FOSSIL CERCOPITHECIDAE OF THE AFAR DEPRESSION, ETHIOPIA: SPECIES SYSTEMATICS AND COMPARISON TO THE TURKANA BASIN

by

STEPHEN R. FROST

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

2001

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

8/15/2001 Eric Delson

Date Chair of Examining Committee

8/15/2001

Date Executive Officer

Terry Harrison

Leslie F. Marcus

Thomas Plummer

John Van Couvering

Supervisory Committee

Abstract

FOSSIL CERCOPITHECIDAE OF THE AFAR DEPRESSION, ETHIOPIA: SPECIES SYSTEMATICS AND COMPARISON TO THE TURKANA BASIN

by

Stephen R. Frost

Advisor: Professor Eric Delson

The fossil Cercopithecidae from the Afar Depression of Ethiopia add considerably to what is known of the family in the African Pliocene and Pleistocene. The sediments that have produced the fossil cercopithecids included in this thesis range in age from 4.4 to 0.25 million years ago (Ma). As most of this material has not been published, it is systematically described. Fossils in this sample represent a minimum of 13 species in 10 genera. At least three of the species and two of the genera are new. The Afar sample also adds to what is known of the other species, including the only relatively complete cranial material of middle Pleistocene *Theropithecus*. There is considerable turnover of species in the sample, with between 1 and 6 being present at any single time interval.

In order to put the Afar sample into a larger context it is compared with the fossil cercopithecid sample from the Turkana Basin, the only other region that spans a similar time interval, has a large cercopithecid sample, and is well controlled chronologically. Fourteen species (from nine genera) are present in the Turkana assemblage, of which probably only three species are shared between the two basins. At higher taxonomic levels the two regions are more similar.

Abstract

When the timing of species turnover is compared between the two basins, both show a large number of species first and last appearances prior to 3.4 Ma. The Afar Depression has a second turnover event between 2.9 and 2.5 Ma, but in the Turkana Basin turnover occurs much later, after 2 Ma, with little change between 3.4 and 2.0 Ma. This lack of synchrony between the two basins suggests that Middle Pliocene turnover was not directly forced by a global climatic event.

Acknowledgments

I thank the members of my committee, Eric Delson, Leslie Marcus, Tom Plummer, John Van Couvering, and Terry Harrison, this dissertation is much improved because of their comments, criticisms, insights and suggestions. I would like to thank all of the faculty and students at NYCEP for all they have done during my time in graduate school that made it possible for me to finish. In particular, Fred Szalay led me to a deeper understanding of evolutionary theory, and how it could be as fascinating as the organisms themselves. Tim Bromage opened my mind and my eyes to many things, including African Pliocene climatic change and biogeography. John Oates introduced me to the complex and rewarding worlds of climatic change and biogeography, and some of the complexities of modern species distributions. Leslie Marcus introduced me to geometric morphometrics, the importance of sample size, and helped me to glimpse "n" dimensions. Carl Terranova helped me to see the importance of distinguishing quantitative questions from qualitative questions. Eric Delson has my particular gratitude for his tireless editing; detailed knowledge of cercopithecid fossils and Neogene paleontology; access to his data, reprints, photographs and extensive cast collection; many discussions about cercopithecid evolution, and mostly for his patience and encouragement. David Reddy has my thanks for his seemingly endless abilities to make things happen.

Kay Behrensmeyer, Rick Potts, and the ETE consortium have my thanks for all of their support, help, and interest. René Bobe has my thanks for all of his advice and many conversations about faunal change in the Pliocene. My thanks also go to some of the people from CSU Long Beach who began my career in fossils, evolution, and geology: Drs. Stanley Finney, George Callisan, David Huckaby and especially Marcus Young-Owl.

Acknowledgments

I am grateful to Tim White for permission to study the Middle Awash Material and to Bill Kimbel for permission to study the material from Hadar. Thanks go to all the members of the Middle Awash Research Project, the IARE, the Institute of Human Origins, and the RVRME for all their hard work in collection and preparation of the Afar material. I thank Tim White, David DeGusta, Yohannes Haile-Selassie and Henry Gilbert for their help in many ways during my study of the Middle Awash material, including some of the identifications.

I thank Zeresenay Alemsegad, Agazzi Negash, Zelalem Asseffa, and Yohannes Haile-Selassie who helped to keep me sane in Addis, through computer break-downs and equipment glitches, and made my experience there far more enjoyable. I thank all of the students at Wits, as well as Jacopo Moggi, all of them helped me in many ways in Johannesburg and otherwise made my time at Wits far better than it would have been. Joe Nigro deserves special thanks for allowing me to destroy his zip drive.

I also thank Chester Tarka and Lorraine Meeker for advice and help with some of the figures, any remaining defects are entirely my doing. I thank Eric Delson for the use of photographs by Chester Tarka. Thanks go to Henry Gilbert for photographs of ARA-VP-1/5, ARA-VP-1/133, ARA-VP-6/1686, and ARA-VP 6/679.

I thank the Ethiopian Centre for Research and Conservation of Cultural Heritage, the Ethiopian Ministry of Information and Culture, and the National Museum of Ethiopia for permission to study the material in their care. My thanks also go to Ato Alemu Ademassu for all of his kind help in the Paleoanthropology lab at the NME. I am grateful to the Office of the President and the Kenya National Museums for access to specimens in their care. I thank Mary Mungu and Nasser Malit for all of their help while at the

KNM. Special thanks go to M. G. Leakey for all her help at the KNM and for kind access to the unpublished Lothagam and Kanapoi material and to a pre-publication draft of her manuscript for the Lothagam cercopithecids.

I thank the many curators and staff of the many institutions who provided access to specimens in their care and for other kind assistance: Drs. Kevin Kuykendal, Lee Berger, Ron Clarke, and Emmanuel Gilissen at the University of the Witwatersrand, Anatomy Department (UWMA), Johannesburg; Drs. Francis Thackeray, Ina Plug, and Heidi Fourier at the Transvaal Museum (TMP), Pretoria, South Africa; Drs. Peter Andrews and Paula Jenkins at British Museum (Natural History), London; staff of the Powell-Cotton Museum, Birchington, UK; Drs. Brigitte Senut, Pascal Tassy, Jacques Repérant and Francis Renoult at the Museum National d'Histoire Naturelle, Paris; the staff of the Musée de la Ville de Lyon, and Dr. Pierre Mein at Lyon University, France; Dr. Wolfgang Maier at the Lehstuhl für Spezielle Zoologie, Universität Tübingen, the Dr. G. Storch of the Forschungsinstitut Senkenberg Museum, Frankfurt, Germany; and Dr. Friedemann Schrenck the Hescheses Landesmuseum, Darmstadt, Germany; Dr. Costin Radulescu at the Institute of Speleology, Bucharest, and Dr. D. Grigorescu at Bucharest University, Romania; and Dr. Richard Thorington and Linda Gordon at the National Museum of Natural History, Washington D.C. I also thank the many other people who provided various sorts of assistance at these institutions, whom I could not name here. The collections of extant cercopithecids housed at the American Museum of Natural History in New York were used for comparative purposes throughout data collection, analysis, and preparation of this thesis. Access was kindly provided by Drs. R.D.E. MacPhee, C. A. Norris, N. Simmons, and Robert Randall. E. Delson's extensive collection of fossil cercopithecid casts, including many specimens from Hadar, the Omo, Koobi Fora and West Turkana, was invaluable during this process.

This research was supported by the Wenner-Gren Foundation (Gr.6436), the L.S.B. Leakey Foundation, a NYCEP fellowship (NSF BIR 9602234), a predoctoral fellowship from the Smithsonian Institution, Evolution of Terrestrial Ecosystems Consortium, and a CUNY Ph.D. program in Anthropology Travel award. I gratefully acknowledge these sources here. Additionally, I acknowledge the LSB Leakey Foundation for Research into Human Origins and the PSC-CUNY Faculty Research Award Program (grant 6-68479) for support of Eric Delson's research on Middle Awash fossil cercopithecids in 1997, which permitted me to accompany him on a short visit to the NME to begin study of these fossils.

Finally, I would like to thank my family for everything under the sun. My parents Alice and Robert have shown unwavering support and belief. To them and to my siblings Mark, Curt, and Robin, I love you all. Most of all, Wendy has my eternal gratitude and love for her help, editing, support, seemingly endless patience, and sacrifices too numerous to count.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

Chapter 1

Introduction

Background

Climatic change has been proposed as a cause of evolutionary process and pattern, most formally in a series of hypotheses Vrba (1992) has called "habitat theory." The first premise of habitat theory is that all animals are habitat specific. That is, they have certain temperature, moisture, and trophic requirements without which they cannot survive. For some taxa these requirements may be relatively broad, for others they may be more narrow. Natural selection will generally act to maintain this relationship between organism and habitat, resulting in morphological stasis rather than anagenetic adaptations to new habitat characteristics. As a result, the common response of most taxa to climatic change is to "passively drift" with their biome as it shifts over their continent.

A second premise is that allopatry is necessary for speciation, and that the majority of allopatry is due to vicariance. Vicariance is the division of a once continuous species range into two or more isolated ranges by the appearance of an isolating barrier within that range. A further assertion is that vicariance is most commonly caused by climatic change. In other words, biotic community interactions on their own are insufficient to cause vicariance. Speciation, extinction, and stasis are all given by Vrba as possible responses to vicariance, i.e. habitat fragmentation. Importantly, anagenesis is not suggested by Vrba as a possible evolutionary response to climatic change.

The net result of the above premises is that most if not all speciation and extinction is due to climatic change. Natural selection and biotic interactions, particularly competition between species, are insufficient to cause speciation or extinction, but will instead tend to maintain an organism's adaptation to its environment. Therefore, under habitat theory, the majority of evolution occurs fairly rapidly and is concentrated during periods of dramatic climatic change in bursts of speciation, extinction, and migration. These evolutionary bursts are called "turnover pulses."

Habitat theory has several implications for mammalian evolution during the Pliocene and Pleistocene. Specifically, most speciation and extinction events should be clustered around particular, relatively restricted time intervals. Those time intervals should be correlated with independently understood large-scale climatic changes, and with simultaneous changes in other unrelated taxa. Furthermore, various species should respond to climatic changes differentially depending on their habitat preferences.

More specifically, Vrba (1985; 1992; 1995; 1999) has proposed that global cooling that occurred between 2.8 – 2.5 million years ago (Ma) (Shackleton et al., 1984; de Menocal, 1995; Denton, 1999) caused a major turnover pulse in African mammals. Habitat theory, therefore, predicts that there should be a relatively large number of first and last appearance of fossil species clustered around this time interval, particularly among more habitat specific mammals.

Several researchers have studied the temporal and geographic distributions of limited taxonomic groups in the Pliocene and Pleistocene of Africa: bovids (Vrba, 1976, 1980, 1985a), suids (Cooke, 1978; Harris and White, 1979; White, 1995; Bishop, 1999), equids (Bernor and Armour-Chelu, 1999), cercopithecids (Delson, 1984, 1988), and hominids (e.g. White, 1995; Kimbel, 1995), as well as taxonomically broader faunal overviews of all Africa (Turner and Wood, 1993) or of one single region (e.g., Wesselman, 1995; Behrensmeyer et al., 1997; Bobe, 1997). There is still considerable debate as to whether a turnover pulse caused by a cooling of global climate occurred between 2.8 – 2.5 Ma (McKee, 1996; Behrensmeyer et al., 1997; Bobe, 1997). All studies aimed at testing a relationship between climate and evolution face many problems, such as those outlined by White (1995). Most of these problems relate the quality of the data involved including: alpha taxonomy; taphonomy; and large gaps in sedimentation.

The studies that focussed specifically on the hypothesized turnover pulse 2.5 Ma have had mixed results. Vrba found evidence of turnover at 2.5 Ma based on bovids (e.g. 1985; 1988; 1995). White (1995) and Bishop (1999) studied the suids and found no support for a turnover pulse 2.5 Ma. White (1995) and Kimbel (1995) both looked at the hominid evidence and found no evidence for a turnover pulse there either.

Vrba's hypothesis was one of the initial motivations for this thesis. Initially I proposed to evaluate the turnover pulse hypothesis with a taxon other than bovids or suids, which had already been examined in this context. The Old World Monkeys, the Family Cercopithecidae, were chosen for this as they are present in most African Pliocene and Pleistocene sites, and are represented by a relatively large number of species during this time interval (Szalay and Delson, 1979; Delson, 1984). Because of the issues pointed out by White (1995), this study was to be based entirely on primary data: every fossil involved in the study would be evaluated directly. This would at least help the alpha taxonomy of the study to be internally consistent, if not more accurate than would a literature based survey, or more cursory analysis.

Primary data collection for this project began in 1997 when I accompanied E. Delson to the National Museum of Ethiopia (NME) to study the fossil cercopithecids from the Middle Awash Paleoanthropological Research Area. During this short trip the potential of the Afar material was realized, and later that year, the Middle Awash and Hadar Material became available for this thesis. The vast majority of this material had not yet been the subject of published descriptions, so systematic description of the Afar sample became the first objective of the thesis. In order to more effectively examine the turnover hypothesis it would be necessary to include a second data set in the analysis. The Turkana Basin was the only viable choice.

During 1999, analysis of the Afar fossil cercopithecid assemblage was conducted during several months in the National Museum of Ethiopia (NME), Addis Ababa. Also while at the NME, specimens from the lower Omo Valley were studied. The Koobi Fora and Nachukui collections were studied during the same year at the National Museums of Kenya (KNM), Nairobi. As analysis of these samples progressed, it became increasingly clear that a rigorous quantitative analysis of the putative turnover pulse at ca. 2.5 Ma would be difficult, at best, based on the cercopithecids alone. This is because many species are represented by very small samples and others are known only from single stratigraphic units, greatly reducing the number of species that could be included in any quantitative analysis. However, it also became clear that the two regions were quite distinct from one another in terms of their cercopithecid fossil records, and comparison of the two would be important in highlighting the uniqueness of each sequence. This comparison is therefore a second objective of this thesis. The relative impact of the ca. 2.5 Ma turnover pulse is evaluated, along with other instances of faunal change in the cercopithecids, in a qualitative manner.

Specific Objectives

The primary purpose of this thesis is to systematically describe the fossil Old World Monkeys (the family Cercopithecidae) from the Afar Depression of Ethiopia, as this has not been done for most of the cercopithecid material. In order to gain a better understanding of the Afar material, and to place it in larger context, it must be compared with a second, broadly equivalent, sample. Therefore, another objective is to compare the Afar material with that from the Lake Turkana Basin. The Turkana Basin is the only region in Africa that spans a similar time interval to the Afar Depression, is well controlled chronologically, and has a large and diverse cercopithecid sample. Lastly, as the material from both regions is well dated, the timing of faunal turnover can be examined within each assemblage and compared between the two assemblages.

Basic Assumptions

Before description of the cercopithecid assemblages from the Afar and Turkana Basins can be conducted, three sets of basic assumptions should be made explicit. First, the higher level taxa of cercopithecids used in this thesis need to be described, along with their relationships to one another. Second, it must be clear exactly which genera are recognized and included in the different higher taxa. Finally, the features used to diagnose fossil material to the various higher taxa need to be given. This information is provided in the first part of Chapter 2.

The stratigraphical and chronological context of the material needs to be known. The second part of Chapter 2 provides a summary description of the sediments that have yielded the cercopithecid fossils discussed. This makes clear both how precise and reliable the chronological information is for the fossils, and therefore the species and higher taxa described. In addition, the position of large gaps in the stratigraphy are presented, as these can effect how precisely the timing of different events are known.

The sample of fossil cercopithecids from the Afar Depression includes specimens collected from several formations in both the Middle Awash and Hadar. The Turkana Basin sample used here includes thousands of specimens collected from the Lower Omo Valley, Koobi Fora, and West Turkana. Both the Afar and Turkana collections are described in Chapter 3, along with the specific methods used to analyze this material both qualitatively and quantitatively.

Description of the Afar Fossil Cercopithecids

Geological, archaeological, paleontological and paleoanthropological research has been conducted in the Afar Basin since the late 1960’s (Taieb, 1974; White, 2000) and it is well known for many important fossil hominid discoveries at Hadar and the Middle Awash. This research has yielded a substantial collection of fossil cercopithecids from sites ranging in age from the Early Pliocene to the Middle Pleistocene. Most of the material from this collection has not been published. Therefore, its systematic description is one of the main goals of this thesis, and is the subject of Chapter 4. Of the Afar material, only the collection of *Theropithecus* from Hadar has been described (Eck, 1993). Some of the other species have been discussed in review articles (Szalay and Delson, 1979; Delson, 1984; 1994; Gundling and Hill, 2000) or included in faunal lists (e.g. Taieb et al., 1976; Kalb et al., 1980; 1982a-c; White et al., 1993; Clark et al., 1994; WoldeGabriel et al., 1994; Kimbel, et al., 1996; de Heinzelin et al., 1999).

