16	1/15		1/18	0/18	
			4/7	1/18	1/19		0/16	0/15		0/18	0/18	
				p=.0032		**3/17**	p=.0156		**2/15**	p=.0509		**4/18**
SkewA	0	1/7		8/18	6/19		6/16	4/15		6/18	5/18	
	1	6/7		7/18	9/19		8/16	10/15		11/18	13/18	
			1/7	2/18	3/19		2/16	1/15		1/18	0/18	
				1/18	1/19		0/16	0/15		0/18	0/18	
				p=.6201		**3/17**	p=.4727		**2/15**	p=.6960		**4/18**
Sprl	0	1/7		5/19	6/19		13/16	9/15		16/18	14/17	
	1	3/7		12/19	10/19		3/16	6/15		2/18	3/17	
	2	3/7		2/19	3/19		0/16	0/15		0/18	0/17	
			4/7	p=.0463		**4/18**	p=.1415		**5/15**	p=.0335		**3/17**
SprlA	0	1/7		5/19	6/19		13/16	9/15		16/18	14/17	
	1	6/7		12/19	10/19		3/16	6/15		2/18	3/17	
			1/7	2/19	3/19		0/16	0/15		0/18	0/17	
				p=.6954		**4/18**	p=.9357		**5/15**	p=.6146		**3/17**

Table 10. Summary of Results for *Gorilla*: Metric Traits. (*K. africanus/E. africanus*)

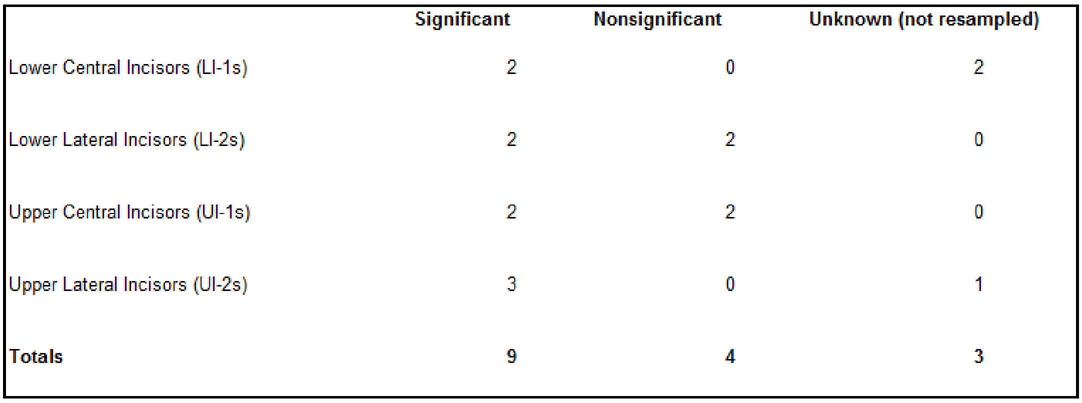


	Significant	Nonsignificant	Unknown (not resampled)
Lower Central Incisors (LI-1s)	2	0	2
Lower Lateral Incisors (LI-2s)	1	3	0
Upper Central Incisors (UI-1s)	2	2	0
Upper Lateral Incisors (UI-2s)	2	1	1
Totals	**7**	**6**	**3**

Table 11. Summary of Results for *Pan*: Metric Traits. (*K. africanus/E. africanus*)

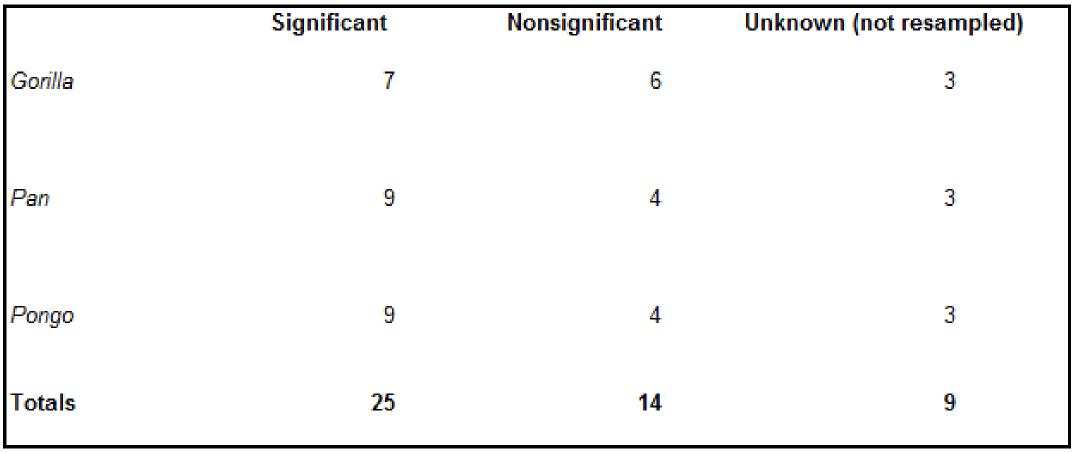
	Significant	**Nonsignificant**	**Unknown (not resampled)**
Lower Central Incisors (LI-1s)	2	0	2
Lower Lateral Incisors (LI-2s)	2	2	0
Upper Central Incisors (UI-1s)	3	1	0
Upper Lateral Incisors (UI-2s)	2	1	1
Totals	**9**	**4**	**3**

Table 12. Summary of Results for *Pongo*: Metric Traits. (*K. africanus/E. africanus*)



	Significant	**Nonsignificant**	**Unknown (not resampled)**
Lower Central Incisors (LI-1s)	2	0	2
Lower Lateral Incisors (LI-2s)	2	2	0
Upper Central Incisors (UI-1s)	2	2	0
Upper Lateral Incisors (UI-2s)	3	0	1
Totals	**9**	**4**	**3**

Table 13. Total Traits by Significance: Metric Results.
(*K. africanus/E. africanus*)



	Significant	Nonsignificant	Unknown (not resampled)
Gorilla	7	6	3
Pan	9	4	3
Pongo	9	4	3
Totals	**25**	**14**	**9**