The Afar sample adds considerably to our knowledge of African Pliocene and Pleistocene cercopithecids. It includes over two thousand fossil cercopithecid specimens that represent a minimum of 13 species from both extant subfamilies. At least three, and possibly four, of these are new. Additionally, many of these specimens provide new information on previously known taxa, such as the only sample of relatively complete crania of *Theropithecus oswaldi* from the Middle Pleistocene. In Chapter 4, the morphology of each species is described, along with its known temporal range and paleogeographic distribution.

Description of Turkana Basin fossil cercopithecids

The paleontological collections from the Turkana Basin are some of the most extensive in East Africa, are well controlled chronologically, and act as a reference against which most other Pliocene and Pleistocene African collections are compared. Most of the fossil cercopithecids of the Turkana Basin have been described previously, in several different publications by multiple authors (Patterson, 1968; Eck and Howell, 1972; Leakey and Leakey, 1973b; 1976; Leakey, 1976; 1982; 1987; 1993; Eck, 1976; 1977; 1987a,b; Eck and Jablonski, 1987; Harris et al., 1988) as well as more briefly mentioned in reviews (Szalay and Delson, 1979; Delson, 1984; 1994; Leakey, 1988; Gundling and Hill, 2000) and site descriptions (e.g. Coffing et al., 1994; Leakey et al., 1995). It was therefore necessary to review the fossils of the Turkana Basin and bring them into a single, consistent framework comparable to that for the Afar cercopithecids, before comparison between the two basins was possible. In addition to taphonomic and collection biases, description of paleontological material often involves error and bias due to the systematist(s) responsible. By having both regions described by a single reviewer, these biases should be more consistent throughout the analysis.

Comparison of the Afar and Turkana Basins

Several aspects of the cercopithecid fossil records from Afar and Turkana regions are compared in Chapter 6. Two primary types of comparison are made. The first consists of comparisons aimed at determining how different the two basins are, and the second focuses on the timing of evolutionary events in the two basins. The two regions share relatively few species, but are more similar at the genus level. In the Early Pliocene they are different in relative abundance of the higher level groups used, but for the rest of the Pliocene and Pleistocene where both basins have samples, they are more similar.

The species of both basins can be divided into different chronological sets, which are separated from one another by periods of faunal turnover. In the Afar Depression, these coincide with gaps in the sedimentary record. Therefore, it is difficult to determine whether they are rapid or gradual. The earliest episode of turnover occurs in the latest part of the Early Pliocene and appears to be fairly synchronous between the two basins. Turnover in the Middle Pliocene is not synchronous between the two basins, occurring prior to 2.5 million years ago (Ma) in the Afar Depression, but after 2.0 Ma in the Turkana Basin. After the Pliocene, the two records are not comparable.

Chapter 7 summarizes and discusses some of the conclusions that can be drawn from this study. The fossil cercopithecids preserved in the Afar Basin add considerably to what is known of the evolution of the family in the Pliocene and Pleistocene. This is particularly true in the Early Pliocene which is not well known elsewhere in Africa. The basins are relatively distinct places in terms of their cercopithecid composition. When the Afar and Turkana Basins are examined together, there is little evidence that climatic change ca. 2.5 Ma cause faunal turnover. At this time there is change in the Afar, but not the Turkana Basin. The 2.5 Ma turnover event in the Afar depression is also no larger than a similar event in the Turkana Basin at 2.0 Ma. Furthermore, there appears to be an important event in the evolution of fossil cercopithecids in the late Early Pliocene, which is not closely correlated with a dramatic change in global climate.

Institutional Abbreviations

BM(NH)	British Museum (Natural History), London
BPI	University of the Witwatersrand, Bernard Price Institute, Johannesburg
KNM	National Museums of Kenya, Nairobi
MNHN	Museum National d'Histoire Naturelle, Paris
NME	National Museum of Ethiopia, Addis Ababa
TMP	Transvaal Museum, Pretoria
UWMA	University of the Witwatersrand, Medical school, Department of Anatomy, Johannesburg

Chapter 2

Background 1: Cercopithecid Phylogeny

This section provides a discussion of the major taxonomic groups within the family Cercopithecidae, or Old World monkeys, and the genera that are included in each taxon. The phylogenetic relationships among these groups will also be discussed, along with the features used to diagnose them. A phylogeny of the suprageneric groups of Cercopithecidae modified from Delson (2000a) is given in figure 2.1. Emphasis will be placed on those features useful for identifying fossils. The morphology of individual genera studied in this thesis is described in chapters 4 and 5. For a thorough discussion of the diagnostic features of the Old World monkeys and the major clades within the family see Delson (1973), Szalay and Delson (1979), Strasser and Delson (1987), Benefit (2000) and Groves (1989; 2000).

There is a large suite of characters that can be used to diagnose the family Cercopithecidae relative to other catarrhines. There are also a number of features that may reflect ancestral catarrhine retentions, which are typical of the family. These have been summarized in a number of sources (e.g. Delson, 1973; 1975; Szalay and Delson, 1979; Strasser and Delson, 1987; Groves, 1989; 2000). Some of these are shown in table 2.1. Possibly the most important characteristic of the Cercopithecidae is bilophodont morphology of the molars. Delson (1973; Szalay and Delson, 1979) has described 4 main morphological types of cercopithecid molars. These molar types are exemplified by different taxonomic groups of cercopithecids: Cercopithecini, Papionini (other than *Theropithecus*), *Theropithecus*, and Colobinae. These groupings are important as they

Table 2.1 Morphological features of the Cercopithecidae. Many features are retentions from the ancestral catarrhine. Probable derived cercopithecid features are underlined. References are as follows: [1]Szalay and Delson, 1979 (and references therein); [2]Strasser and Delson, 1987; [3]Strasser, 1988. See these sources for illustration.

- C typically sexually dimorphic and often large.[1]
- C has a mesial, compressed sulcus that continues onto the root in males.[1,2]
- P_3 mesiobuccal honing flange long.[1,2]
- P^3 may have a long mesiobuccal flange.[1,2]
- dp^3 often has a mesiobuccal extension.[1]
- dp_3 has paraconid, typically a paralophid.[1]
- M_3 has a hypoconulid.[1]
- dp_4-M_2 lack a hypoconulid.[1,2]
- dp^3-M^3 mesial width greater than distal.[1]
- dp_3-M_2 mesial width less than distal.[1]
- M_3 mesial width greater than distal.[1]
- Molars bilophodont.[1,2]
- Cheek teeth elongated.[2]
- Cranial vault low and globular.[2]
- Interorbital breadth wide, and face generally wide.[1,2]
- Nasals short and face moderately projecting.[1,2]
- Piriform aperture tall.[2]
- Maxilla contributes to lacrimal canal.[1,2]
- Ethmoid in orbit.[1]
- Mandibular ramus vertical.[1]
- Median mental foramen present.[2]
- External tail present.[1]
- Vertebral column with many lumbar and few sacral elements.[1]
- Thorax laterally compressed.[1]
- Clavicle short.[1]
- Scapula positioned dorsolaterally.[1]
- Ulnar olecranon process long.[1]
- Ulnar styloid process articulates with carpus.[1]
- External pollex long.[2]
- Pelvis narrow, with elongate ilium.[1]
- Distal tibiofibular joint syndesmotic (variably synovial in arboreal species).[3]
- Pedal functional axis through digit 3.[2]
- Astragalar trochlea asymmetrical and moderately wedge-shaped.[3]
- Pressure facet for fibulocalcaneal ligament present.[3]
- Posterior calcaneal facet short, tightly curved, less medially oriented, squared proximally, sides equal in length.[2,3]
- Anterior calcaneal facets doubled.[2]
- Proximal calcaneus long, and proximal calcaneal facet short.[3]
- Facet for *os peroneum* consistantly present on cuboid.[3]
- Hallucal facet of entocuneiform medially oriented, kidney-shaped, with small helical groove.[2,3]
- Proximal ectocuneiform-cuboid facet longer than distal.[2,3]

Table 2.1 (Continued)

- Medial malleolar facet of astragalus does not reach plantar surface.[3]
- Astragalar facet for spring ligament extends far laterally.[3]
- Proximal calcaneal facet of astragalus strongly curved.[3]
- Astragalus lacks separate *m. flexor fibularis* groove.[2,3]
- Entocuneiform facet of navicular plantar length longer than dorsal.[3]
- Male ischial callosities contiguous in midline (but separate in some groups).[2]
- Female sexual swellings present, but lost in many groups.[2]*m. flexor fibularis* inserts into digits 1,3 and 4.[2,3]
- 2n=44 chromosomes.[1]

often represent the finest taxonomic level to which isolated teeth can be assigned. The molar morphology of each of these groups is described below. These four taxa, and their respective molar morphologies, will be referred to as Delson's dental groups.

The extant Cercopithecidae are conventionally divided into two subfamilies: the Colobinae and Cercopithecinae (Delson, 1975; Szalay and Delson, 1979; Strasser and Delson, 1987; Fleagle, 1988). A large number of dental, skeletal and soft tissue characters differentiate these subfamilies. Molecular evidence generally corroborates the morphological data in this regard (Disotell, 1996; 2000).

Of the two subfamilies, the Cercopithecinae are more diverse in number of extant species and genera. They are also generally more abundant at most fossil sites. Some of the most obvious differences between the subfamilies are in the alimentary anatomy. The Cercopithecinae are characterized by the presence of cheek pouches, and relatively simple stomach morphology. Several features used to diagnose the Cercopithecinae are listed in table 2.2.

Dentally, the Cercopithecinae are distinct from the Colobinae. The lower incisors are unique among primates in lacking enamel on their lingual surfaces (Delson, 1975; Gantt et al., 1999). The upper incisors are generally spatulate so that the apex of the

Table 2.2 Morphological features of the Cercopithecinae. Some are likely to be ancestral for the family. Probable derived cercopithecine features are underlined. References are as for table 1.

- M_x trigonids long.[1,2]
- Cusps bunodont, notches (lingual/buccal on M_x/M^x) shallow (i.e. medium cuspal relief).[1,2]
- Molar flare moderate to strong (reduced in some Cercopithecini).[2]
- I^x enlarged, I^1 spatulate and flaring in anterior view.[1]
- I_x lack lingual enamel.[2]
- Interorbital breadth narrow, and face generally narrow.[1,2]
- Face long and projecting.[1,2]
- Nasals long and narrow.[1,2]
- Face tall, especially zygomae.[1]
- Vomer part of medial orbital wall.[1]
- Cranial vault low.[2]
- Choanae tend to be high and narrow.[1]
- Mandibular ramus inclined posteriorly.[1]
- Mandibular corpus deepens mesially.[1,2]
- Median mental foramen present in mandibular symphysis.[1] (polarity changed in ref.2, see above).
- Cheiridia usually short.[1]
- Moderate supraradial and supraulnar fossae.[1]
- Supraradial notch smaller than supraulnar.[1]
- Radial notch of ulna is doubled.[1]
- Medial malleolar facet of astragalus extends to plantar surface.[3]
- Astragalocalcaneal joint not helical.[1]
- Distal astragalocalcanial facet strongly curved relative to spring ligament.[3]
- Pedal functional axis through ray 3.[3]
- Entocuneiform hallucal facet lacks helical groove and plantar and medial buttressing.[3]
- Buccal pouches.[1,2]
- Chromosome number variable,[1] but 2n=42 may be ancestral.[2]

crown is significantly broader than at the cervix. The upper lateral incisor is large in comparison to those of colobines and is not caniniform (Szalay and Delson, 1979). The molars have relatively low and bunodont cusps. The buccal notches of the upper molars and lingual notches of the lowers are shallow, and the crown beneath them is comparatively tall. The molars also have relatively long trigonids, or mesial foveae (Szalay and Delson, 1979; Strasser and Delson, 1987).

Cercopithecine crania are distinguished from those of the colobines by a number of morphological features. The interorbital breadth in narrow, the midface is long, and often forms a “snout”. This is reflected in the nasal bones, which are comparatively narrow and elongate. The lacrimal often completely surrounds the lacrimal fossa and may extend onto the face (although these features have been shown to be variable within species (see Benefit and Mcrossin, 1990). The mandibular symphysis is pierced by a median mental canal. The mandibular ramus is typically posteriorly inclined as well. (Szalay and Delson, 1979; Strasser and Delson, 1987).

The Cercopithecinae are divided into two primary clades, typically ranked as tribes. Cercopithecini includes the guenons, talapoin, patas and swamp monkeys (the genera *Cercopithecus*, *Miopithecus*, *Erythrocebus* and *Allenopithecus* respectively). The second tribe, Papionini, includes the remaining genera (*Papio*, *Lophocebus*, *Theropithecus*, *Cercocebus*, *Mandrillus*, *Parapapio, Pliopapio, Gorgopithecus*, *Macaca*, *Procynocephalus,* and *Paradolichopithecus*) (Strasser and Delson, 1987; Disotell, 1996; 2000; Fleagle, 1988).

The Cercopithecini are distinguished from the papionins by relatively few morphological features, these are given in table 2.3. The ischial callosities are widely separated, and the females lack sexual swellings (except in *Miopithecus* and *Allenopithecus*). They are highly variable in the number of chromosomes, but all species have a diploid number greater than 42 (Dutrillaux, et al., 1988). The canines of the females are slender and relatively masculine in morphology with a large mesial sulcus. They are still significantly smaller than those of the males. The molar morphology of the Cercopithecini is the first of Delson’s four dental categories. The molar crowns are

Table 2.3 Morphological features typical of the Cercopithecini. Probable derived features are underlined. References as for Table 2.1, and [4]Groves, 1989; [5]Dutrillaux, et al., 1988.

- I^2 small relative to I^1 (except for *C. aethiops* and *E. patas*).
- Female C's slender and "masculine" in morphology.[4]
- M_3 lacks hypoconulid (variably absent in some non-cercopithecin species).[1,2]
- M^3 reduced distally.[1]
- Molar flare low (except in *Allenopithecus*), cheek teeth relatively elongate.[1,2]:
- Face may be less elongate than Papionini.[1]
- Choanae wider.[1]:
- Tail long.[1]
- Female sexual swellings absent (except in *Miopithecus*, and somewhat in *Allenopithecus*).[1]
- Ischial callosities separate.[1]
- Chromosomes highly variable and tachytelic (2n=48 – 72).[1,2,5]

straight sided and lack basal flare. They are also comparatively long and narrow. The most distinctive dental feature of the Cercopithecini relative to the Papionini is the loss of the M_3 hypoconulid. Associated with this is reduction in size of the distal half of the M^3.

Within the Cercopithecini, the genus *Allenopithecus* is sometimes placed in a separate subtribe, the Allenopithecina. The remaining genera are then placed in the Cercopithecina (Strasser and Delson, 1987, Delson, 2000a). *Allenopithecus* is separated from the other Cercopithecini by its highly flaring molars. This may be partially a primitive retention from the common cercopithecine ancestor, but its degree of flare is even greater than most papionins, being comparable to that of *Cercocebus*, and *Lophocebus* (see figure 4.7-4.8). It also retains the apparently primitive feature of female sexual swellings. It has a diploid number of 48 chromosomes, which is the lowest number of any cercopithecin.

The other cercopithecine tribe, the Papionini, constitutes the majority of the East African fossil record. Many morphological features of the papionins are likely to be primitive for cercopithecines. The morphological features typical of papionins are given

---

Table 2.4 Morphological features typical of the Papionini. Possible derived features are underlined. References as for Table 2.3.

- I^x large and spatulate.[1]
- I^2 inclined apically and mesially.[1]
- I^2 large relative to I^1.
- Female C_x incisiform.[4]
- P_3 elongate with large distal fovea.[1]
- P_4 wide with inflated mesiobuccal area, with metaconid larger than protoconid.[1]
- dp^3-M^3 mesial width greater than distal.[1]
- dp_3-M_1 mesial width less than distal.[1]
- $M_{2\text{-}3}$ mesial width greater than distal.[1]
- Molars generaly as for Cercopithecinae.[1]
- Molar flare increased.[1]
- Molar tooth margin is symmetrical in distal view.[1]
- Accessory cuspules common in molar notches.[1]
- M_3 often has tuberculum sextum.[1]
- Cranium more elongate, and further development of associated traits under Cercopithecinae.[1,2]
- Piriform aperture wide.[2]
- Postcranium more derived towards terrestriality than for Cercopithecinae.[2]
- Ischial callosities often contiguous or continuous across midline.[1]
- Female sexual swelling pronounced (except for small *Macaca*).[1]
- $2n=42$.[1,2]

---

in table 2.4. *Macaca* and its fossil relatives, *Paradolichopithecus* and *Procynocephalus*, are recognized as the subtribe Macacina. This taxon has an entirely Eurasian and North African distribution. The remaining papionin genera are placed in the subtribe Papionina, which is nearly entirely sub-Saharan in distribution (the only exceptions are *Papio* in Southern Arabia and isolated populations in the central Sahara. There are also rare fossils of *Theropithecus* from India and Spain).

There has been a fair amount of difference in interpretation of the generic level phylogeny of the papionins over the last several decades. *Theropithecus* was previously placed in its own third tribe based on large morphological differences, primarily in the cranium and dentition (Maier, 1971; Jolly, 1972). It has since been moved into the

Papionini (Delson, 1975; Strasser and Delson, 1987) and is considered by some to be the sister taxon to *Papio* (Delson and Dean, 1993; Disotell, 1994; the first authors include *Mandrillus* in *Papio*, the second separates *Mandrillus* at the genus level). Some authors include *Lophocebus* as a subgenus of *Cercocebus* (*e.g.* Szalay and Delson, 1979), while others separate them as two distinct genera (Groves, 1978; 1989; Disotell, 1996; 2000). Furthermore, in the majority of molecular analyses to date *Cercocebus* is found to be the sister taxon of *Mandrillus* (distinct from *Papio*) and *Lophocebus* the sister taxon to a *Papio/Theropithecus* clade (Disotell, 1994; Harris, 1997; Harris and Disotell, 1998). Several morphological features have been described that are consistent with the molecular phylogeny (Fleagle and McGraw, 1999). For the purposes of this thesis, *Lophocebus* and *Cercocebus* are recognized as full genera, as is *Mandrillus*. These distinctions are useful as there is little evidence for the occurrence of either *Cercocebus* or *Mandrillus* in the East African record, but there are several fossils known that are likely referable to *Lophocebus* and *Papio*, and there is a very large amount of *Theropithecus* known. For all of the papionin genera, except *Theropithecus*, molar morphology is essentially the same as described for the subfamily above, and constitutes the second of Delson's dental groups. There is some variability in basal flare, with *Lophocebus* and *Cercocebus*, and possibly *Mandrillus* having greater flare than the other genera.

The morphology of the individual papionin genera included in this thesis will be discussed in chapters 4 and 5; however one genus merits discussion here, due to its highly derived morphology, its singular importance in the East African fossil record, and because it represents the third of Delson's dental categories. *Theropithecus* is

Table 2.5 Morphological features of *Theropithecus*. Derived features are underlined. References are as follows: [1]Szalay and Delson, 1979; [6]Jablonski, 1986; [7]Eck and Jablonski, 1987; [8]Delson and Dean, 1993.

- Anterior dentition reduced, I's (C's in T. oswaldi).[1,7,8]
- Cheek teeth high crowned with increased cuspal relief. [1,7,8]
- Foveae deeply excavated and notches deeply incised.[1,7]
- Trigonid foreshortened, but deep.[1]
- Cusps columnar, separated by deep basins. [1,7,8]
- M^x/M_x lingual/mesial cleft deeply excavated and flattened at base.[1,8]
- Lophids and trigonids angled mesiolingually.[1]
- M_2 (some M_1) large accessory distal cuspule present.[1]
- Molar buccal margin forms a mesiodistal crest (lingual margin in uppers). [1,7,8]
- Posterior molar eruption delayed.[1]
- Sagittal crest positioned anteriorly. [1,7,8]
- Narrow postorbital breadth, i.e. large amount of postorbital constriction. [1,7,8]
- Wide zygomatic arches and large temporal fossae.[7,8]
- Muzzle profile "hollow" concave, with steep anteorbital drop.[1,2]
- Zygomata vertical.[1]
- Zygomata positioned anteirorly.[8]
- Posterior maxilla deep.[1,8]
- Temporomandibular joint elevated relative to occlusal plane.[7,8]
- Premaxilla short, incisor alveoli vertically oriented.[1]
- Basioccipital wide.[8]
- Reverse curve of spee.[7]
- Mandibular ramus vertical, coronoid expanded. [1,7,8]
- Mandibular symphysis long.[7]
- Intermembral index 97 (*T. gelada* only).[2]
- Forelimb, especially humerus, elongate.[1]
- Humeral medial epicondyle short and retroflexed.[1]
- Olecranon process expanded and retroflexed.[1]
- Phalanges short and stout, including hallucal.[1]
- Pollex long (only known in *T. gelada* and *T. brumpti*).[1,6]
- Extra sitting pads ventral to ischial callosities.[1]
- Pectoral area of naked skin with catamenial swelling in females.[1]

distinguished from other cercopithecids by a suite of adaptations for graminivory (see table 2.5). The most obvious of these are the in the molars, which are high crowned (for a primate, not hypsodont in the ungulate sense) with relatively tall, columnar cusps. The buccal clefts of the lowers and lingual clefts of the uppers are deeply excavated with flattened "floors". When the teeth wear down they produce a complex pattern of folded

Table 2.6 Morphological features of the Colobinae. Many features are retentions from the ancestral catarrhine or cercopithecid. Probable derived colobine features are underlined. References as for table 2.1.

- Incisors small.[1]
- I^1 rhomboidal.[2]
- I^2 small and caniniform.[1]
- I_x with lingual enamel.[1]
- I_2 conical with "lateral prong".[1]
- P_3 broad.[1]
- P_4 mesiobuccal region more flange-like, and may be angled relative to the tooth row.[1]
- P_4 metaconid less tall and wide than protoconid.[1]
- dP_3 may reduce distal fovea.[1]
- Molars with high relief, M_x lingual notches deep, nearly to cervix. (except *C. kimeui*).[1,2]
- Molar flare low.[2]
- M^x distal margin asymmetrically curved.[1]
- M_x trigonid basin mesiodistally shortened.[1,2]
- Accessory cuspules rare.[1]
- M_x mesial width less than distal, except for M_3.[1]
- M_3 hypoconulid only rarely absent, (except *Presbytis* typically lacks it).[1]
- Face short (*Nasalis* and some fossil exceptions).[1,2]
- Interorbital broad, face broad in general (except *Nasalis* and some fossils).[1]
- Nasals short (except *Nasalis*).[2]
- Lacrimal bone typically within the orbit.[1,2]
- Lacrimal fossa extends onto maxilla.[1,2]
- Ethmoid in the orbit.[1]
- Mandibular corpus deep, and tapers anteriorly (or sometimes is of even depth).[1,2]
- Mandibular ramus subvertical, and gonial area often expanded inferiorly.[1]
- Median mental foramen absent (except. *P. verus* and some African fossils).[1,2]
- Digits elongate.[1]
- Lower ankle joint secondarily helical.[1]
- Supraradial fossa deeper and larger than supraulnar.[1]
- Distal humaral articular surface wide.[1]
- Radial articulation of the ulna shallow, and typically single.[1]
- External pollex reduced.[1,2]
- Pedal functional axis through rays 3 and 4.[2]
- Proximal ectocuneiform-cuboid facet shorter than distal.[2,3]
- Proximal calcaneal facet of astragalus elongate and more strongly curved.[3]
- Astragalar head strongly laterally rotated.[3]
- Astragalar facet for spring ligament limited laterally.[3]
- Astragalus with separate *m. flexor fibularis* groove.[2,3]
- Astragalus with well developed *m. flexor tibialis groove*.[3]
- Entocuneiform facet of Navicular plantar length much longer than dorsal.[3]
- Foregut expanded and three-chambered for fermentation.[1,2]
- Ischial calosities widely separate.[1]
- Sexual swellings lacking (except in *Piliocolobus* and *Procolobus*).[1,2]
- 2N=44 (except Nasalis where 2N=48).[1]

enamel and dentine that efficiently shears abrasive grass blades. The incisors are small compared to other papionins. In the cranium, there is a suite of features related to an emphasis on molar chewing. These include an anteriorly positioned sagittal crest, large infratemporal fossae, and anteriorly positioned zygomata. In the postcranium, there are a series of adaptations for terrestriality. Additionally, the hand has the highest opposability index of any catarrhine, due to a relatively short second digit (Maier, 1972). Additionally the femur is distinctive in that it often possesses a "reverse" carrying angle (Krentz, 1993).

The subfamily Colobinae is morphologically very distinct from the Cercopithecinae. The most important difference is the enlarged, multi-chambered stomach that allows bacterial foregut fermentation of cellulose and other plant fibers, in a manner not entirely unlike that of ruminants. There is also some evidence for convergence of stomach enzymes between colobines and ruminant artiodactyls (Messier and Stewart, 1997). A summary of the morphological features of the colobines is given in table 2.6. Whereas the cercopithecines are relatively derived in their incisor morphology and more primitive in their molar morphology, the colobines appear to show the opposite pattern. The incisors are generally small, and their crowns are not flaring in labial view. The upper second incisors may preserve the primitive catarrhine condition (Szalay and Delson, 1979; Strasser and Delson, 1987). They are relatively small in comparison to the first, narrow, and caniniform. The molar teeth are more derived, however, and represent the fourth of Delson's dental groups. They have tall cusps and low lingual notches leading to a large amount of cuspal relief above the rest of the crown. The cross-lophs are strongly developed, yielding a more strongly bilophodont pattern.

Within the colobine subfamily two main clades are typically recognized, often at the subtribal level. The two groups appear to be separated geographically, with the Presbytina in Asia and the Colobina in Africa (Delson, 1975; Szalay and Delson, 1979, Strasser and Delson, 1987). Alternatively, Groves (1989) has argued that *Nasalis* is the sister taxon to all of the other colobines, each group being put into its own subfamily (Groves considers the colobines a family). In this study, the Colobinae will be divided into the Colobina and Presbytina.

Different recent taxonomies have recognized from one to three genera for the extant Colobina. All researchers recognize three taxa: a black and white group, a red group, and the olive colobus. Disagreement centers around whether red colobus are more closely related to the black and white group or to the olive colobus. Following Strasser and Delson (1987) and Groves (1989) two genera will be recognized here. The red and olive colobus monkeys will be united in the genus *Procolobus*, in the subgenera *P.(Piliocolobus)* and *P.(Procolobus)* respectively. The genus *Colobus* is composed of only the black and white group. This classification of African colobines is largely based on soft tissue anatomy, but there are cranial and mandibular features that support these groups as well (see chapters 4 and 5 for more thorough description of these features).

The Presbytina are considerably more diverse than the Colobina, with different classifications recognizing from three (Szalay and Delson, 1979) to nine genera (Jablonski, 1998). These forms can be divided into two main groups, that on preliminary evidence, seem to represent clades: the odd-nosed colobines and the “normal” langurs (Disotell, 1996; 2000). The odd-nosed forms are the genera *Pygathrix* (including *P.*

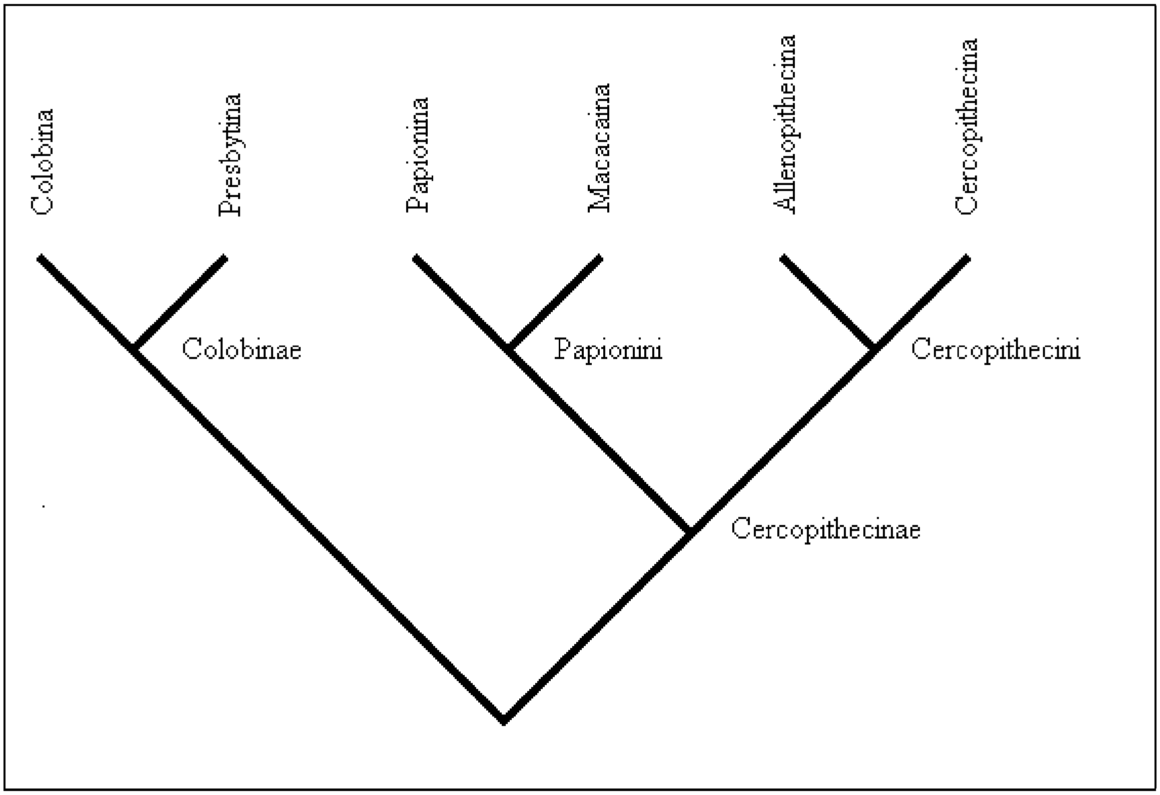
(Rhinopithecus)) and *Nasalis* (including *N. (Simias)*), with the "normal" langurs being *Presbytis* and *Semnopithecus* (including *S. (Trachypithecus)*).

There are a few features of the dentition and postcranium that appear to separate the two subtribes (Szalay and Delson, 1979; Strasser and Delson, 1987; Strasser, 1988). In all of these features the Colobina appear to possess the derived state relative to the Presbytina. Therefore the latter group may not represent a holophyletic unit. The P^3 of colobinans has a reduced protocone, whereas it is well developed in the presbytinans. The M_3 of the African colobines appears to have a distal lophid that is wider than the mesial. The M_3 proportions are reversed in the Asian genera, a condition similar to that in cercopithecines. In the postcranium there is reduction of the length of the thumb. The Asian forms have a thumb that is small in comparison to that of cercopithecines, and the African genera lack an external thumb. In the foot, the Presbytina show a reduction in the size of the proximal cuboidal facet when compared to that of cercopithecines. In the Colobina, the proximal cuboidal facet is typically absent. This feature is variable within species, and these differences are only observable with relatively large sample sizes.

African Plio-Pleistocene fossil colobines are considerably more diverse than the extant Colobina: there are several forms that were much larger than the extant species (Delson *et al.*, 2000), some of which seem to have been adapted for more terrestrial locomotion (Birchette, 1982; Delson, 1994). Others have lower crowned molars that may indicate a less folivorous diet than many extant species (Leakey, 1982; Benefit, 2000). In addition to the general lack of osteological and dental features known to separate the subtribes, many of the characters that can be used require either large samples or elements that are rarely preserved. As a result, it is not clear whether all fossil African colobines are members of the Colobina, or whether some may be more closely related to specific Asian taxa (Leakey, 1982; 1987). As a result, the fossil genera *Microcolobus*, *Libypithecus*, *Kuseracolobus*, *Rhinocolobus*, *Paracolobus* and *Cercopithecoides* are not placed within either subtribe, nor are the Asian fossils *Mesopithecus* and *Dolichopithecus*.

As reviewed above, the phylogenetic relationships of the higher-level cercopithecid clades are reasonably well resolved. There is no question about the holophyly of the two subfamilies (Szalay and Delson, 1979; Strasser and Delson, 1987; Groves, 1989; Disotell, 1996; 2000). There is also little question that the Cercopithecini are a holophyletic group, and the sister taxon to the Papionini (Groves, 1989 is a dissenting opinion, counting *Allenopithecus* as a papionin). Within the papionins, several genetic studies support the holophyly of the two papionin subtribes (Harris and Disotell, 1998; Morales et al., 1998; Tosi, 2000). Whether the two colobine subtribes represent holophyletic groups awaits further analysis, as do the interrelationships of the guenons. The generic relationships of the papionins are perhaps the most contentious, although recent molecular evidence strongly supports the close relationship of *Lophocebus* to *Papio* and *Cercocebus* to *Mandrillus* (Harris and Disotell, 1998). These unsettled generic-level phylogenies do not present an insurmountable problem for this thesis as all of the involved genera are diagnosable (provided preservation of the necessary anatomy) on the basis of skeletal and dental morphology.

Figure 2.1 Phylogeny of major cercopithecid clades. Modified from Delson (2000). See test for discussion.



Background 2: Brief Chronostratigraphy of the Afar and Turkana Basins

The purpose of this section is to introduce the basic geology, and most importantly for this thesis, the chronostratigraphy of the major paleontological collecting regions where the fossils discussed were collected. The stratigraphy and formations of the Afar basin have been documented by several authors, and these are synthesized here. Some of the earliest surveys of the region are those of Taieb (1974). Since then the geology and stratigraphy of the Hadar formation has been well documented (e.g. Taieb et al., 1976; Aronson and Taieb, 1981; Tiercelin, 1986; Walter and Aronson, 1993; Walter, 1994; Kimbel et al., 1996). Several papers on the stratigraphy and paleontology of the middle Awash have also been published (e.g. Kalb et al., 1980; 1982a,c; Clark et al., 1984; 1994; Adamson and Williams, 1987; Kalb 1993; White et al., 1993; WoldeGabriel et al., 1994; de Heinzelin et al., 1999; Renne, et al., 1999). The general stratigraphy of the Turkana Basin has also been thoroughly described, and will only be briefly reviewed below. Some recent syntheses include those of Brown (1994; 1995), Brown and Feibel (1991) and Harris et al. (1989).