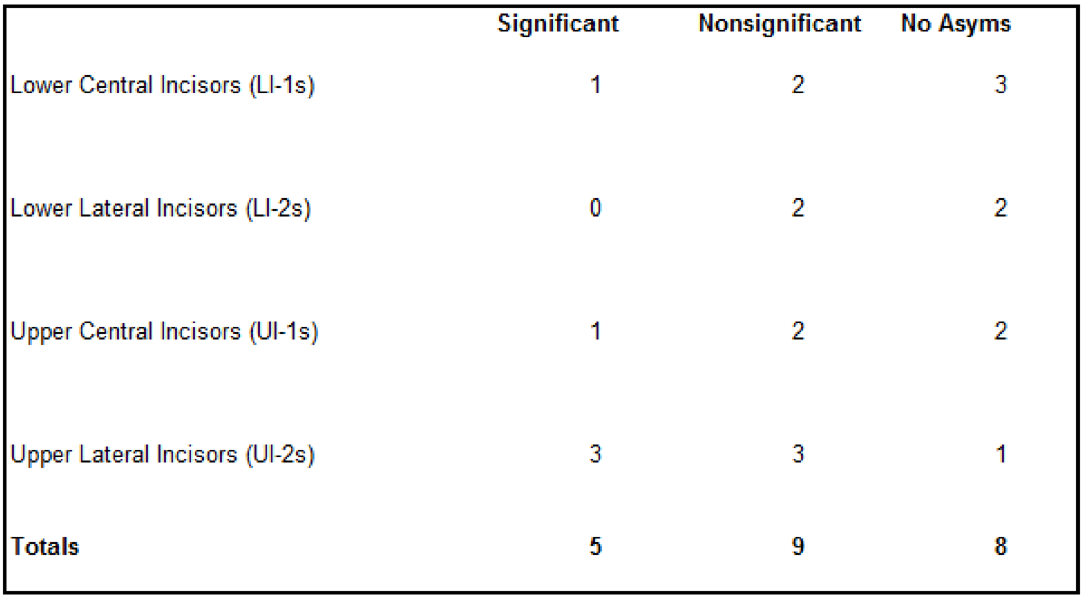
Table 14. Summary of Results for *Gorilla*: Non-metric Traits. (*K. africanus/E. africanus*)

	Significant	Nonsignificant	No Asyms
Lower Central Incisors (LI-1s)	1	5	0
Lower Lateral Incisors (LI-2s)	0	4	0
Upper Central Incisors (UI-1s)	0	5	0
Upper Lateral Incisors (UI-2s)	3	4	0
Totals	**4**	**18**	**1**

Table 15. Summary of Results for *Pan*: Non-metric Traits. (*K. africanus/E. africanus*)

	Significant	Nonsignificant	No Asyms
Lower Central Incisors (LI-1s)	2	3	1
Lower Lateral Incisors (LI-2s)	0	3	1
Upper Central Incisors (UI-1s)	1	4	0
Upper Lateral Incisors (UI-2s)	3	4	0
Totals	**6**	**14**	**2**

Table 16. Summary of Results for *Pongo*: Non-metric Traits. (*K. africanus/E. africanus*)



	Significant	**Nonsignificant**	**No Asyms**
Lower Central Incisors (LI-1s)	1	2	3
Lower Lateral Incisors (LI-2s)	0	2	2
Upper Central Incisors (UI-1s)	1	2	2
Upper Lateral Incisors (UI-2s)	3	3	1
Totals	**5**	**9**	**8**

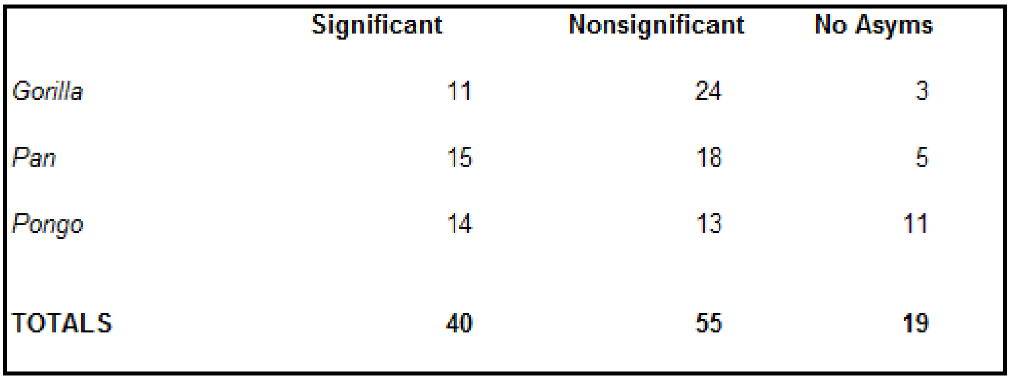
**Table 17. Total Traits by Significance: Non-metric Results.
(*K. africanus/E. africanus*)**

	Significant	Nonsignificant	No Asyms
Gorilla	4	18	0
Pan	6	14	2
Pongo	5	9	8
Totals	**15**	**41**	**10**

Table 18. Grand Total of Metric and Non-metric Significant vs. Nonsignificant Results: (*K. africanus/E. africanus*)

	Significant	**Nonsignificant**	**No Asyms**
Metric	25	14	9
Non-metric	15	41	10
TOTALS	**40**	**55**	**19**

Table 19. Grand Totals of Significant vs. Nonsignificant Results: Extant Genera. (*K. africanus/E.africanus*)

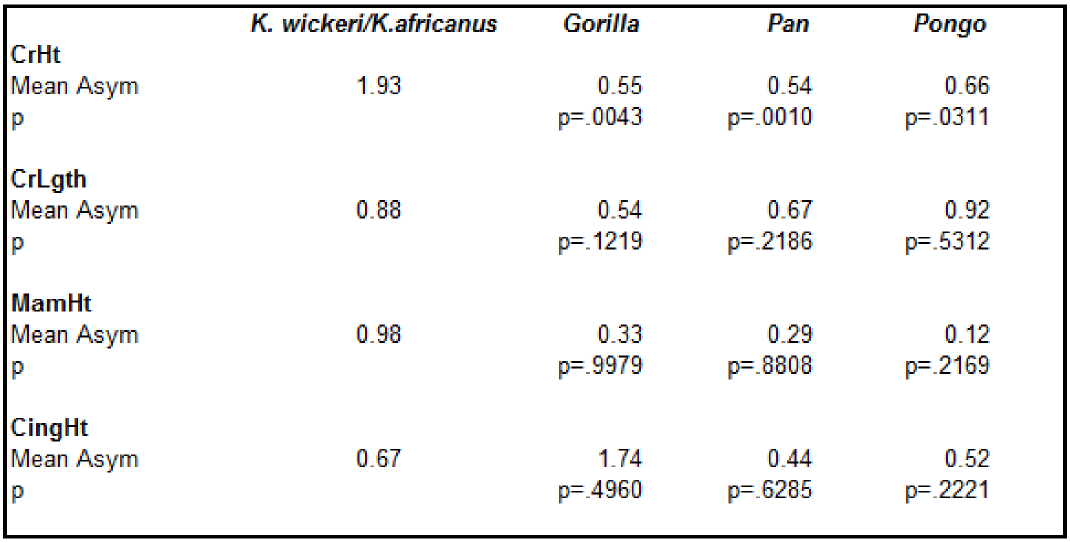


	Significant	Nonsignificant	No Asyms
Gorilla	11	24	3
Pan	15	18	5
Pongo	14	13	11
TOTALS	**40**	**55**	**19**

Table 20. Unexpected Nonsignificant Results Falsifying Alternative Hypothesis. (*K. africanus/E.africanus*)