Afar Depression

The Afar depression is located in Northern Ethiopia and Southeastern Eritrea (see figure 2.2). It is roughly triangular in outline, and represents the only subaerial triple rift junction on Earth today. It is at the junction of the East African rift system, the Red Sea rift and the Gulf of Aden. It is bounded to the East by the Red Sea, to the South by the Somali Plateau and to the Northwest by the Ethiopian Plateau (see figure 2.3).

Figure 2.2. Location of the Afar and Turkana Basins within East Africa. Reproduced from Delson et al., 2000b (Courtesy of E. Delson).

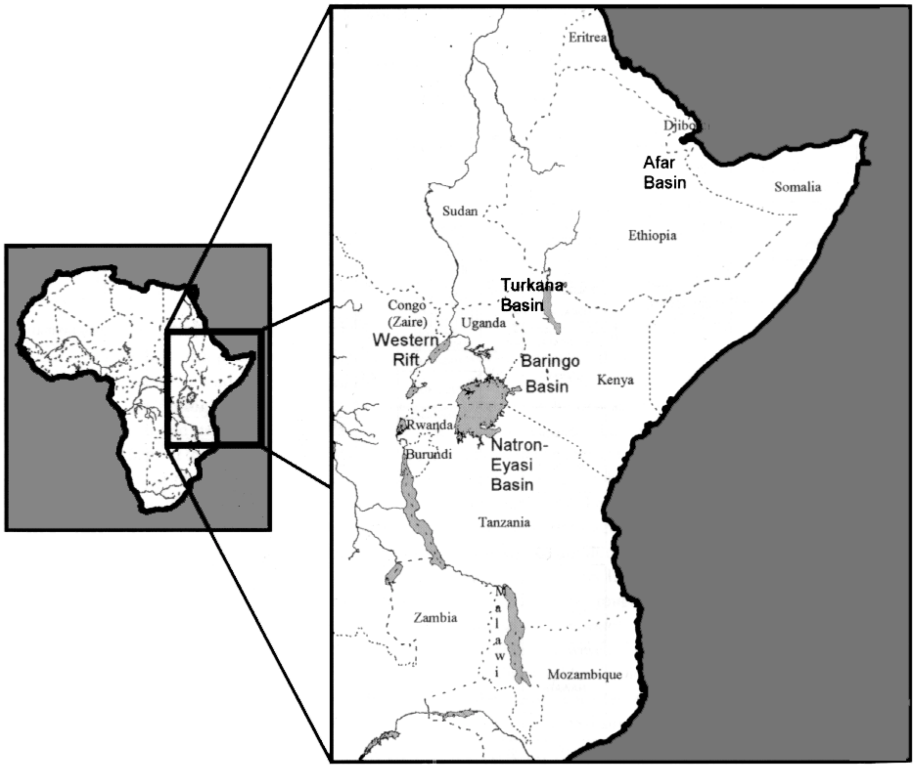


Figure 2.3 Map of the Ethiopian rift, including the Afar Depression, showing its boundaries. Reproduced from White, 2000. (Courtesy of T. White).

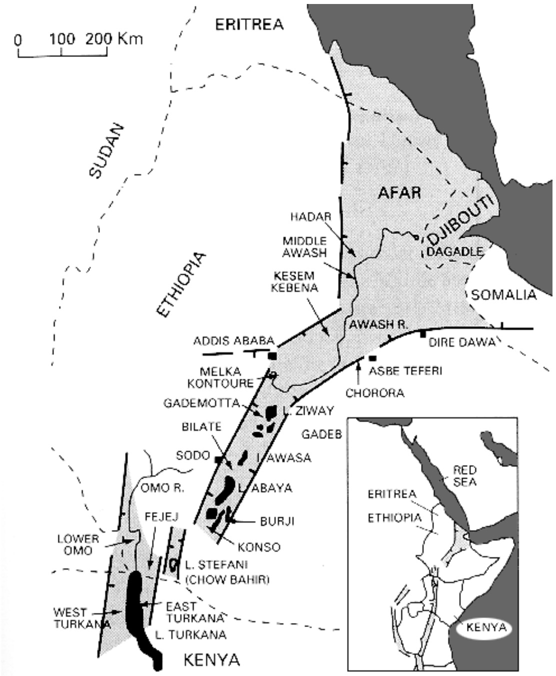
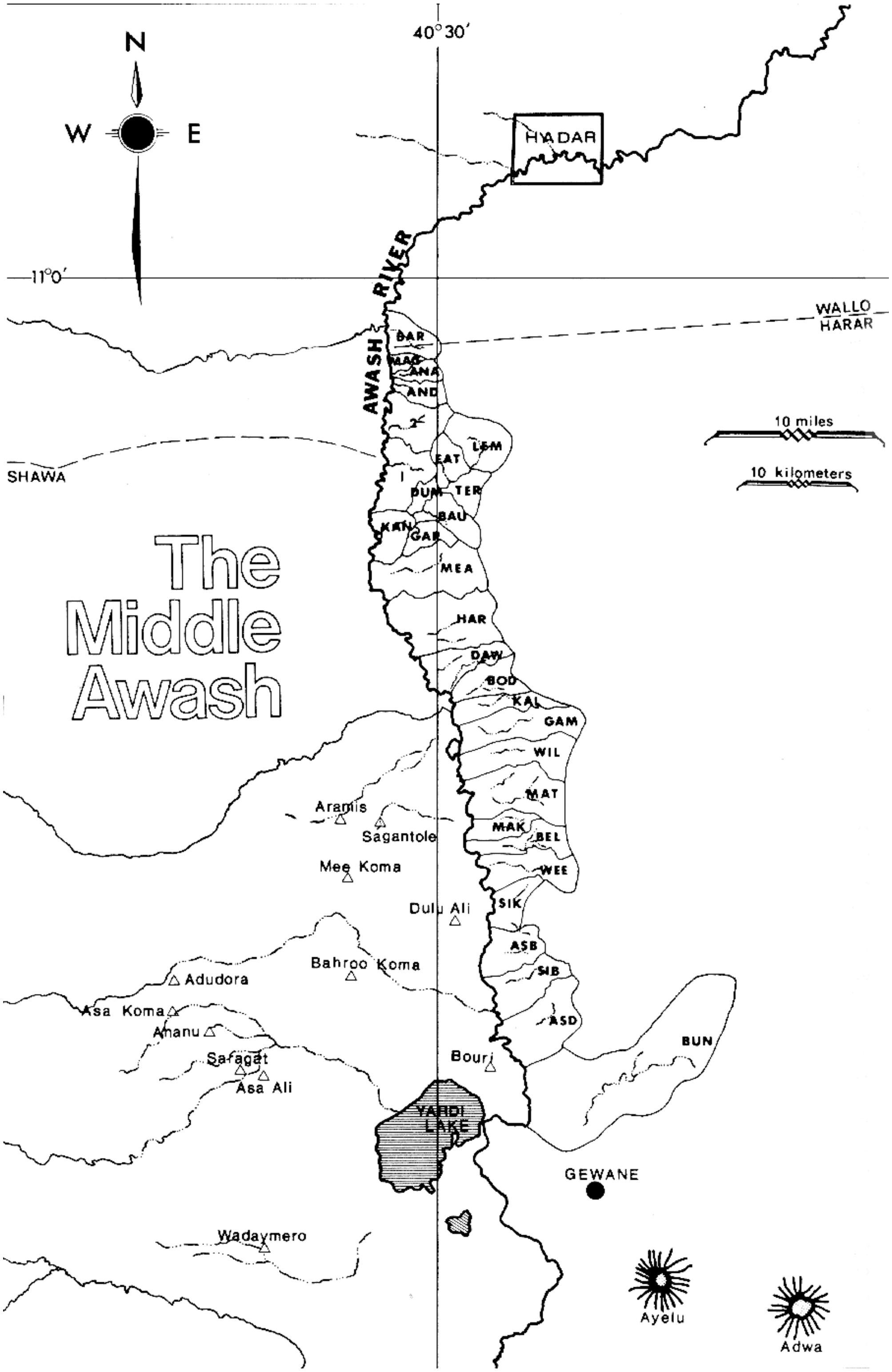


Figure 2.4 Map of the Middle Awash, also showing the location of Hadar. Three letter abreviations for drainages on the figure match those in Chapter 3 for the locality names.



The fossil cercopithecids described in this study derive from two main paleontological research areas that lie within the Afar Basin: the Middle Awash and Hadar (shown in figure 2.4). These regions are well known for the many important hominid discoveries, including those of *Australopithecus afarensis* and early *Homo* from Hadar; and *Ardipithecus ramidus*, *Australopithecus afarensis, Australopithecus garhi*, and "archaic" *Homo sapiens* from the Middle Awash (Conroy et al., 1978; Johansen et al., 1982; Asfaw, 1987; White et al., 1994; 1995; 2000; Kimbel et al., 1994; 1996; Asfaw et al., 1999). Two other sites in the Afar region were not included in this thesis. Their stratigraphy is not discussed here. The first is the area of the Gona just west of Hadar (Semaw et al., 1997). Another is the site of Asbole in the Busidima-Dikika research area located South of the Gona and North of the Middle Awash (Alemseged and Geraads, 2001).

The Middle Awash paleoanthropological research area lies along the Eastern and Western banks of the Awash River Valley, between the village of Gewane and the Busidima-Dikika research area. The valley is an elongate graben, bounded by the Ethiopian escarpment to the West and to the East by a lower basaltic escarpment (Asfaw et al., 1990). Sediments in the Middle Awash are from the Upper Miocene through Upper Pleistocene and include several distinct formations (Kalb *et al*., 1982c; Kalb, 1993; Renne *et al*., 1999; White, 2000). These sediments are mostly lacustrine, fluvial, alluvial and pedimentological, and are heavily tectonically disturbed, forming a complex series of exposures and vertebrate fossil localities (Kalb *et al.,* 1982b; White *et al.,* 1993; Clark *et al.,* 1994; WoldeGabriel *et al.,* 1994, de Heinzelin *et al*., 1999; Renne *et al*., 1999). As a result, vertebrate collecting localities in the Middle Awash tend to represent thin slices of time, separated from one another by relatively large temporal gaps. There a number of tuffs in the sequence that have been radiometrically dated and/or correlated to dated tuffs from Hadar, the Turkana Basin, and the Gulf of Aden. Along with paleomagnetic correlations, these give good chronological control to most of the localities studied, even if the stratigraphy among different localities is complex (White *et al.,* 1993; Clark *et al.,* 1994; WoldeGabriel *et al.,* 1994; Brown, 1994, 1995; de Heinzelin *et al*., 1999; Renne *et al*., 1999). The dates for these tuffs are shown in figure 2.5, and correlations to the Turkana Basin are shown in figure 2.7.

The oldest sediments containing vertebrate fossils in the Afar region are in the Chorora Formation. The Chorora fauna has recently been described by Alemseged et al. (2000) and is of Late Miocene age overlying volcanic rocks dated to 9.0 Ma (Asfaw et al., 1990). There are no cercopithecoids. In the Middle Awash proper the oldest levels are in the Adu-Asa formation, which is of terminal Miocene age (Kalb, 1993; Kalb et al., 1982a). The Adu-Asa formation is largely exposed along the Western margin area of the Middle Awash. This formation was originally described with three members, from oldest to youngest they are the Adu, Asa, and Kuseralee Members. The Kuseralee Member has been transferred by Renne et al. (1999) to the bottom of the Sagantole Formation.

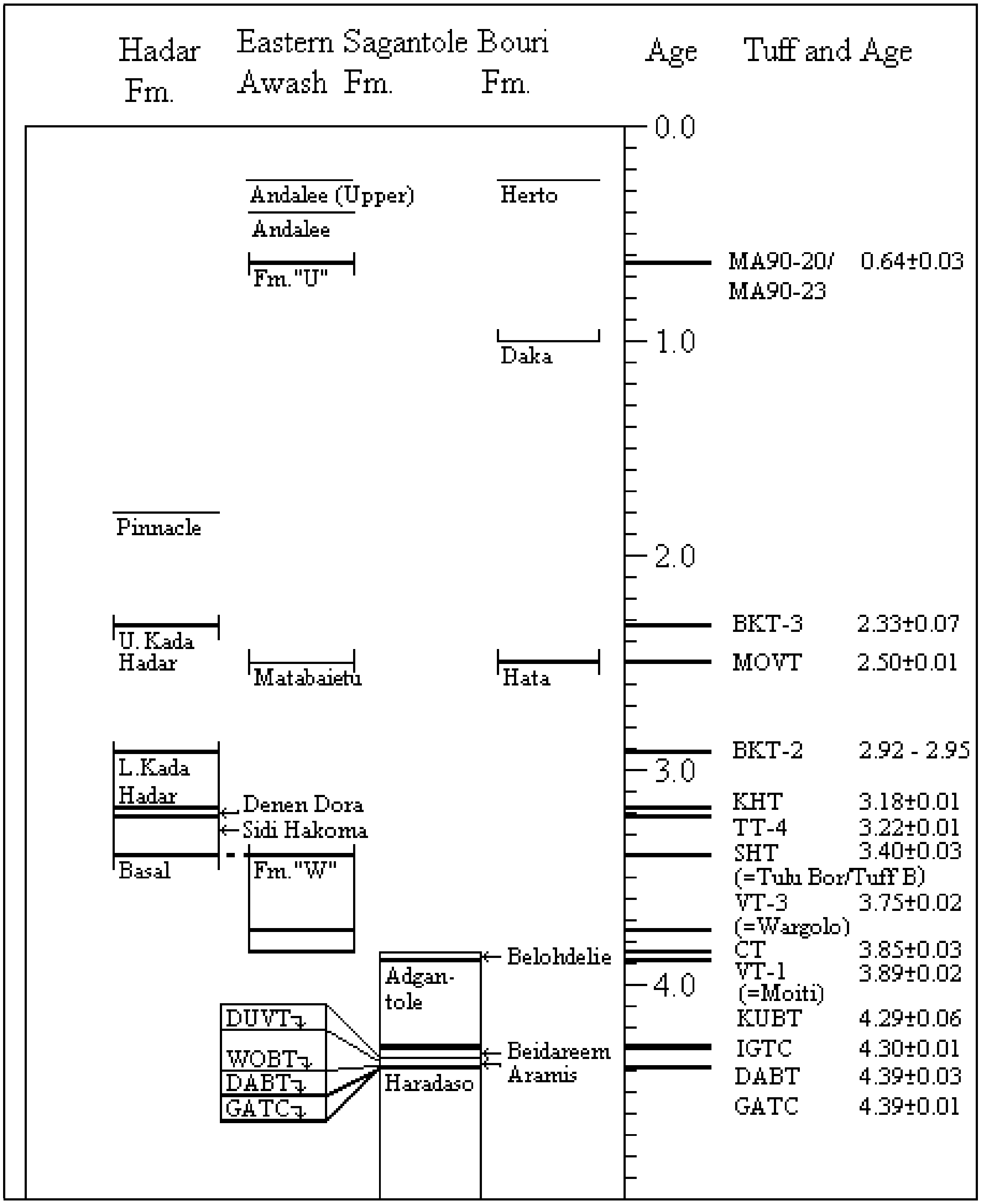
The Sagantole Formation is exposed mainly in the area of the Central Awash Complex (Kalb et al., 1982a; 1993; Renne et al., 1999). The Central Awash Complex is a horst, or upfaulted block, positioned West of the Awash River. It is terminal Miocene through Early Pliocene in age and consists largely of lacustrine, alluvial and volcaniclastic sediments with tephras and basalt. Its base has been dated to 5.6 Ma. The top has been dated to 3.89 Ma. There are seven members, from lowest to highest:

Kuseralee, Gawto, Haradaso, Aramis, Beidareem, Adgantole, and Belohdelie. They are individually described by Renne et al. (1999).

This thesis includes only those fossils recovered superior to the Gàala Vitric Tuff Complex (GATC), which defines the base of the Aramis Member (Renne et al., 1999; see figure 2.5). The GATC has been dated to 4.39 ± 0.01 Ma (WoldeGabriel et al., 1994). The sediments of the Aramis Member are largely fluvial and alluvial from overbank and/or floodplain deposition. There are also shallow lacustrine environments near the top of the member. The largest single assemblage of cercopithecids discussed in this study derives from between the GATC and the overlying Daam Atu Basaltic Tuff (4.39 ± 0.03 Ma). This assemblage is, therefore, very well constrained chronologically. WoldeGabriel et al. (1994) reconstructed the sediments of the GATC/DABT interval as being deposited in a relatively wooded environment. There are also small samples of cercopithecids from the Aramis member above the DABT. Most of these are isolated teeth. The age of the top of the Aramis Member is not precisely known, but is older than 4.3 Ma as the Igida Crystal Tuff in the overlying Beidareem Member has been dated to 4.30 ± 0.01 Ma (Renne et al., 1999). The overlying Beidareem Member is largely lacustrine and composed of basaltic tuffs, with no cercopithecid fossils recovered.

The Adgantole Member overlies the Beidareem. It is largely subaerial in sedimentation, with silt, clay, sand and conglomeratic deposits. There is a small cercopithecid sample from this member that dates to between 4.29 Ma and 4.18 Ma based on the underlying Kullunta Basaltic Tuff and on paleomagnetic correlation respectively (Renne et al., 1999).

Figure 2.5 Chronostratigraphy of different Afar Formations. Dated tuffs are shown by bold lines, and their chronological position is marked on the scale to the right, where the name is given, along with their ages. Any correlations to the Turkana Basin are labelled in parentheses. References for the dates on the tuffs are: Unnamed tuff MA90-20/MA90-23 (Clark et al., 1994); BKT-3 (Kimbel et al., 1996); MOVT (de Heinzelin et al., 1999); BKT-2 (Kimbel et al., 1994); KHT, TT-4 (Walter, 1994); SHT (Walter and Aronson, 1993); SHT,VT-3,CT,VT-1 (White et al., 1993); KUBT, IGTC, DABT (Renne et al., 1999); GATC (WoldeGabriel et al., 1994).



The Belohdelie Member overlies the Adgantole and has its best exposures on the Eastern side of the Awash, where a small collection of cercopithecids was recovered in the Wee-ee and Wilti Dora drainages. Its sediments are largely lacustrine in nature (Adamson and Williams, 1987; Renne et al., 1999). The base of this member is defined as the base of the Vitric Tuff 1 (VT-1) and its top is the base of the Cindery Tuff (CT). These tephra have been dated to 3.89 and 3.85 Ma respectively (White et al., 1993) and the VT-1 has been correlated to the Moiti Tuff in the Turkana Basin.

On the Eastern side of the Awash River, above the Sagantole Formation, lie a series of sediments informally designated Formation “W” by White et al. (1993). The base of this unit is the Cindery Tuff (CT). After deposit of the CT, there is a shift in sedimentation from primarily lacustrine to primarily pedi-alluvial (Adamson and Williams, 1987; Renne et al., 1999). Sedimentation rates are much lower after this shift. Above the CT lies the VT-3, which has been dated to 3.75 Ma (White et al., 1993), and chemically correlated to the Wargolo Tuff in the Turkana Basin (Haileab and Brown, 1992). There is a small collection of cercopithecids from Formation “W” below the VT-3 and above the CT, which is therefore dated to between 3.75 and 3.85 Ma.

Above the VT-3 lies a tuff which has been correlated to the Sidi Hakoma Tuff (SHT) at Hadar and the Tulu Bor (=Tuff B) in the Turkana Basin (White et al., 1993). The SHT has been dated to 3.4 Ma at Hadar (Walter and Aronson, 1993), and this age has been confirmed isotopically in the Middle Awash as well (White et al., 1993). There is a comparatively large sample of cercopithecids that have been collected from below the SHT in the Maka, Matabaietu, Wee-ee and Bunketo catchments. Because of an erosional unconformity between the Maka sands and the underlying VT-3, the most reliable age for these fossils is closer to 3.4 Ma than to 3.75. The fauna from this level supports an age close to 3.4 Ma as well (White et al., 1993).

Largely fluvial sediments East of the Awash river in the Wilti Dora, Gamedah, and Matabaietu catchments were described as the Matabaietu Formation (Kalb et al., 1982c; Kalb, 1993). These sediments have yielded vertebrate fossils including hominids (Asfaw et al., 1999) and a large number of cercopithecids. These have been dated to approximately 2.5 Ma (Asfaw et al., 1999; White, 2000). Vrba (1997) has suggested on the basis of the bovids that some of the sites in these sediments (MAT-VP-1 and 2) may date to closer to 2 Ma, and another (MAT-VP-6) may be older, dating to approximately 2.9 Ma. Vrba (1997) also notes, however, that current stratigraphic evidence suggests all of these sites are close to 2.5 Ma.

Also on the East side of the Awash River, Middle Pleistocene sediments from Bodo, Dawaitoli, and Hargufia were termed the Bodo Member of the Wehaietu Formation by Kalb et al. (1982c; 1993). These were placed in the informally designated Unit “U” by Clark et al. (1994). They are largely fluvial in nature, and in fault contact with older sediments to the East. A tuff near the base of Unit “U” has been isotopically dated to 0.64 ±0.03 Ma (Clark et al., 1994). Most of the fossils overlie this tuff, but are probably close in age.

Sediments from the Andalee and Issie catchments have been described as the Andalee Member of the Wehaietu Formation by Kalb et al. (1982a; 1982c; Kalb, 1993). These are younger than Unit “U” and are divided into a lower and upper unit. The lower unit is probably Middle Pleistocene in age and marked by the presence of *Theropithecus oswaldi leakeyi*, which is absent from upper Andalee. There may also be a difference in the archeological material from the upper and lower Andalee beds. The stone tools from the lower unit, initially described as Sangoan (Kalb et al., 1982a), are probably late Achulean, whereas the tools from the upper Andalee Member are more consistent with Middle Stone Age (A. Brooks and J. Yellen, personal communication). There has been no chronometric age determined for the Andalee Member. The lower Andalee sediments are younger than Unit "U" (Kalb, 1993), but how much younger is not clear. The upper Andalee beds may be significantly younger than the lower given the absence of *Theropithecus* and possible difference in the stone tools. If the lithics from the upper Andalee unit are in fact Middle Stone Age, then it is likely to be younger than approximately 250 Ka. If this is correct, then the lower Andalee beds are likely to be between 600 and 250 Ka, with a midpoint of approximately 425 Ka. Kalb et al. (1982a) biochronologically dated the lower Andalee Beds to the late Middle Pleistocene.

The Bouri Formation is located on the Western side of the Awash River, South of Aramis. It is divided into three members, the Hata, Daka, and Herto representing approximately 80 m of sediment (de Heinzelin et al., 1999). The oldest member is the Hata (short for Hatayae). It is composed mostly of fluvial sediments, deposited near a shallow fluctuating lake. In the lower part of the Hata Member, the Maoleem Vitric Tuff (MOVT) has been isotopically dated to 2.5 (± 0.01) Ma. Based on magnetostratigraphic correlation and biochronology the vertebrate material collected from this member is all close to 2.5 Ma in age. Based on paleomagnetics they are unlikely to be older than 2.6 Ma or younger than 2.45 Ma. The base of the overlying Daka (short for Dakanihylo) Member has been dated to 1.0 Ma. The youngest member in the Bouri Formation is the

Herto. It has not been radioisotopically dated, but contains late Achulean/Middle Stone Age artifacts.

Downstream (North) along the Awash River from the Middle Awash lies Hadar. The Hadar Formation consists of a series of stratified sediments representing riverine, channel fill and floodplain sediments deposited near a large lake. Sedimentation at Hadar is generally more continuous than in the Middle Awash. This formation is divided into four members (Basal, Sidi Hakoma, Denen Dora, Kada Hadar) separated by tuffs. The Sidi Hakoma Tuff (SHT) forms the base of the Sidi Hakoma Member, the Triple Tuff 4 (TT-4) is the base of the Denen Dora Member, and the Kada Hadar Tuff (KHT) is the base of the Kada Hadar Member (Aronson and Taieb, 1981). These tephra along with the Bourouki Tuffs 2 and 3 (BKT-2 and BKT-3) and the Kadada Moumou Basalt have been radiometrically dated (Walter and Aronson, 1993; Walter, 1994; Kimbel *et al.*, 1996), and the Sidi Hakoma Tuff has been correlated to the Tulu Bor at Koobi Fora (Brown, 1992). The ages of these are shown on figure 2.5. The ages of the members are thus, 3.4 to 3.22 Ma for the Sidi Hakoma, 3.22 to 3.18 for the Denen Dora, and 3.18 to 2.92 for the lower part of the Kada Hadar Member.

After 2.92 Ma sedimentation decreases. There is a large unconformity between the BKT-2 and BKT-3 in the Kada Hadar Member, dividing the Kada Hadar Member into upper and lower parts. From the Sidi Hakoma up to the unconformity, sedimentation is by a meandering river system, with several lacustrine transgressions from a nearby lake. Above the unconformity sedimentation is dominated by coarse-grained conglomerates, with lacustrine sediments absent (Kimbel et al., 1996).

The paleoenvironment in the Sidi Hakoma Member was dominated by dry bush or woodland with denser vegetation near streams. The Denen Dora Member was typified by gallery forests and wetlands. Dry bush to woodland was again predominant in the lower part of the Kada Hadar Member. After the unconformity in the upper part of the Kada Hadar Member open environments predominated, but with some wetlands and bushland (Kimbel, et al., 1996). There are sizable collections of cercopithecids from the Sidi Hakoma through lower Kada Hadar Members, as well as smaller samples from the Basal Member and upper Kada Hadar Member. Those from the upper Kada Hadar Member are close in age to the BKT-3 Tuff dated to 2.33 ± 0.07 Ma. There are also cercopithecid fossils from a site called Pinnacle, which is substantially younger than the BKT-3. This site is probably latest Pliocene to Early Pleistocene in age (Eck, personal communication).

There are also a few sites in the Hadar region that are not tightly controlled as to their stratigraphic position relative to the main part of the Hadar Formation. A large collection of cercopithecid teeth and fragmentary postcrania was collected from the site of Ahmado. Kalb (1993) described a tuff at the base of the Ahmado beds, from which the cercopithecid fossils were recovered, that may correlate with the base of the Sidi Hakoma Member. A colobine partial skeleton (often referred to as the Leadu Colobine), and a few dental remains of *Theropithecus*, were discovered at the site of Leadu several kilometers north of Hadar. The exact age of this material and how it correlates to the main Hadar section is unclear, but the presence of *Theropithecus* similar in size to that from the main part of the Hadar Formation suggests a broadly similar age. The site of Geraru has produced a few cercopithecids, and is thought to correlate with the upper part of the Hadar formation (Kalb, 1993).

Turkana Basin

The Turkana basin in Northwestern Kenya and Southern Ethiopia is a segment of the East African Rift System (see figure 2.2). The basin is occupied by Lake Turkana, which at its current level has no outlet. Sediments around the basin span from the late Cretaceous through the Recent (Brown, 2000). The Omo Group of Plio-Pleistocene formations is located in the Northern Turkana Basin. It includes the Usno, Mursi, and Shungura Formations in the lower Omo River Valley in Ethiopia and in Kenya, the Koobi Fora and Nachukui Formations located in Kenya on the eastern and western sides of Lake Turkana respectively (see figure 2.6). Southeast of Lake Turkana are the ca. 4+ Ma sites of Kanapoi and Ekora (M.G. Leakey and R.E.F. Leakey, 1976; Leakey *et al.*, 1995). The Turkana sediments are some of the most thoroughly studied in East Africa, and have been described and summarized many times (*e.g.* de Heinzelin, 1983; Harris et al., 1988; Brown and Feibel, 1986; 1991; Feibel *et al.*, 1989; Brown, 1994, 1995; and references therein). As a result, they will only be discussed very briefly, with emphasis on the sediments that yielded cercopithecid fossils discussed in the later chapters. They span the time interval from the late Miocene to the present, with the period from 3.5 Ma to about 1.0 Ma being particularly well represented.

The three main formations of the Omo group, the Shungura, Koobi Fora, and Nachukui, are each divided into a number of members, each of which has a tuff at its base. In most cases the member and its basal tuff share a name (e.g. Tuff B is at the base

---

Figure 2.6 Map of the Turkana Basin showing the relative positions of the formations of the Omo Group. A is the Shungura Formation, B the Nachukui, and C the Koobi Fora.

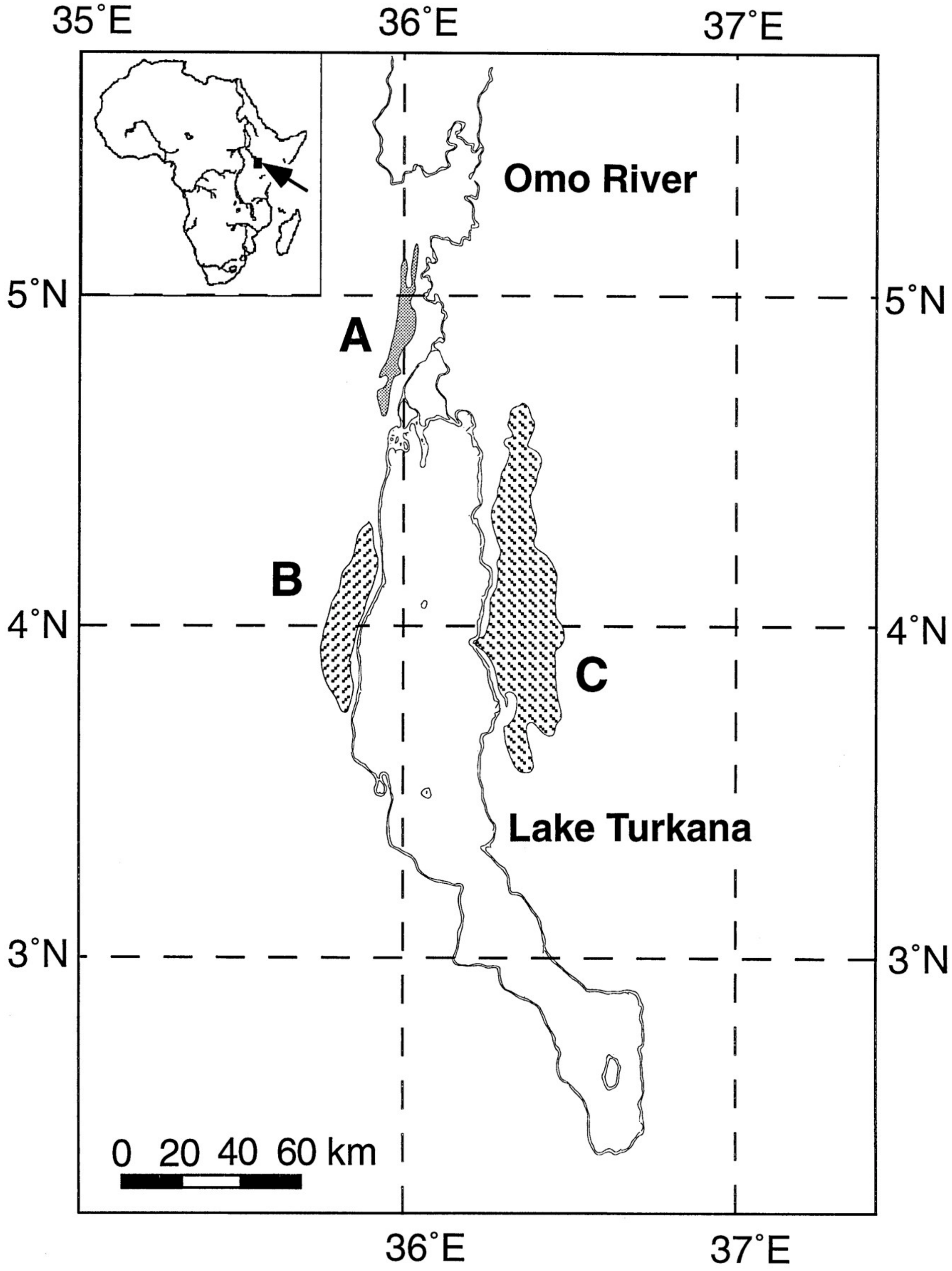
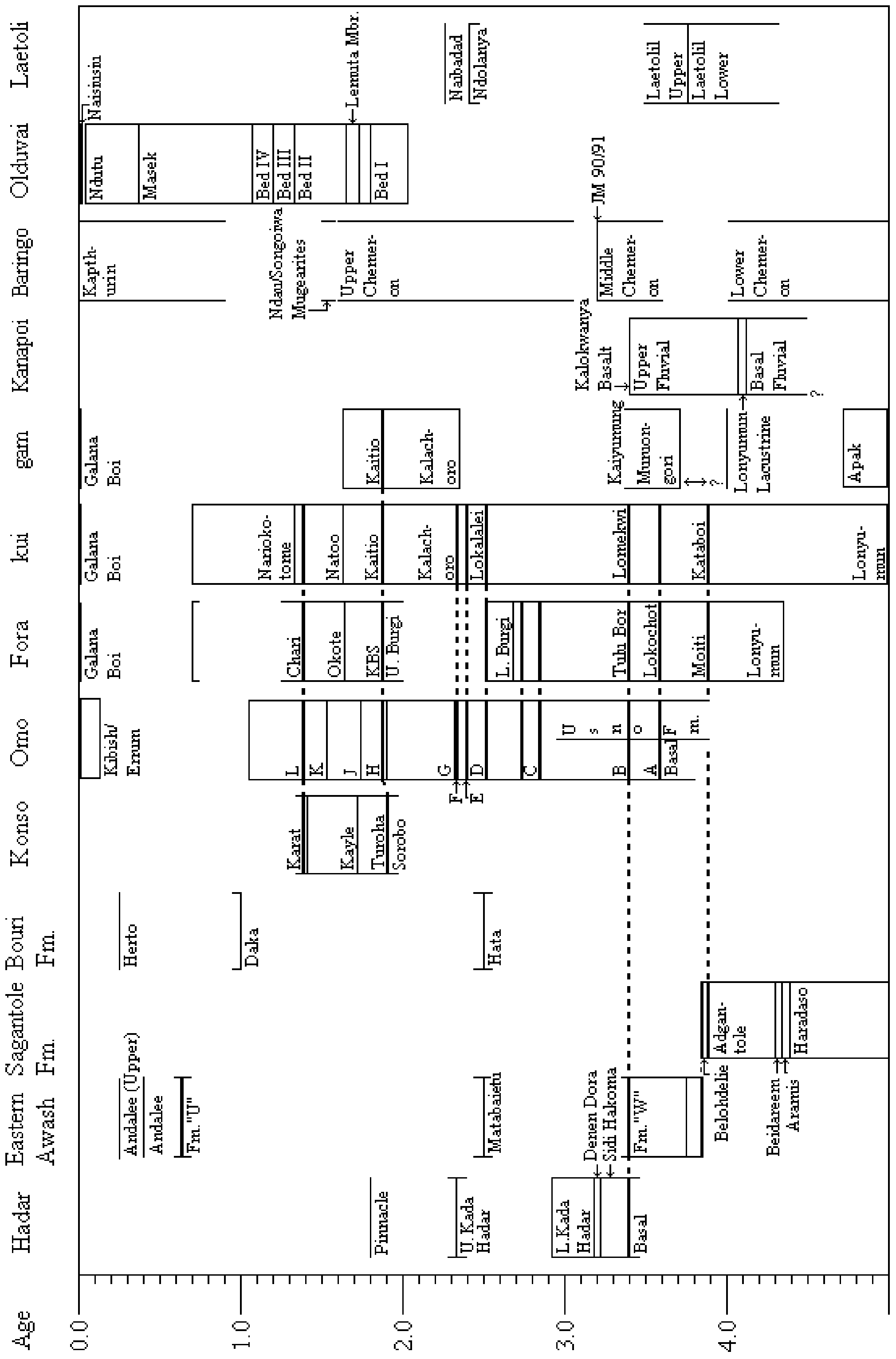