Tooth and Trait: Metric	**Genus** **Non-signif (unexpected) result**	**Genus** **Signif (expected) result**
LI-1 Crown Height	*Gorilla*	*Pan, Pongo*
UI-1 Crown Length	*Pongo*	*Gorilla, Pan*
UI-1 Mamelon Height	*Gorilla*	*Pan, Pongo*
UI-2 Crown Length	*Gorilla, Pan*	*Pongo*
Tooth and Trait: Non-metric		
LI-1 Margin Shape	*Gorilla*	*Pan, Pongo*
LI-2 Skew	*Gorilla, Pan*	*Pongo*
UI-1 Margin Shape	*Gorilla*	*Pan, Pongo*
UI-2 Vertical Ridges	*Gorilla*	*Pan, Pongo*
UI-2 Skew (0,1,2)	*Pongo*	*Gorilla, Pan*
UI-2 Spiraling (0,1,2)	*Pan*	*Gorilla, Pongo*

**Table 21. Upper Central Incisor Asymmetry: Metric.
(*K. wickeri/K.* (*E.*) *africanus* with Extant Apes)**

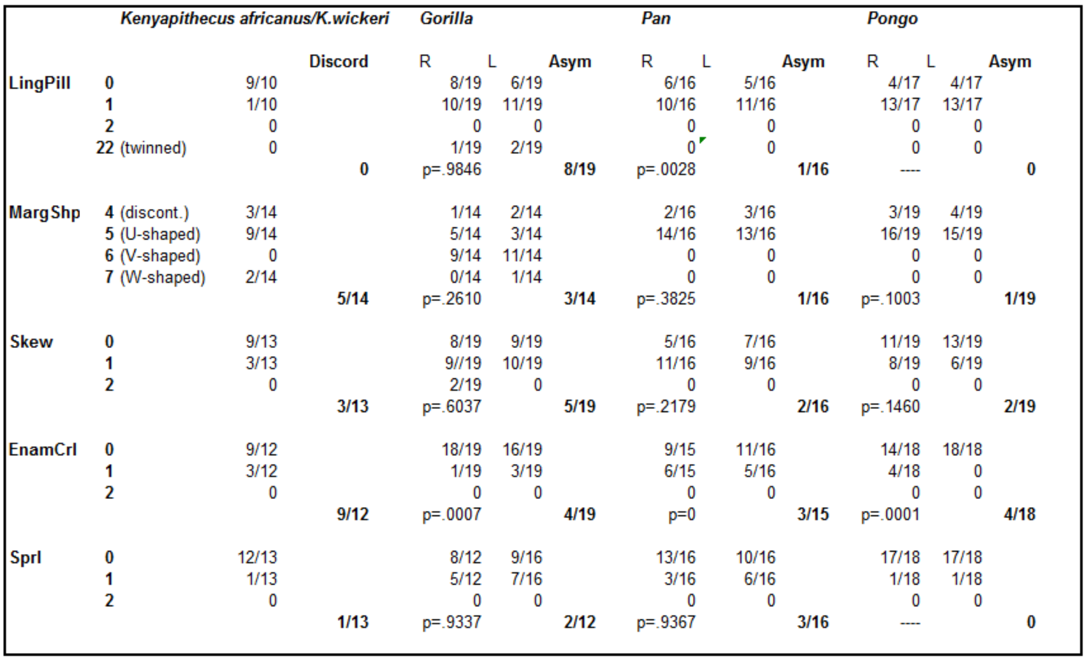


	K. wickeri/K.africanus	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	1.93	0.55	0.54	0.66
p		p=.0043	p=.0010	p=.0311
CrLgth				
Mean Asym	0.88	0.54	0.67	0.92
p		p=.1219	p=.2186	p=.5312
MamHt				
Mean Asym	0.98	0.33	0.29	0.12
p		p=.9979	p=.8808	p=.2169
CingHt				
Mean Asym	0.67	1.74	0.44	0.52
p		p=.4960	p=.6285	p=.2221

Table 22. Upper Lateral Incisor Asymmetry: Metric.
(*K. wickeri/K.* (*E.*) *africanus* with Extant Apes)

	Kenyapithecus africanus/K.wickeri	*Gorilla*	*Pan*	*Pongo*
CrHt				
Mean Asym	0.79	0.61	0.47	0.74
p		p=.2016	p=.5904	p=.3691
CrLgth				
Mean Asym	0.63	0.75	0.69	0.48
p		p=.6740	p=.5841	p=.1678
MamHt				
Mean Asym	0.85	0.31	0.83	0.24
p		unknown	unknown	unknown
CingHt				
Mean Asym	0.87	0.75	0.35	0.48
p		p=.3028	p=.0052	p=.0259

Table 23. Upper Central Incisor Asymmetry: Non-metric. (*K. wickeri/K.* (*E.*) *africanus* with Extant Apes)



		Kenyapithecus africanus/K.wickeri		*Gorilla*			*Pan*			*Pongo*		
			Discord	R	L	**Asym**	R	L	**Asym**	R	L	**Asym**
LingPill	**0**	9/10		8/19	6/19		6/16	5/16		4/17	4/17	
	1	1/10		10/19	11/19		10/16	11/16		13/17	13/17	
	2	0		0	0		0	0		0	0	
	22 (twinned)	0		1/19	2/19		0	0		0	0	
			0	p=.9846		**8/19**	p=.0028		**1/16**	----		**0**
MargShp	**4** (discont.)	3/14		1/14	2/14		2/16	3/16		3/19	4/19	
	5 (U-shaped)	9/14		5/14	3/14		14/16	13/16		16/19	15/19	
	6 (V-shaped)	0		9/14	11/14		0	0		0	0	
	7 (W-shaped)	2/14		0/14	1/14		0	0		0	0	
			5/14	p=.2610		**3/14**	p=.3825		**1/16**	p=.1003		**1/19**
Skew	**0**	9/13		8/19	9/19		5/16	7/16		11/19	13/19	
	1	3/13		9//19	10/19		11/16	9/16		8/19	6/19	
	2	0		2/19	0		0	0		0	0	
			3/13	p=.6037		**5/19**	p=.2179		**2/16**	p=.1460		**2/19**
EnamCrl	**0**	9/12		18/19	16/19		9/15	11/16		14/18	18/18	
	1	3/12		1/19	3/19		6/15	5/16		4/18	0	
	2	0		0	0		0	0		0	0	
			9/12	p=.0007		**4/19**	p=0		**3/15**	p=.0001		**4/18**
Sprl	**0**	12/13		8/12	9/16		13/16	10/16		17/18	17/18	
	1	1/13		5/12	7/16		3/16	6/16		1/18	1/18	
	2	0		0	0		0	0		0	0	
			1/13	p=.9337		**2/12**	p=.9367		**3/16**	----		**0**

Table 24. Upper Lateral Incisor Asymmetry: Non-metric. (*K. wickeri/K.* (*E.*) *africanus* with Extant Apes)