Figure 2.7 Chronostratigraphy of major East African Pliocene and Pleistocene Formations with Fossil cercopithecids. Only correlated tuffs are shown as bold lines. Correlations between formations are show with dashed lines. The names of members are shown in the figure. Formation names are shown at the top.



of Member B in the Shungura Formation and the Tulu Bor Tuff is at the base of the Tulu Bor Member). The Shungura Formation has a Basal Member, followed by Members A-L (skipping I). Each of these is further divided into several units denoted by an integer, e.g. G – 13 for the thirteenth Unit in Member G. This formation is relatively continuous and spans the time range from over 3.6 Ma through 1.05 Ma. There are very large cercopithecid samples from the upper part of Member B though the lower part of Member G. Above G – 13 and below B-10 samples are very small (Eck, 1976; Bobe, 1997). Deposition in the lower part of the formation was relatively continuous, and fluvial in nature, until G-13. While samples are large in this part of the Shungura Formation, depositional environments are relatively high energy and the fossil specimens are fragmentary, the majority being represented by isolated teeth (Bobe, 1997). In the upper part of Member G, sedimentary conditions are lacustrine. Then from G – 28 through L – 6 sedimentation is generally fluvial again, with the top of Member L being lacustrine (de Heinzelin, 1983).

Also in the lower Omo Valley is the Usno Formation. It is divided into 20 numbered sedimentary units. The top of Usno unit 6 (designated U-6) has been correlated with Tuff A (=Lokochot) and dates to 3.6 Ma, and U-10 has been correlated with Tuff B (=Tulu Bor, Sidi Hakoma), and is therefore 3.4 Ma. U-13 has been correlated to B-3 in the Shungura Formation, which paleomagnetic studies have correlated to the top of the Mammoth subchron, and therefore about 3.08 Ma (de Heinzelin, 1983). Most of the fossils from the Usno formation derive from U-12 and are therefore dated to between 3.4 and 3.08 Ma. The holotype of *P. quadratirostris* Iwamoto, 1982 was likely collected from Unit U-8 or 9 (Delson and Dean, 1993) and therefore dates to between 3.4 and 3.6 Ma.

The Koobi Fora Formation is divided into eight members, which are shown in Figure 2.7. Sedimentation in this formation is also relatively continuous, except for two large unconformities. One is in the middle of the Burgi Member accounting for approximately 500 Kyr, and informally divides this member into lower and upper parts. Another unconformity of approximately 500 Kyr duration is in the Chari Member below the Silbo Tuff (Brown and Feibel, 1986). The Lokochot Member has produced a small sample of fossil cercopithecids. Larger samples come from the Tulu Bor, the upper part of the Burgi, the KBS, and the Okote Members. At Allia Bay, a sizeable sample of cercopithecids was also recovered from the Lonyumun Member (Coffing et al., 1994). For most of the Koobi Fora Formation, sedimentary conditions were fluvial, but with brief lacustrine episodes common. There were also longer periods of lake conditions in the upper part of the Lokochot Member and for the duration of the Burgi Member above the unconformity (Brown and Feibel, 1986). This may have contributed to the relatively large number of more complete specimens and partial skeletons from the upper Burgi Member. The sequence above the KBS Tuff is generally characterized by more lateral variability than the lower part of the formation.

The Nachukui Formation is also divided into eight members, which are shown in figure 2.7. Only the Lomekwi Member has produced sizable samples of cercopithecids. It spans a long time interval, and is often divided into lower, middle and upper sections (Harris et al., 1988). The upper members of the formation have produced relatively small samples, all identifiable to *Theropithecus oswaldi* (Harris et al., 1988). The Lonyumun

Member is largely lacustrine. The lower part of the overlying Kataboi is generally fluvial, but with lacustrine conditions at the top that correlated with the transgression seen in the Lokochot. The Lomekwi Member is largely fluvial, with the more Western exposures (i.e. away from the lake) generally preserving more conglomerates. In the middle of Kalachoro Member, a major lacustrine event occurs. This is the same transgression as is preserved in the upper part of Member G in the Shungura Formation and in the upper Burgi Member of the Koobi Fora Formation. Above this event, there are generally alternating fluvial and lacustrine conditions in the Nachukui Formation. The Nariokotome Member, however preserves more volcaniclastic conglomerates, but also has several levels preserving stromatolites.

The different formations of the Omo group have been dated radiometrically and correlated to one another based upon tephrostratigraphy (see Brown, 1994). The ages and tephrostratigraphic correlations for the main formations of the Northern Turkana Basin are shown in figure 2.7 (taken from Brown, 1994; 1995) along with several other East African sites that have yielded fossil cercopithecids. The Konso stratigraphy and correlations are from Katoh et al. (2000). Asfaw et al. (1991) listed *Theropithecus* and *Papio* as being present at Konso. The stratigraphy of Lothagam is from Leakey et al. (1996), and the cercopithecids from Lothagam are described in Leakey et al. (in press). The stratigraphy for Kanapoi is taken from Leakey et al. (1995). The only published specimen is described by Patterson (1968) and discussed by Leakey and Delson (1987). Recent excavations have recovered a far larger sample of cercopithecids from Kanapoi, but this material has not been described. It is briefly summarized in Leakey et al. (1995). The stratigraphy for the Baringo Basin is from Hill (1995), but with some modifications from Gundling and Hill (2000). The cercopithecids from the Baringo Basin are best summarized in Gunding and Hill (2000). The stratigraphy from Laetoli is from Hay (1987) and Drake and Curtis (1987). Leakey and Delson (1987) described the fossil cercopithecids from Laetoli.

Chapter 3

Materials and Methods

Materials

The main objective of this thesis is the systematic description of a large sample of fossil cercopithecids, specifically those from the Middle Awash and Hadar in the Afar Depression of Ethiopia. In order to provide a basis of comparison, a systematic description of the fossil cercopithecids from the Turkana Basin is also presented. Therefore a brief description is given here of the different Afar fossil collections as well as those from the Turkana Basin.

The Afar Sample

This collection was made by several different research groups over a period spanning from 1972 to the present. The study sample includes only that material which was available as of 1999, and dated to less than 4.4 Ma. All of the fossil material collected from the Afar depression is housed at the National Museum of Ethiopia (NME). A sample of 2087 cercopithecid specimens from the Afar region were studied. This sample included 690 specimens from Hadar and surrounding areas that were collected by the International Afar Research Expedition (IARE) from 1972-1977; and from Hadar by the Institute of Human Origins (IHO) from 1990-1994. In 1975-1976 the Rift Valley Research Mission in Ethiopia (RVRME) collected 298 fossil cercopithecid specimens from the Middle Awash. The Middle Awash Research Project collected and catalogued 1099 specimens between 1981 and 1999, from sites dated to 4.4 Ma or younger.

The different collections at the NME are accessioned under different systems. All of the Hadar material follows the same numbering conventions. Each locality is assigned a number preceded by the letters “AL” which stand for “Afar Locality”. Within each locality, individual specimens are numbered sequentially. Thus, the colobine cranium and mandible from Leadu has the number AL2-34, because it is the 34th fossil from locality 2 (this specimen is associated with a partial skeleton, many of the elements of which have been assigned separate numbers, these are given in the description in chapter 4. However, as it represents a single individual it is generally referred to by the first number assigned). The stratigraphic positions of the IARE and IHO localities are shown by member on Table 3.1. The stratigraphic positions of many specimens are known to a specific unit within a given member, but this level of precision is not shown in the table. Where this affects the age estimation of specific fossils or taxa this is noted in the description in chapter 4.

The material collected by the RVRME follows a similar format, but the locality numbers are preceded by the letters “KL”. Originally they were only preceded by the letter “L” (see Kalb et al., 1982), but a “K” was added by the NME to distinguish these specimens from those collected by the American part of the International Omo Research Expedition. The stratigraphic positions of the different RVRME localities are shown in Table 3.1. These are based on the descriptions by Kalb et al. (1982c; Kalb, 1993).

The Middle Awash Research Project collections follow a different numbering system. They begin with a three-letter prefix, which specifies the drainage or area name from which they were collected, followed by a number for the specific locality within that area. This is then followed by an individual specimen number. Thus the specimen number for the holotype of *Pliopapio alemui*, ARA-VP-6/933 means that it was collected at Aramis locality 6, and was the 933rd specimen. The locality abbreviations used for this numbering system are given in Table 3.2 and the stratigraphic positions of the different localities are shown in Table 3.1.

Some of the Afar material has been referred to in various publications. Specimens of *Theropithecus oswaldi darti* from Hadar available prior to 1990 were described by Eck (1993). Other material from Hadar has been mentioned or figured in various reviews of the cercopithecid fossil record (Szalay and Delson, 1979; Delson, 1984; 1994) and included in several faunal lists (Taieb et al., 1976; Kimbel et al., 1996). Cercopithecids from the RVRME collections from various sites in the Middle Awash area have been briefly described in several publications (e.g. Kalb et al., 1980; 1982a; 1982b). The Middle Awash Research Project specimens from Aramis have been published (Frost, in press), and many of the others have been mentioned in various faunal lists (Clark et al., 1984, 1994; White et al., 1993; WoldeGabriel et al., 1994; de Heinzelin et al., 1999).

The Turkana Basin Sample

The Turkana basin sample used in this thesis, derives from four formations, and was collected by many different research groups. There are over 6,000 cercopithecid specimens from the Omo collections alone (Eck, 1977). From Koobi Fora, there are over 450 catalogued entries, but as a large number of these involve multiple elements or even partial skeletons, they account for approximately 2000 separate fossils (Bobe, pers com.). The Nachukui Formation collections include about 100 specimens (Harris et al., 1988).

All of the collections of the International Omo Research Expedition are housed at the NME. They were assigned specimen numbers under two systems. Material collected by the French contingent was accessioned under a system that combined the

Table 3.1 Stratigraphic positions for localities from different Afar collections. For ages of the different stratigraphic levels see chapter 2. Abbreviations used in the Middle Awash locality names are given in table 3.2. To save space, “-VP-“ has been removed from locality names. The stratigraphic position of the RVRME localities is taken from Kalb et al. (1982c) and Kalb (1993).

Stratigraphic Level	Middle Awash Locs.	RVRME Localities	Hadar Localities
U. Andalee		KL183	
Andalee		KL187-191	
Unit "U"	BOD1,DAW1,HAR1	KL6,272,279,281,286,337	
Pinnacle			AL532,537,539,551,552,558-560,563,571,577,578,601,603, 606,608
U. Kada Hadar			AL416,593,596,621,623,653, 666
Matabaietu Fm.	GAM1,MAT1-6,WIL2-3	KL1,5,11,13,16,18,19,22,29, 37-40,43-46,50,52,55,57,64, 65,74,75,142,157,231,232, 234,235,243,244, ?KL157	
Hata Mb.	BOU8,12,15		
Gerararu			AL18,74,99
Leadu			AL2
Kada Hadar			AL205,288,363,370,415,430, 437,438,444,526-528,685,693, 700
Denen Dora			AL55,56,58,113,116,118-120, 133,134,153,154,156,158,161-163,173,174,177,178,183,185-188,196,201,207,221,238,241, 269, 281,282,284-286,300, 304,307-310,315-319,321,322, 329,330,333,341,362,366,391, 392,414,426,431,433, 435, 486,487,545,604
Sidi Hakoma			AL52,108,109,112,126-129, 132,134,137,142-145,147,148, 165,166,175,193,198-208,211, 213,217,222,223,225,231,236, 237,244,248, 249,252,253,256, 259,266,270,277,280,289,327, 345,353,377,383,390,400,404, 406,411,412,422,445,465,468, 525,660
Ahmado			AL100
Basal			AL124,272,401-403
"W" Sub-SHT	BUN2,MAK1,MAT7, WEE5	KL123	
"W" VT-3/CT	BOD3		
Belohdelie Mb.	WEE1-2,WIL1	KL155	
Adgantole Mb.	ARA14		
Aramis supra DUVT	ARA15	KL221	
Aramis DUVT/WOBT	ARA2,11		
Aramis WOBT/DABT	ARA7		
Aramis DABT/GATC	ARA1,6,7,17,KUS2, SAG7		

Table 3.2 Three letter abbreviations used in catalog numbers and locality names of Middle Awash specimens.

Abbreviation	Area Name
ARA	Aramis
BOD	Bodo
BOU	Bouri
BUN	Bunketo
DAW	Dawaitoli
GAM	Gamedah
HAR	Hargufia
KUS	Kuseralee
MAK	Maka
MAT	Matabaietu
SAG	Sagantole
WEE	Wee-ee
WIL	Wilti Dora

locality number, which always began with “Omo”, followed by the year of collection and the individual specimen number. Individual specimen numbers were assigned in sequence for a given year. For example, the holotype of *Rhinocolobus turkanaensis* is Omo 75 ’69 1012, which was collected from the French locality Omo 75, in 1969 and was fossil number 1012 for that year. The American collections are numbered under a different system. Each locality was assigned a number preceded by a letter. This letter is typically an “L” for locality, but “W” and “B” were used for the White Sands and Brown Sands localities in the Usno Formation, and “F” or “P” were used if the specimens were collected by geological surveys. For each specimen then, the locality number is followed by an individual specimen number. For example, the specimen number for a well-known *T. brumpti* skull is L345-287, which is the 287th specimen from locality L345. Finally, there are nine cercopithecid specimens collected by Arambourg from the Omo Valley in the 1930’s, which are housed at the Museum National d’Histoire Naturelle, Paris, and are numbered OMO 001 through OMO 009.

The collections from Koobi Fora and West Turkana are both housed at the National Museums of Kenya (KNM), and are assigned accession numbers under a common system. Each begins with a two-letter code followed by the accession number. Specimens from Koobi Fora all begin with the letters “ER” (for East Rudolf as the region was formerly known) and those from the Nachukui Formation all begin with “WT” (for West Turkana). Specimens from Kanapoi follow the same system, but have the two-letter code “KP”. The specimen from the nearby site of Ekora uses the Kanapoi letters (KNM-KP 287).

Qualitative Data

All of the specimens from the Afar sample were identified as far as possible to anatomical element and to taxon. Often it was possible to identify specimens to species, or in the case of some *Theropithecus* specimens, to subspecies. Occasionally, this was possible entirely on the basis of the morphology preserved in a given specimen. In most cases, however, such identifications were based on the total sample. More fragmentary material was identified to species largely by association. For instance, at many sites there are isolated molars or gnathic fragments that can be definitively identified as *Theropithecus*, but can not be allocated to either *T. oswaldi* or *T. brumpti*. However, these would be identified to *T. oswaldi* in this case because all of the more complete diagnosable material represented this species, while none represented *T. brumpti*. On the other hand, large colobine teeth from levels dated to between 3.4 and 3.0 Ma were left unidentified to species because of the presence of two similarly-sized colobine species at these levels whose dentition are indistinguishable.

For each specimen, qualitative descriptions were made. In addition to a general anatomical description, notes were made of features relevant to either functional morphology or taxonomy, or that were otherwise outstanding, such as state of preservation. As a part of this qualitative description, all specimens were entered into a Microsoft Access database so that they could be quickly and easily referenced. This database includes fields for museum number, collection locality and stratigraphy, geologic age, anatomical element, taxonomic identification, whether it is associated with other elements, comments and citations. Catalogues were available for the Hadar and Middle Awash Research Project collections. This greatly speeded this step of the analysis. However, all specimens were studied and entered into the database whether catalogued or not.

For both documentation and publication purposes, digital photographs were made of a large sample of the material. These also facilitated comparison of material housed in different institutions while traveling during data collection, and for reference during write-up where casts were not available. The photographs were made using a Pixera Professional digital camera system (http://www.pixera.com/PixeraCatalog/Professional/Professional.html) mounted on a tripod and connected directly to a notebook computer. Standard 35 mm camera lenses of 28 and 50 mm focal length were mounted on the Pixera using a C-mount adapter. When mounted on the Pixera, these lenses were equivalent to 135 and 200 mm focal length. This meant that the camera was mounted at a relatively large distance from the photographed object, typically from 1 to 2 meters for an object of 10 to 20 cm in length. This minimized the distortion to the images caused by parallax, and facilitated a relatively large depth of field. In all photographs, a black velvet background was used where available. When this was not available, black cloth was substituted. The subjects were illuminated with two Lowell Tota-lites. All photographs were made with a centimeter scale in view. The scale was mounted at mid-height for the object being photographed.

Different elements were photographed in different orientations. Crania were generally photographed in lateral and dorsal views while aligned in the Frankfurt plane, and in ventral view perpendicular to the occlusal plane. Mandibles were photographed from occlusal and lateral views, and sometimes from anterior views. Proximal humeri were photographed in lateral view, while distal humeri were photographed in anterior and posterior views. Proximal femora were photographed in posterior view, as were distal tibiae. Other elements were photographed in non-standard views that attempted to maximize the amount of anatomy presented in a given photograph.

Quantitative Data

A number of different types of quantitative data were collected. These included both standard distance measurements made with calipers, and 3-d coordinate data. The caliper data were collected using needle-point Fowler digital calipers (read to 0.01 mm), with a PC serial port interface, and Fowler Software Wedge for Windows (T.A.L. Enterprises, 1991) that allowed input of measurements directly into standardized templates in Excel. This minimized errors due to data recording and entry, and also greatly enhanced the speed with which the data could be collected.

Caliper measurements were collected on teeth, mandibles, humeri, femora, and calcanei. For specific measurements collected, see tables 3.3-3.6. In general, these

Table 3.3 Dental measurements collected for this analysis.

Incisors and Canines	Measurement	Description
	Width	maximum bucco-lingual dimension
	Length	maximum mesio-distal dimension
	Height	crown height from cervix to apex, measured from buccal side
Upper Premolars		
	Width	maximum bucco-lingual dimension
	Length	maximum mesio-distal dimension
	Intercusp	distance between paracone and protocone
	Height	crown height from cervix to apex of paracone, measured on the buccal side
Lower Third Premolar		
	Width	maximum bucco-lingual dimension
	Length	maximum mesio-distal dimension, measured at the alveolar margin, does not
	Flange Length	distance from apex of protocone to the end of mesiobuccal flange
	Height	crown height from cervix to apex of protoconid, measured on the lingual side
Lower Fourth Premolar		
	Width	maximum bucco-lingual dimension
	Length	maximum mesio-distal dimension
	Intercusp	distance between protoconid and metaconid
	Notch Height	height of the lingual notch above the cervix
	Height	height of the metaconid above the cervix
Molars and Deciduous Premolars		
	Mesial Width	maximum bucco-lingual dimension across the mesial loph(id)
	Mesial Notch Width	maximum bucco-lingual dimension across the mesial loph(id), but taken at the height of the buccal notch for uppers and lingual
	Distal Width	maximum bucco-lingual dimension across the distal loph(id)
	Distal Notch Width	as for Mesial Notch Width, but taken across the distal loph(id)
	Length	maximum mesio-distal dimension
	Mesial Intercusp	distance between paracone and protocone on uppers, protoconid and metaconid on
	Distal Intercusp	distance between metacone and hypocone on uppers, hypoconid and entoconid on
	Buccal Intercusp	distance between paracone and metacone on uppers, protoconid and hypoconid on
	Lingual Intercusp	distance between paracone and hypocone on uppers, metaconid and entoconid on
	Notch Height	height of the notch above the cervix, buccal notch on uppers, lingual on lowers
	Height	crown height above the cervix to paracone apex on uppers, metaconid apex on lowers

Table 3.4 Measurements taken on humeri.

Measurement	Description
Length to Head	Maximum length from the capitulum to the proximal surface of the head
Length to Gtr. Tuberosity	Maximum length from the capitulum to the proximal surface of the greater tuberosity
Proximal ML	Maximum medio-lateral dimension of the proximal humerus including the tuberosities
Head ML	Maximum medio-lateral dimension of the articular surface of the head
Proximal AP	Maximum anterio-posterior dimension of the proximal humerus including the tuberosities
Head AP	Maximum anterio-posterior dimension of the articular surface of the head
Biepicondylar Breadth	Maximum medio-lateral width across the epicondyles
Distal Articular Breadth	Maximum medio-lateral width across the capitulum and trochlea
Trochlear Breadth	Maximum medio-lateral width of the trochlea
Trochlear Length	Maximum proximo-distal length of the medial trochlear flange
Distal Humeral Depth	Maximum anterio-posterior depth of the distal humerus at the capitulum
Olecranon Fossa Depth	Maximum medio-lateral width of the olecranon fossa
Brachioradialis to Capitulum	Length from the capitulum to the proximal end of the brachioradialis origin
Brachioradialis to Head	Length from the head to the proximal end of the brachioradialis origin
Midshaft ML	Maximum medio-lateral dimension of the midshaft
Midshaft AP	Maximujm anterio-posteiror dimension at the midshaft

Table 3.5 Measurements taken on femora.

Measurement	Description
Length to Head	Maximum length from the lateral condyle to the proximal surface of the head
Length to Grt. Trochanter	Maximum length from the lateral condyle to the proximal tip of the greater trochanter
Head AP	Maximum anterio-posterior dimension of the head
Head ML	Maximum medio-lateral dimension of the head
Head PD	Maximum proximodistal dimension of the head
Mediolateral width	Maximum medio-lateral dimension from the head to the lateral surface of the greater trochanter
Shaft ML	Maximum medio-lateral dimension of the midshaft
Shaft AP	Maximum anterio-posterior dimension of the midshaft
Bicondylar width	Maximum mediolateral dimension across both condyles
Distal Depth	Maximum anterio-posterior depth of the distal femur

Table 3.6 Measurements taken on calcanei.

Measurement	Description
Length	Maximum proximo-distal dimension
Proximal Length	Distance from the distal limit of the trochlea to the proximal tip of the tuberosity
Trochlear Length	Length of the trochlea
Distal Length	Distance from the proximal limit of the trochlear facet to the distal end of calcaneus

measurements follow those of Delson (1973). For dental specimens, the degree of wear was recorded for premolars, molars and deciduous premolars. For molars, wear on each of the four principal cusps is scored on a numeric scale from 0-4. An unworn cusp is scored as 0 and a cusp with all of the occlusal enamel is worn off is scored as 4. The values for the four cusps are then summed to yield a molar wear state from 0 to 16. The system for premolars works the same way, but as they only have two principal cusps they are on a scale from 0 to 8. Lower third premolars are not scored for wear. Delson (1973) provides further description and figures for the system of scoring dental wear.

E. Delson made available his database with equivalent caliper measurements on approximately 4000 specimens. These included several specimens previously measured by Delson from Hadar, the Middle Awash, the Omo, and Koobi Fora. For this study, all teeth that were adequately preserved from the Afar sample were measured. Additionally, comparative data were collected on several hundred extant and fossil specimens from many institutions during the course of this study (see acknowledgments for a list), yielding a combined comparative sample approaching 5000 specimens.

On relatively complete cranial remains three-dimensional coordinate data (landmarks) were collected using a Microscribe 3-DX digitizer (http://www.microscribe.com/aboutms3d/products.html) following a protocol described by Singleton (in press) and to be more thoroughly described by Frost et al. (in prep). Landmark coordinates were recorded directly into Microsoft Excel using a standard

Table 3.7 Cranial landmarks collected for all specimens. The number corresponds to the order in which they are collected, and matches those of Figure 2. *Landmarks numbered 30 and higher are collected in the ventral orientation, all others are collected in the dorsal orientation.

Number	Point	DEFINITION
MIDLINE		
1.	Inion	Most posterior point of cranium, when viewed in the Frankfurt horizontal, be it on sagittal/nuchal crest or not
2.	Bregma	Junction of coronal and sagittal sutures, on sagittal crest if necessary
3.	Glabella	As viewed in Frankfurt horizontal
4.	Nasion	Fronto-nasal suture in midline
5.	Rhinion	Most anterior point in midline on nasals (i.e. “end” of the nasals).
6.	Nasospinale	Inferiormost midline point of piriform aperture.
7.	Prosthion	Anteroinferior point on projection of premaxilla between central incisors.
30.*	Opisthion	Posterior most point of foramen magnum.
31.	Basion	Anterior most point of foramen magnum.
32.	Staphylion	Midline point on palate on line tangent to anteriormost points on choanae
33.	Incisivion	Midline point at the anteriormost point of the maxilla (=posterior end of the incisive foramen),extrapolated if broken or asymmetrical
BILATERAL (Rgt/Left)		
8./19.	Prosthion2	Antero-inferiormost point on pre maxilla, equivalent to prosthion, but between central and lateral incisors
9./20.	Premax-max superior	Where premaxillo-maxillary suture meets nasal bone, or aperture, if it does not continue to the nasal bone
10./21.	Zygo-max inferior	Anteroinferior point of zygomaticomaxillary suture, in antero-lateral view
11./22.	Zygo-max superior	Anterosuperior point of zygomaticomaxillary suture (taken at orbit rim)
12./23.	Dacryon	Junction of frontal, lacrimal and maxilla
13./24.	Mid-torus inferior	Point on inferior margin of supraorbital torus (superior margin of orbit) roughly at middle of orbit
14./25.	Mid-torus superior	Superior to MTI on superior most point of spraorbital torus when viewed in Frankfurt horizontal (see Line I)
15./26.	Frontomalare orbitale	Where frontozygomatic suture crosses the inner orbital rim.
16./27.	Frontomalare temporale	Where frontozygomatic suture crosses lateral edge of zygoma (LEZ) if suture isn’t straight, project course of middle third laterally to LEZ
17./28.	Porion	(in Frankfurt horizontal--defines) top of auditory meatus
18./29.	Zygo-temp superior	Superior point of zygomatico-temporal suture on lateral face of zygomatic arch
34./40.	Postglenoid	Tip (or midpoint of area)
35./41.	Zygo-temp inf	Inferolateral point of zygomaticotemporal suture on lateral face of zygomatic arch
36./42.	Distal M3	Distal midpoint projected (laterally) onto alveolar margin
37./43.	M1-2 contact	Projected (laterally) onto alveolar margin.
38./44.	Mesial P3	Most mesial point on P3 alveolus, projected onto alveolar margin
39./45.	Premax-max inf	Where premaxillomaxillary suture crosses alveolar margin

template. For each specimen 45 standard craniometric landmarks were recorded in the form of three-dimensional coordinate data. For a list and descriptions see table 3.7.

Data was collected in two separate views, each with the specimen mounted in a fixed position relative to the digitizer. In the first view, the specimen is mounted in approximately the Frankfurt Horizontal. The first 29 landmarks were collected from the dorsal aspect of the specimen while mounted in this position. The specimen was then turned over and remounted ventral side up, with the occlusal plane approximately horizontal. The remaining sixteen of the landmarks were collected from the ventral aspect of the cranium. These orientations used were chosen for convenience during data collection and do not affect subsequent analysis, because the data are later reoriented during the generalized procrustes analysis.

Four additional registration points were collected in both the dorsal and ventral orientations. Because the landmarks were collected with the specimen mounted in two different positions, the 29 landmarks from the dorsal aspect of the cranium are in a separate coordinate system from those collected on the ventral aspect. The registration points were used to align data collected in the ventral position onto the same coordinate system as those collected in the dorsal position (i.e. the dorsal and ventral halves are “fit” together into a “complete” landmark configuration). This was accomplished by applying a least squares superimposition of the four ventral orientation points onto the four dorsal points.

These complete, “registered” configurations were combined with a database collected during this study and by the NYCEP morphometrics group, to yield a complete cranial data set of 1442 cercopithecid specimens from both extant subfamilies and all six of the subtribes described in Chapter 2. A generalized procrustes analysis (GPA) (Dryden and Mardia, 1998) was performed on this data set using Morpheus (Slice, 1998). Centroid sizes from this analysis were stored, along with the superimposed coordinates, in two forms, one with all specimens scaled to unit centroid size and another with the original size of each specimen retained. Centroid size is a unitless measure. It is defined as the square root of the sum of squared distance of each landmark to their centroid (Dreyden and Mardia, 1998).

Centroid sizes were used to estimate overall cranial size for comparative purposes and in species description. Chord distances between various combinations of landmarks were computed using the Pythagorean theorem (i.e. $d^2 = (x_1-x_2)^2 + (y_1 - y_2)^2 + (z_1-z_2)^2$). Distances could then be easily compared among specimens or taxa. When distances are used in the text, the pairs of landmarks are described. These chord distances should be equivalent to caliper measurements, but were not used in combination with caliper measurements for this study. Multivariate analysis of the coordinate data will be the subject of later work, and is not included in this thesis.

Most of the quantitative analyses used in this thesis were performed using SAS version 8.0 (SAS Institute, 1999; http://www.sas.com/products/sassystem/index.html). Caliper data were loaded directly into SAS from the Excel spreadsheets, and the coordinate data were loaded from text files. In SAS chord distances and ratios were computed as well as means, ranges, ANOVAs, regressions or other computations as needed during systematic descriptions and comparison.

Chapter 4

Systematic Paleontology of the Afar Cercopithecidae

The Pliocene and Pleistocene sample of fossil Cercopithecidae from the Afar Depression of Ethiopia is the largest in East Africa outside of the Turkana Basin. As described in chapter 3, the sample included in this study consists of over 2,000 specimens spanning a time range from 4.4 Ma through ~0.25 Ma. The geology of the Afar Basin and the strata from which this sample derives have been described in chapter 2.

The only specimens from the Afar region of Ethiopia that have been described in detail is the sample of *Theropithecus oswaldi darti* from Hadar (Eck, 1993) and the recently described species from Aramis (Frost, in press). The other Hadar monkeys have been discussed in a number of review articles by Delson (Szalay and Delson, 1979; Delson, 1984; 1994; 2000). The material from Aramis, Wee-ee, Maka, Bouri, Matabaietu, Makaamitalu, Bodo, and Andalee has been included in species lists and summary descriptions (Kalb et al., 1980; 1982a; 1982b; White et al., 1993; Clark et al., 1994; WoldeGabriel et al., 1994; Kimbel, et al., 1996; de Heinzelin et al., 1999). By and large, however, this material is undescribed. This chapter describes all of the material that was available during my data collection in 1999.

In the discussion to follow, range data are provided, in Ma. The first range listed is the range for confidently assigned specimens only. Following this range, a second range in parentheses may be provided if there is tentatively allocated material that would extend the known range. Additionally, the range based on the Afar material is provided if it differs from the total range. If no separate listing is given, then the Afar range is identical to the overall known range of the taxon.

Family Cercopithecidae Gray, 1821

Subfamily Cercopithecinae Gray, 1821

Tribe Cercopithecini Gray, 1821

Genus *Cercopithecus* Linnaeus, 1758

(= or including *Lasiopyga* Illiger, 1811. *Cercocephalus* Temminck, 1853. *Petaurista* Reichenbach, 1862. *Diademia* Reichenbach, 1862. *Mona* Reichenbach, 1862. *Chlorocebus* Gray, 1870. *Cynocebus* Gray, 1870. *Diana* Troussart, 1878. *Rhinostictus* Troussart, 1897. *Otopithecus* Troussart, 1897. *Pogonocebus* Troussart, 1897. *Allochrocebus* Elliot, 1913. *Insignicebus* Elliot, 1913. *Melanocebus* Elliot, 1913. *Neocebus* Elliot, 1913. *Rhinostigma* Elliot, 1913.)

Type species: *Cercopithecus diana* Linnaeus, 1758

Other included species (following P. H. Napier, 1981): *C. aethiops* Linnaeus, 1758; *C. cephus* Linnaeus, 1758; *C. nictitans* Linnaeus 1766; *C. mona* Schreber, 1774; *C. petaurista* Schreber 1774; *C. ascanius* Audebert, 1799; *C. mitis* Wolf, 1822; *C. pogonias* Bennett, 1833; *C. campbelli* Waterhouse, 1838; *C. erythrotis* Waterhouse, 1838; *C. erythrogaster* Gray, 1866; *C. neglectus* Schlegel, 1876; *C. wolfi* Meyer, 1891; *C. preussi* Matschie, 1898; *C. lhoesti* Sclater, 1899; *C. hamlyni* Pocock, 1907; *C. denti* Thomas, 1907; *C. dryas* Schwartz, 1932; *C. salongo* Thys van den Audenaerde, 1977.