	Kenyapithecus africanus/K. wickeri			*Gorilla*			*Pan*			*Pongo*		
			Discord	R	L	Asym	R	L	Asym	R	L	Asym
IncisShp	0	1/9		11/18	10/18		7/16	8/15		8/18	8/18	
	1	8/9		7/18	8/18		9/16	7/15		10/18	10/18	
			8/9	p=0		**1/18**	p=0		**1/15**	----		**0**
VertRidge	0	3/9		12/18	15/18		3/16	5/15		12/18	14/18	
	1	6/9		6/18	3/18		13/16	10/15		6/18	4/18	
	2	0		0/18	0/18		0/16	0/15		0/18	0/18	
			3/9	p=.2221		**3/18**	p=..1264		**2/15**	p=.0686		**2/18**
MargShp	4	0		5/18	4/19		3/16	3/15		4/17	3/17	
	5	4/9		7/18	10/19		10/16	9/15		11/17	10/17	
	6	0		6/18	4/19		3/16	3/15		1/17	3/17	
	7	5/9		0/18	1/19		0/16	0/15		1/17	1/17	
			4/9	p=.1530		**4/19**	p=.0125		**1/15**	p=.1096		**4/17**
Skew	0	1/9		8/18	6/19		6/16	4/15		6/18	5/18	
	1	5/9		7/18	9/19		8/16	10/15		11/18	13/18	
	2	3/9		2/18	3/19		2/16	1/15		1/18	0/18	
			4/9	1/18	1/19		0/16	0/15		0/18	0/18	
				p=.0930		**3/17**	p=.0365		**2/15**	p=.0928		**4/18**
SkewA	0	1/9		8/18	6/19		6/16	4/15		6/18	5/18	
	1	8/9		7/18	9/19		8/16	10/15		11/18	13/18	
			1/9	2/18	3/19		2/16	1/15		1/18	0/18	
				1/18	1/19		0/16	0/15		0/18	0/18	
				p=.7368		**3/17**	p=.6044		**2/15**	p=.7369		**4/18**
SprI	0	2/9		5/19	6/19		13/16	9/15		16/18	14/17	
	1	3/9		12/19	10/19		3/16	6/15		2/18	3/17	
	2	4/9		2/19	3/19		0/16	0/15		0/18	0/17	
			7/9	p=.5772		**4/18**	p=.0023		**5/15**	p=.0001		**3/17**
SprIA	0	2/9		5/19	6/19		13/16	9/15		16/18	14/17	
	1	7/9		12/19	10/19		3/16	6/15		2/18	3/17	
			7/9	2/19	3/19		0/16	0/15		0/18	0/17	
				p=.5772		**4/18**	p=.0023		**5/15**	p=.0001		**3/17**

Table 25. Summary of Results for *Gorilla*: Metric Traits.
(*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	**Nonsignificant**	**Unknown (not resampled)**
Upper Central Incisors (UI-1s)	1	4	0
Upper Lateral Incisors (UI-2s)	0	3	1
Totals	**1**	**7**	**1**

Table 26. Summary of Results for *Pan*: Metric Traits. (*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	**Nonsignificant**	**Unknown (not resampled)**
Upper Central Incisors (UI-1s)	4	3	0
Upper Lateral Incisors (UI-2s)	1	2	1
Totals	**5**	**5**	**1**

Table 27. Summary of Results for *Pongo*: Metric Traits. (*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	Nonsignificant	Unknown (not resampled)
Upper Central Incisors (UI-1s)	1	4	0
Upper Lateral Incisors (UI-2s)	1	2	1
Totals	**2**	**6**	**1**

Table 28. Total Traits by Significance: Metric Results (*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	**Nonsignificant**	**Unknown (not resampled)**
Gorilla	1	7	1
Pan	5	5	1
Pongo	2	6	1
Totals	**8**	**18**	**3**

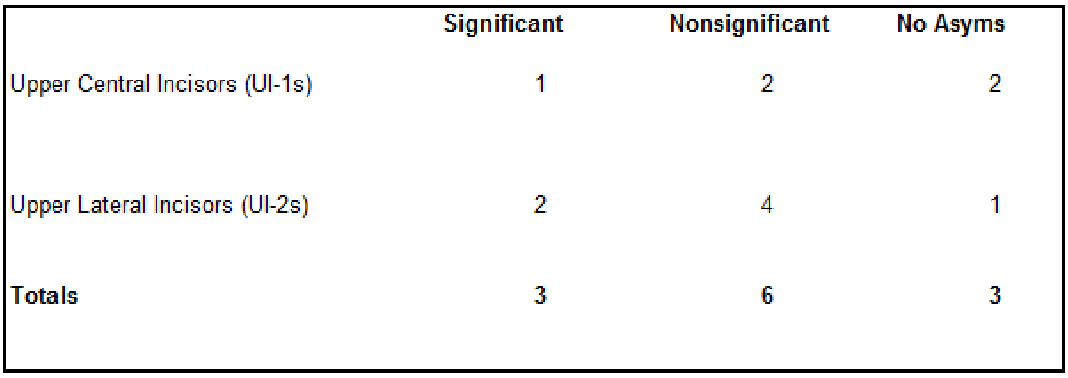
Table 29. Summary of Results for *Gorilla*: Non-metric Traits.
(*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	Nonsignificant	No Asyms
Upper Central Incisors (UI-1s)	1	4	0
Upper Lateral Incisors (UI-2s)	1	6	0
Totals	**2**	**10**	**0**

Table 30. Summary of Results for *Pan*: Non-metric Traits. (*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	Nonsignificant	No Asyms
Upper Central Incisors (UI-1s)	2	3	0
Upper Lateral Incisors (UI-2s)	5	2	0
Totals	**7**	**5**	**0**

Table 31. Summary of Results for *Pongo*: Non-metric Traits. (*K. wickeri/ K.* (*E.*) *africanus*)

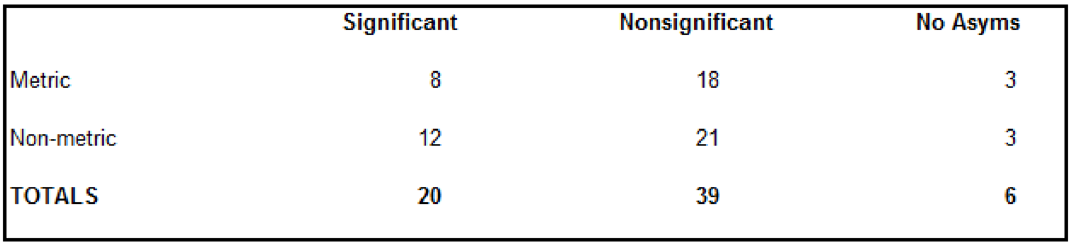


	Significant	Nonsignificant	No Asyms
Upper Central Incisors (UI-1s)	1	2	2
Upper Lateral Incisors (UI-2s)	2	4	1
Totals	**3**	**6**	**3**

**Table 32. Total Traits by Significance: Non-metric Results.
(*K. wickeri/ K.* (*E.*) *africanus*)**

	Significant	Nonsignificant	Unknown (not resampled)
Gorilla	2	10	0
Pan	7	5	0
Pongo	3	6	3
Totals	**12**	**21**	**3**

Table 33. Grand Totals of Metric and Non-metric Significant vs. Nonsignificant Results: (*K. wickeri/ K.* (*E.*) *africanus*)



	Significant	**Nonsignificant**	**No Asyms**
Metric	8	18	3
Non-metric	12	21	3
TOTALS	**20**	**39**	**6**

Table 34. Grand Totals of Metric and Non-metric Significant vs. Nonsignificant Results: Extant Genera. (*K. wickeri/ K.* (*E.*) *africanus*)

	Significant	**Nonsignificant**	**No Asyms**
Gorilla	3	17	1
Pan	12	10	1
Pongo	5	12	4
TOTALS	**20**	**39**	**6**

Table 35. Unexpected Nonsignificant Results Falsifying Alternative Hypothesis. (*K. wickeri/ K.* (*E.*) *africanus*)

Tooth and Trait: Metric	**Genus** **Non-signif (unexpected) result**	**Genus** **Signif (expected) result**
UI-2 Cingulum Height	*Gorilla*	*Pan, Pongo*
Tooth and Trait: Non-metric		
UI-1 Lingual Pillar	*Gorilla*	*Pan*
UI-1 Spiraling	*Gorilla, Pan*	
UI-2 Incisor Shape		*Gorilla, Pan*
UI-2 Skew (0,1,2)	*Gorilla, Pongo*	*Pan*
UI-2 Spiraling (0,1,2)	*Gorilla*	*Pan, Pongo*
UI-2 Spiral A	*Gorilla*	*Pan, Pongo*

APPENDIX B

Plates 1-33.

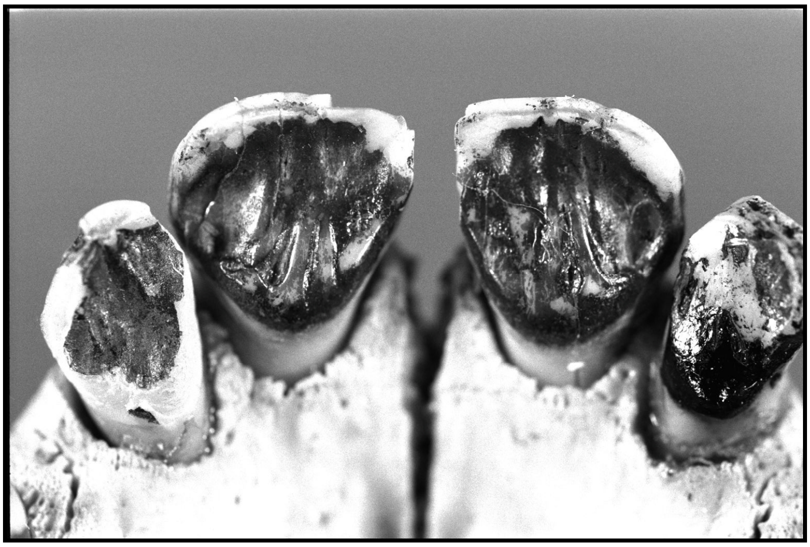


Plate 1. Differential wear on upper incisors of *Gorilla*, ID# USMNH 176225. Note the extreme wear on the right upper lateral incisor of this adult male.

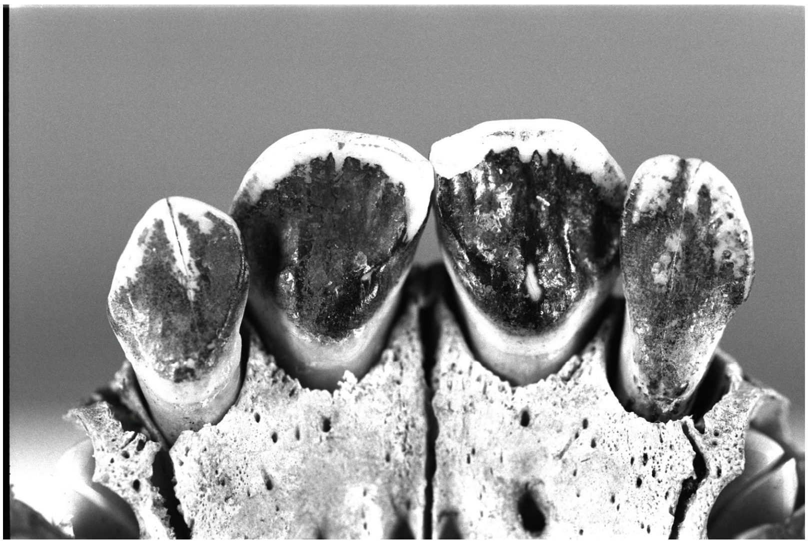


Plate 2. Fluctuating asymmetry on this subadult male *Gorilla*, ID# USMNH 252578, both environmental and genetic. Environmental: Note how both cingula on the left UI-1 and UI-2 are worn more than on the right ones. Genetic: Note that the left UI-1 is broader than its antimere on the right. The left UI-2, though more worn, is taller than its antimere on the right. Note permanent canines, just beginning to erupt.

Plate 3. Variation in antimeric pairs in lower incisors of *Gorilla*, ID# USMNH 252578. Note the lack of a lingual pillar on the left LI-1 and strong presence of one on the right LI-1. Note also slight incisor spiraling on both LI-2s, more pronounced on the left. (Note deciduous canines, with unerupted permanent canines in crypts.)

Plate 4. Slight asymmetries between antimeric pairs in *Gorilla*, ID# USMNH 241232. Although these incisors are relatively symmetrical, the left UI-1 is wider than the right, and the left UI-2 has a more well defined lingual pillar than the right. Wear has reduced the height of the left UI-1

Plate 5. Lower incisors of the same individual in Plate 4. Pre-mortem chipping on distal aspect of the left UI-2 and a slightly more U-shaped margin on the left UI-1 (as compared to the pronounced V-shaped margin on the right UI-1) give slight asymmetry to these otherwise fairly symmetrical-appearing antimeres.

Plate 6. Asymmetry in antimeric pairs in *Gorilla*, ID# USMNH 545032. This is an adult male, Maganga, from one of Diann Fossey's groups. He has twinning (actually an unusual tripling) of the cingular border on the right UI-2, with a normal border on the left UI-2. There is also slight winging of the right UI-1, with none on the left UI-1.

Plate 7. This is Rafiki, an adult male *Gorilla*, ID# USMNH 545028, in one of Diann Fossey's groups before he was killed by poachers and later exhumed. Note asymmetry between antimeres and twinned basal swelling and lingual pillar on left UI-1, with normal-appearing right antimere. Note the unusual twinned cingulum on both UI-2s.

Plate 8. This is Limbo, another adult male *Gorilla* (ID# USMNH 545034) studied by Diann Fossey. He, too, was killed by poachers and later exhumed. Note the symmetry of his upper incisors. There is evidence of slight differential wear on his left UI-1 and UI-2, relative to their antimeres.

Plate 9. Asymmetry between antimeric pairs in *Gorilla*, ID# USMNH 396936. Note the size disparity of the left and right upper incisor pairs.

Plate 10. This small juvenile male *Gorilla*, ID# USMNH 239684, exhibits extreme asymmetry in his lower incisor row. Note the congenital absence of the left LI-2 and malformation of the left LI-1.

Plate 11. Enamel curling on lateral marginal ridges and slight spiraling on both UI-1s in this adult male *Pan*, ID# USMNH 220327. Incisor spiraling on UI-2s, one trait used to diagnose the genus “*Equatorius*,” can be found on other incisors and is an occasional variation seen in extant apes as well as in *Kenyapithecus africanus.* Enamel curling on marginal ridges on UI-1s, supposedly diagnostic of *K. wickeri*, has also been found on other incisors in both extant and Miocene apes.

Plate 12. Asymmetry between antimeric pairs in the lower incisors of this same individual (see Plate 6). Note the size disparity between the LI-1s, in particular.

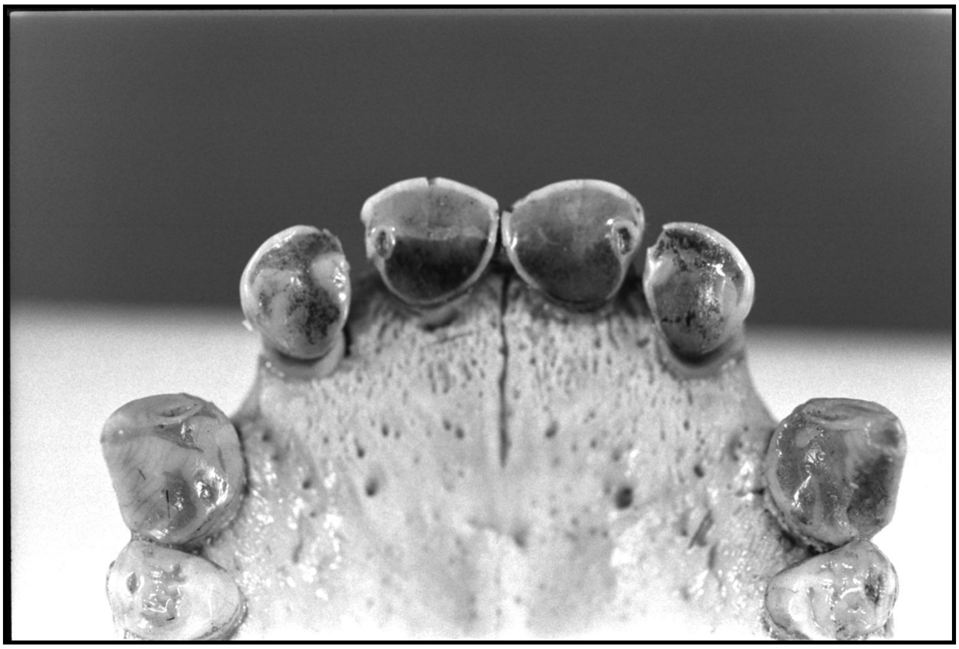


Plate 13. These fairly symmetrical, moderately worn upper incisors in this adult female *Pan*, ID# USMNH 220062, nevertheless show evidence of having had enamel curling on the lateral marginal ridges.

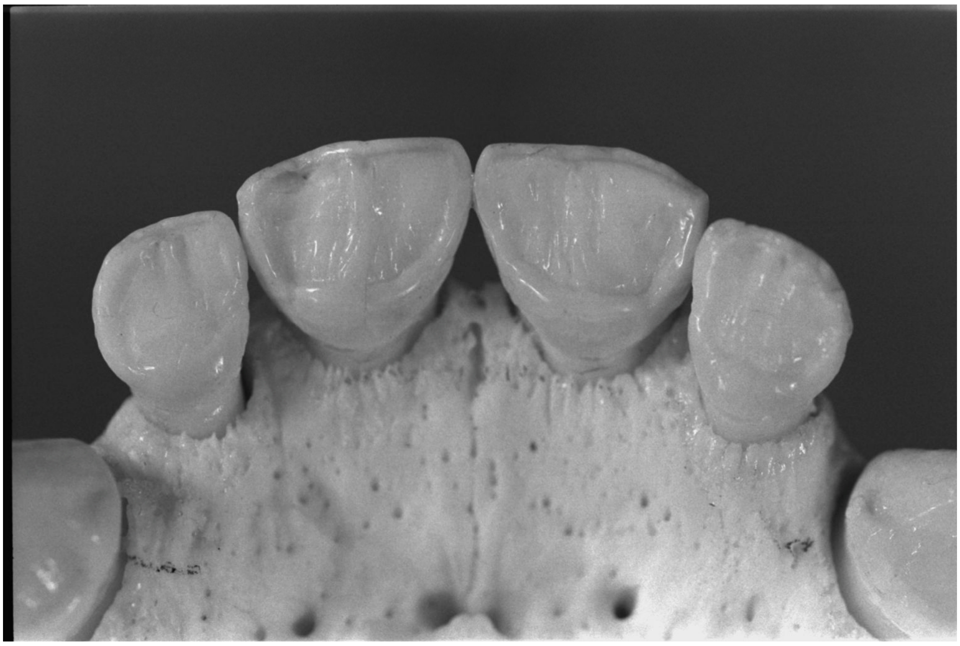


Plate 14. Minor asymmetries in upper incisors in *Pan*, ID# USMNH 282763. These mostly unworn incisors nevertheless show slight asymmetry between antimeric pairs. Right UI-1 and UI-2 have single lingual pillars, whereas left UI-1 and UI-2 lack definitive lingual pillars and instead have low-relief vertical ridges. Additionally, there is slight spiraling of cingula of the right UI-1, UI-2, and left UI-1 and no cingulum spiraling on the left UI-2.

Plate 15. Asymmetry in antimeric pairs in lower incisors of this young adult *Pan*, ID# USMNH 282763. Note the disparity in size between the LI-1s.

Plate 16. Spot the curation mistake in the upper incisor row of this subadult male specimen of *Pan*, ID# USMNH 176236. Note deciduous canines, with unerupted permanent canines in crypts.

Plate 17. Asymmetry in antimeres in upper incisor row of this adult male *Pan*, ID# USMNH 305820. Note the difference in cingulum size between antimeric pairs of the UI-2s. The left UI-2 has a distinct lingual pillar that is lacking in its right antimere.

Plate 18. Relatively symmetrical lower incisor row in the same individual (see Plate 17).

Plate 19 . Asymmetry in antimeric pairs in *Pongo*, ID# USMNH 142169. Even allowing for breakage of apex of right UI-1 crown in this adult female, it can be extrapolated that the left UI-1 was taller and wider than the right, despite greater wear on the left-side antimeres. Both UI-2s are caniniform in shape. Note also that enamel in *Pongo* is thick, compared to the thin-enameled African apes, making incisor relief less pronounced.

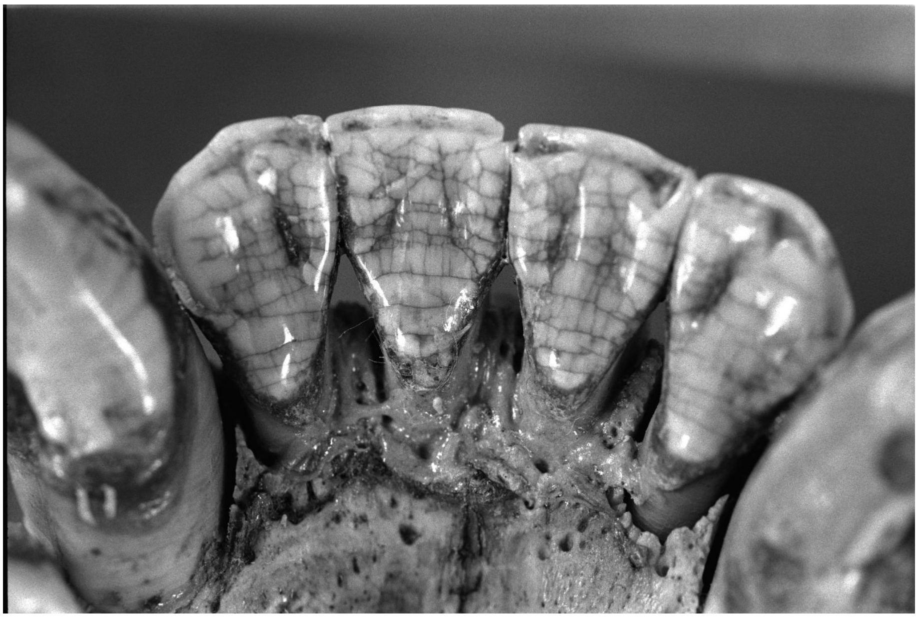


Plate 20. Relatively symmetrical antimeres in the lower incisor row in this adult female *Pongo*, ID# USMNH 142169*.* In general, orangutans had fewer asymmetries in antimeric pairs than either of the African apes. Note the extremely tall, narrow basal swellings, characteristic of *Pongo.*

Plate 21 . Differential wear on the lower incisors of *Pongo*, ID# USMNH49850/143587. The left LI-1 and LI-2 are more worn than their antimeres on the right. Note the tall cingulids with horizontal rugae.

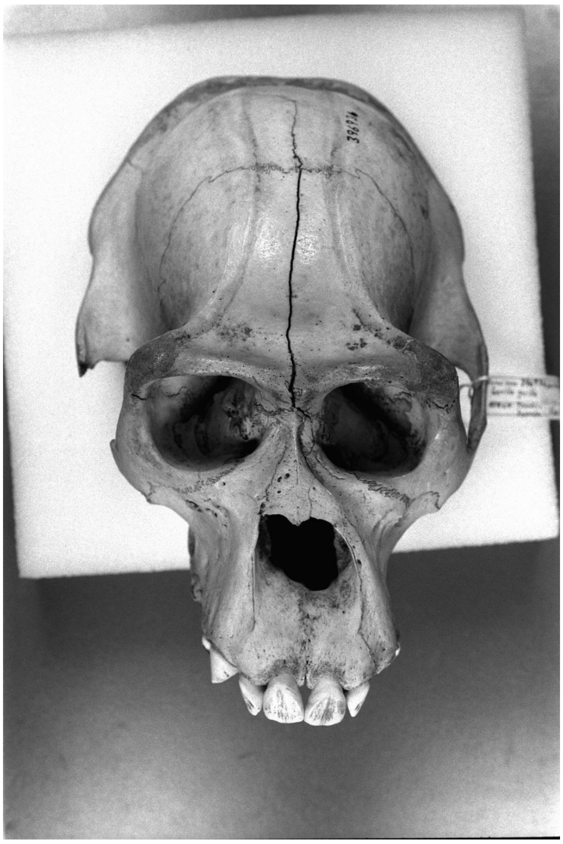


Plate 22. Fluctuating asymmetry in the midface of this adult female *Gorilla*. A growth anomaly of this degree of severity is probably the result of illness or trauma in youth. Note the skull fracture; she, too, was a victim of poaching.

Plate 23. *Kenyapithecus africanus*, ID# KMNH MB20573. This left LI-2 reveals a tusk-like morphology, one indicator that this Miocene species was most likely a hard-object feeder. At one time, before an LI-2 *in situ* in a *K. africanus* mandible was found, many isolated LI-2s of this species had been misattributed as being “suid” and were placed in a drawer with fossil pigs.

Plate 24. *Kenyapithecus africanus*, ID# KMNH MB24766, Bed 3. Left LI-2. This tooth exhibits very little wear or chemical erosion.

Plate 25. *Kenyapithecus africanus*, ID# KMNH MB32333, Bed 5. Right LI-2. Although chronologically younger than the tooth in Plate 23, fossils from Bed 5 typically exhibit more chemical erosion than fossils from Bed 3 at Maboko Island.

Plate 26. The specimen first named *Equatorius africanus*, ID# TH28860, from Kipsaramon, Tugen Hills. This portion consists of a mandibular fragment containing the left LI-1 and both LI-2s. Note the tusk-like morphology, similar to that of *Kenyapithecus africanus.* To date, there are no known lower incisors of *K. wickeri* with which to compare these.

Plate 27. *Kenyapithecus africanus*, ID# KMNH mb32331. Right UI-1. Note the moderate enamel curling (flange) on the mesial ridge of this tooth, supposedly diagnostic of *K. wickeri.*

Plate 28. *Kenyapithecus africanus*, ID# MB29097. This moderately worn left UI-1 exhibits a strong basal swelling, moderate vertical ridges, despite wear.

Plate 29. *Kenyapithecus africanus*, ID# MB104. Note the very slight enamel curling on the mesial ridge of this left UI-1.

Plate 30. Comparison of MB20726 (*Kenyapithecus africanus*), TH28860 (“*Equatorius*” *africanus*, and FT49 (*K. wickeri*) (right) with *K. africanus,* mb32331 (left) and MB104 (below). The medial apex of the UI-1 of *Equatorius* was chipped, possibly pre-mortem. Note the gradation of enamel flanging from strongly present to absent.

Plate 31. *Equatorius africanus*, ID# TH28860 from Kipsaramon, Tugen Hills. Note incisor spiraling on this left UI-2, supposedly diagnostic of this species.

Plate 32. Left: *Kenyapithecus africanus* (mb9729) from Maboko Island. Right: *K. wickeri* (FT49) from Fort Ternan and *Equatorius africanus* (TH28860) UI-2s from Kipsaramon. Although FT49 lacks a spiraled cingulum and TH28860 has a strongly spiraled cingulum, mb9729 has an intermediate morphology, with a slightly spiraled cingulum.

Plate 33. Effects of wear. These three *Kenyapithecus africanus* fossil U-2s show the effect of wear and chemical erosion on the morphology of the cingulum.

APPENDIX C

COPYRIGHT PERMISSIONS

RE: Copyright permission?

Friday, April 1, 2011 1:20 PM
From: "begun" <begun@chass.utoronto.ca>
To:
"Candy Davis" <roundapes@yahoo.com>

Dear Candace,

Thanks for asking about this. I was not sure but now I know for the future. Since you are using only an except from the copyrighted work you simply need to hold on to the permission from Kay. You should probably include it in your thesis as well, and of course, the references. The same holds for Retallack. Good luck with your defense.

Regards,
David

On 22/03/2011 15:44, Candy Davis wrote:
> Dear Dr. Begun:
>
> My name is Candace A. Davis. I am a Ph.D. Candidate in Anthropology at Southern Illinois University, with a specialty in African Miocene apes. I am about to defend my dissertation and am trying to tie up the loose ends the Graduate School needs in order to submit it to them. One item I need is copyright permissions to use two maps from two articles in JHE (2002), issue 42. Dr. Kay Behrensmeyer (the senior author of one of them) has suggested that as JHE officially owns the copyrights to these articles, I also need to contact you, the senior editor of the Journal.
>
> The maps I wish to use are from Behrensmeyer K. et al. 2002. Geology and geochronology of the middle Miocene Kipsaramon site complex, Tugen Hills, Kenya. J Hum Evol 42:11-38 (map found on p. 12) and from Retallack GJ et al. 2002. Paleosols and paleoenvironments of the middle Miocene, Maboko Formation, Kenya. J Hum Evol 42:659-703 (map found on p. 669). I have not yet heard back from Dr. Retallack yet, but Dr. Behrensmeyer's reply follows below.
>
> I will be defending my dissertation on March 31st. The Graduate School's deadline to have everything submitted to them is mid-April. So I would appreciate your help. Thank you very much in advance!
>
> Sincerely,
> Candace A. Davis, Ph.D. Candidate
> Department of Anthropology'
> Southern Illinois University at Carbondale

RE: Copyright permission?

Thursday, March 24, 2011 2:01 PM
From:
"Greg Retallack" <gregr@uoregon.edu>
Add sender to Contacts
To:
"'Candy Davis'" <roundapes@yahoo.com>
Dear Candace,

Yes there is no problem with using the map you mention for your dissertation, or for publication. Sadly it was done so long ago that I cannot offer electronic copy better than scanning the journal.

Regards, Greg Retallack

-----Original Message-----
From: Candy Davis [mailto:roundapes@yahoo.com]
Sent: Monday, March 21, 2011 10:33 AM
To: gregr@uoregon.edu
Subject: Copyright permission?

Dear Dr. Retallack:

I am about to finish my Ph.D. in Anthropology at Southern Illinois University at Carbondale, IL and am putting the finishing touches on my dissertation, entitled:

BILATERAL ASYMMETRY IN INCISORS:
IMPLICATIONS FOR MIOCENE HOMINOID SPECIES DIAGNOSIS.

Dr. Brenda Benefit was the chair of my M.A. thesis committee and is a member of my Ph.D. committee. (Dr. Robert Corruccini is my dissertation committee chair.)

There is a map of you have that shows some of the Miocene fossil primate sites on p. 669 of your 2002 article, co-authored with Drs. Benefit, McCrossin, and Wynn: Paleosols and paleoenvironments of the middle Miocene: Maboko Formation, Kenya (J Hum Evol 42:659-703) that I would like to have permission to use (and acknowledge appropriately) in my dissertation, if you wouldn't mind.

If this would be possible, could you please send me an e-mail ASAP so I can include this with the material I turn in to the Department of Graduate Studies? I plan to graduate in May 2011 and am trying to get everything I need as quickly as I can before the mid-April deadline. Thank you in advance.

Yours truly,

Candace A. Davis, M.A., Ph.D. Candidate
Department of Anthropology
Southern Illinois University at Carbondale

RE: Copyright permission?

Monday, March 21, 2011 2:36 PM
From:
"Behrensmeyer, Kay" <BEHRENSA@si.edu>
Add sender to Contacts
To:
"'Candy Davis'" <roundapes@yahoo.com>
Dear Ms. Davis,

I hereby grant you permission, as senior author of the paper mentioned below, to use this figure in your dissertation, with the understanding that appropriate credit and citation will be included in the caption.

Since JHE officially owns the copyright, you probably also should ask them for this one-time use, appending my permission email to any correspondence to the journal editor.

Sincerely yours,

Anna K. Behrensmeyer

-----Original Message-----
From: Candy Davis [mailto:roundapes@yahoo.com]
Sent: Monday, March 21, 2011 1:43 PM
To: Behrensmeyer, Kay
Subject: Copyright permission?

Dear Dr. Behrensmeyer:

I am about to finish my Ph.D. in Anthropology at Southern Illinois University at Carbondale, IL and am putting the finishing touches on my dissertation, entitled:

BILATERAL ASYMMETRY IN INCISORS:
IMPLICATIONS FOR MIOCENE HOMINOID SPECIES DIAGNOSIS.

Dr. Brenda Benefit was the chair of my M.A. thesis committee and is a member of my Ph.D. committee. (Dr. Robert Corruccini is my dissertation committee chair.)

There is a map of you have that shows some of the Miocene fossil primate sites relevant to my research on Kenyapithecus (Equatorius) africanus and K. wicker on p. 12 of your 2002 article, entitled: Geology and geochronology of the middle Miocene Kipsaramon site complex, Muryur Beds, Tugen Hills, Kenya. (J Hum Evol 42:11-38.) One of my committee members suggested that having maps of the region would be very helpful to me to illustrate for the readers of my dissertation where Maboko Island, Fort Ternan, and Kipsaramon are geographically, relative to one another. When I found the map in your article, I thought it would be a good choice. Therefore, I am asking for copyright permission to reproduce your map, acknowledging it appropriately, of course, in my dissertation.

If this would be possible, could you please send me an e-mail of permission ASAP so I can include this with the material I turn in to the Department of Graduate Studies? I plan to graduate in May 2011 and am trying to get everything I need as quickly as I can before the Graduate School's mid-April deadline for turning in my completed dissertation, plus all copyright permissions. Thank you in advance.

Yours truly,

Candace A. Davis, M.A., Ph.D. Candidate
Department of Anthropology
Southern Illinois University at Carbondale

VITA

Graduate School
Southern Illinois University

Candace A. Davis Date of Birth: October 29, 1948

1001 N Bridge
Carbondale, Illinois 62901
roundapes@yahoo.com

University of Illinois at Chicago
Bachelor of Arts, Anthropology, May 1971

Special Honors and Awards
Graduated with High Honors in Anthropology

Southern Illinois University at Carbondale
Master of Arts, Anthropology, May 2002

Southern Illinois University at Carbondale
Doctor of Philosophy, Anthropology, August 2011

Dissertation Title:
Bilateral Asymmetry in Incisors: Implications for Miocene Hominoid Species Diagnosis

Major Professor: Robert S. Corruccini