Generic diagnosis:

A highly speciose genus of small African cercopithecins, generally larger than *Miopithecus* and smaller than *Erythrocebus*. It is distinguished from *Miopithecus* and *Allenopithecus* by a lack of female sexual swellings during oestrus. The neurocranium is less elongate than that of *Erythrocebus* and lacks the slope from the foramen magnum to the choanae. The molars lack basal flare, which is similar to other cercopithecin genera, but different from *Allenopithecus*. The postcranium lacks the specializations for terrestriality seen in *Erythrocebus*. The tail is always longer than head and body length, also unlike *Erythrocebus*.

Cercopithecus sp. indet.

(= or including *Cercopithecus* cf. *aethiops* Kalb, 1982a)

Afar specimens included: see appendix 1.

Range: ~3.3 Ma- Recent

Afar range: ~0.4-0.25 Ma

Distribution: <u>Asbole</u>; <u>Andalee Mbr., Wehaietu Fm.</u>; Members B, C, G, J, Shungura Fm.; Usno Fm.; KBS Mbr., Koobi Fora Fm.; Kanam East; Taung, Upper.

Description:

All of the material assigned to this taxon comes from the sites of Andalee (KL187-KL191) and Issie (KL183), which are within the lower and upper parts of the Andalee Member of the Wehaietu Formation respectively (Kalb et al., 1982a; 1982c). The material from Andalee has been discussed briefly by Kalb et al. (1982a). Cranial material is represented by a few relatively complete maxillary specimens. KL191-87 (see plate 1) is a left maxilla and lower face of a female with the complete left dentition, except for the tip of the canine. KL191-174 is a right maxilla and anterior portion on the zygomatic bone with P^4-M^2. The inferior orbital rim, lateral surface of the rostrum, and a small portion of the palatal process are preserved. There are 14 additional partial maxillae (appendix 1).

In both cranial and dental size, this species is in the larger end of the size range of *C. aethiops*, and several other species of *Cercopithecus*. It is larger than *C. ascanius* and *C. nictitans.* It is substantially larger than *Miopithecus talapoin* and smaller than *Erythrocebus patas*. Dental dimensions are given in table 4.1.

Maxilla

Overall, the preserved morphology of the face is similar to that of *Cercopithecus aethiops*, but also to most other species of *Cercopithecus*, which are not strongly differentiated from one another in their cranial morphology. The infraorbital region in KL191-174 preserves three infraorbital foramina. As is typical of all Cercopithecini, other than *C. lhoesti* and some *C. nictitans* (personal observation), both males and females lack maxillary ridges. Both postcanine and suborbital fossae are also absent. What is preserved of the rostral profile is therefore smoothly curving, and rather tall. The muzzle dorsum is not preserved, but based on what is present they would have been arched in cross-section and not flattened. This is similar to most species of *Cercopithecus*, but distinct from *C. lhoesti*.

Table 4.1 Summary dental dimesnions for *Cercopithecus* sp. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.18. For descriptions of measurements see chapter 3.

	Cercopithecus sp. Andalee												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^1	3	4.5	0.1	4.4	4.6	6.3	1.5	5.1	8.0	5.0	0.4	4.6	5.5
P^3	2	4.3	0.6	3.9	4.8					3.6	0.2	3.4	3.7
P^4	5	5.2	0.5	4.7	5.9					4.4	0.4	3.9	5.0
M^1	8	5.7	0.3	5.1	6.1	5.2	0.5	4.2	5.5	6.0	0.3	5.5	6.4
M^2	7	6.6	0.4	6.0	7.1	6.1	0.4	5.7	6.7	6.8	0.3	6.5	7.4
M^3	3	5.8	0.7	5.4	6.6	4.7	0.6	4.2	5.4	6.1	1.0	5.3	7.2
M^x	1					5.9				6.7			
dP^3	2	4.1	0.3	3.8	4.3	3.9	0.1	3.8	3.9	5.3	0.0	5.3	5.3
dP^4	2	4.8	0.5	4.4	5.2	4.5	0.4	4.2	4.8	5.4	0.4	5.1	5.7
I_1	5	4.0	0.2	3.8	4.3	5.2	1.5	3.9	7.8	3.2	0.2	3.0	3.4
I_2	6	3.9	0.2	3.6	4.1	5.0	0.9	4.2	6.7	3.2	0.3	2.7	3.7
C_1 (?)	2	5.0	0.7	4.5	5.5	7.0				3.4	0.3	3.2	3.6
C_1 (?)	2	6.5	1.7	5.3	7.7	10.0				5.3	0.5	5.0	5.7
P_3 (?)	3	3.1	0.2	2.9	3.4	6.6	0.5	6.0	7.0	4.9	0.4	4.4	5.2
P_3 (?)	3	3.5	0.5	3.0	4.0	9.9	0.9	9.3	11.0	5.7	1.3	4.7	7.3
P_4	11	4.1	0.7	3.5	5.4					5.0	0.5	4.2	6.1
M_1	11	4.8	0.2	4.3	5.2	4.9	0.3	4.4	5.4	5.9	0.5	4.8	6.9
M_2	14	5.8	0.6	4.7	6.6	5.6	0.5	4.8	6.2	6.5	0.5	5.7	7.2
M_3	14	5.5	0.5	5.0	6.8	4.7	0.6	4.0	5.8	6.5	0.6	5.9	8.5
M_x	1	5.0				3.9							

As expected for a cercopithecine of this size, the rostrum is short, but relatively longer than that of most similarly sized colobines. It is also shorter than that of *Erythrocebus*, and slightly shorter than that of *Allenopithecus*. The premaxillae project relatively far anteriorly and there is a modest diastema between the lateral incisor and the canine. Only a small portion of the piriform aperture is preserved on KL191-87. It probably was oriented at an angle of about 45° relative to the occlusal plane, but there is a lot of error in this estimate due to the fragmentary nature of the specimen.

The maxillary dental arcade is roughly parabolic in shape even in males, with the incisors extending in an arc well anterior to the canine. The M^2 is typically the most laterally placed tooth. The M^3 is typically medial to M^2, especially when the buccal margins are compared. The canine bulges slightly lateral to the P^3 in females, and a bit more so in males. In lateral view, the anterior portion of the dental arcade curves superiorly, making its profile markedly convex-down.

Zygomatic region

The anterior surface of the zygomatic process is positioned above the distal M^1 or mesial M^2 in most specimens, and is generally more distal in males. This position is similar to that of other guenons, but significantly more anteriorly placed relative to *Erythrocebus* and most papionins. The anterior surface of the zygoma does not jut out laterally, but instead curves smoothly posteriorly and laterally away from the maxilla. It is unmarked by suborbital fossae. The inferior border is often slightly posterior to the inferior orbital rim.

Mandible

There are 23 mandibular fragments of *Cercopithecus* sp. from Andalee and Issie (appendix 1), the most complete of these, which formed the basis of the description below, are: KL191-58 (see plate 1) a nearly complete mandible of a male individual, glued at the symphysis. It preserves the anterior part of the right ramus, a small piece of the left, the entire inferior margin of the corpus, and the left P_3-M_3 and right C-P_3,M_{2-3}. KL183-7 is a right corpus fragment of a male individual preserving from the symphysis to the M_2, with the P_4-M_2. The margin is largely present but crushed. KL191-106 is a laterally crushed male mandible with the left P_4-M_3 and right I_1-P_3. The inferior margin is present except below the left M_{2-3}. Left P_4-M_3 are preserved as are the right I_1-P_3. KL188-7 is a right corpus fragment of a male individual preserving from the symphysis posteriorly to below the M_2; the P_3-M_2 are preserved. The most compete female specimen is KL191-105 (plate 1) a right corpus fragment with P_3-M_3. KL183-6 is most of the right corpus and a small part of the ramus of a female individual, it is edentulous except for the M_{2-3}. KL191-86 is a symphyseal fragment of a female preserving the left canine through the damaged right canine.

The symphysis is long, sloping and forms a smoothly curving arc in profile view. The slope is similar to most species of *Cercopithecus*, including *C. aethiops*. Relative to the rest of the corpus, the symphysis is quite deep. Mental ridges are faint or absent, and a median mental foramen is present. The incisive alveoli are slightly proclined, which is typical of *Cercopithecus*. The plenum alveolare is short, extending posteriorly only to the middle of the P_3, and slopes steeply posteroinferiorly. The inferior transverse torus is also only modestly developed. It extends further posteriorly than the superior, typically to the middle of P_4.

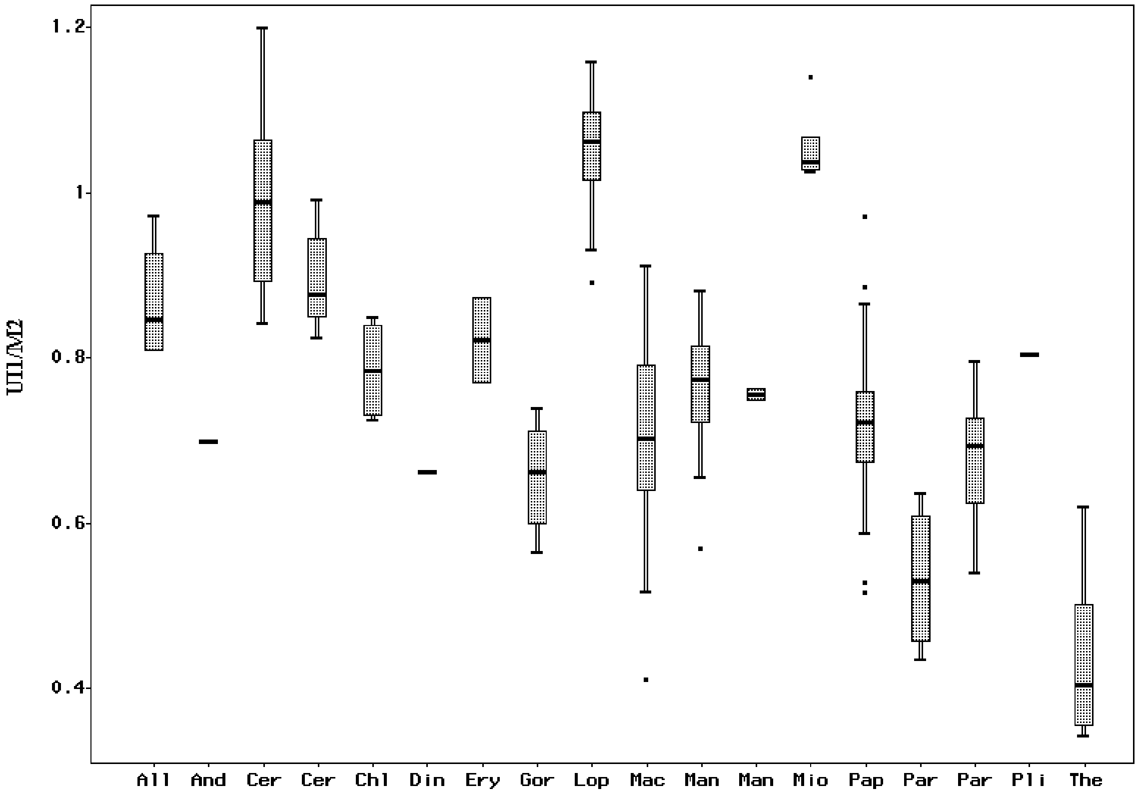
As for most species of *Cercopithecus*, the corpus is shallow, but relatively deeper than that of *Erythrocebus*. It is deepest at the posterior limit of the symphysis, roughly below the premolars. It then shallows considerably posterior to this, until about the M_3. The lateral surface of the corpus lacks fossae, or in some males has slight fossae. In superior view, the oblique line merges with the corpus at approximately the level of M_2 and a modest extramolar sulcus is present.

The anterior border of the ramus slopes more posteriorly than it does in most modern *Cercopithecus*, but less so than in *Colobus*. In lateral view there is often a retromolar gap. The ramus is relatively short in height, and the coronoid process is tall. The attachment for the masseter muscle is only weakly developed. There appears to have been a fairly deep triangular fossa on the lateral surface of the ramus. The gonial region is not expanded.

Dentition

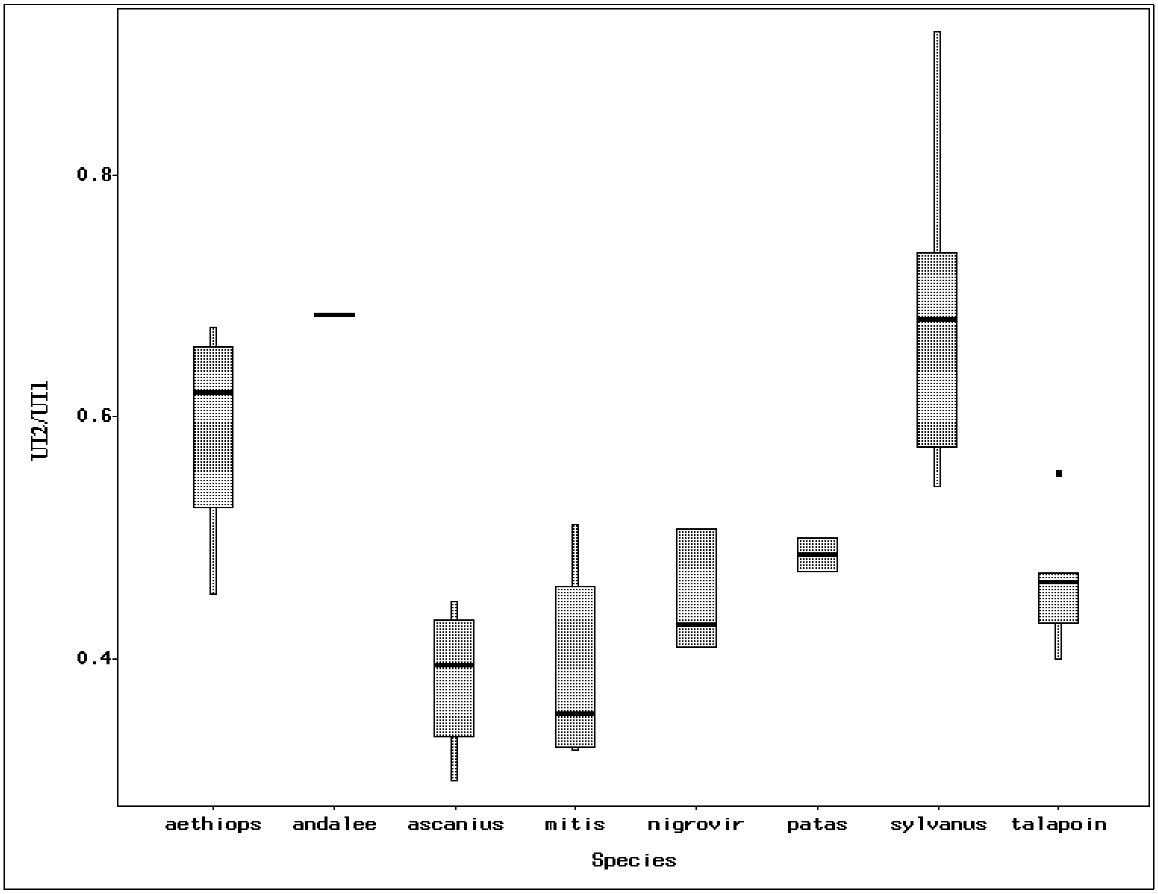
The morphology of the upper incisors is typical for the subfamily. The I^1 crown is spatulate and lacks a lingual cingulum. In anterior view, it is broad and flaring. Relative to the size of the molars it is similar to most papionins and *C. aethiops*, but smaller than in other species of *Cercopithecus* (see figure 4.1). The I^2 is more asymmetrical and its crown tilts mesially. The I^2 is also significantly shorter, mesiodistally, than the I^1. In this characteristic the guenon from Andalee is similar to *C. aethiops*. The I^2 is, however, significantly broader relative to the I^1 than in other species of *Cercopithecus* and *M. talapoin* (see figure 4.2). The lower incisors are typical for the subfamily, being relatively tall and narrow in anterior view, and less flaring than the uppers. They lack lingual enamel. The I_2 is more asymmetrical than the I_1. The labial surface is curves more tightly distally than that of the I_1 and the lateral border slopes more mesially.

Figure 4.1 Length of the I^1 vs. Mesial Width of the M^2. The central bar represents the median, or 50th percentile. The bottom and top of each box represent the value at the 25th and 75th percentiles respectively, and the whiskers extend to the farthest observation that is less than 1.5 times the length of the box. Any individuals outside of the whisker range are marked separately. Genera are shown on the X-Axis as follows: All = *Allenopithecus*, And = *Cercopithecus sp.* from Andalee; Cer = *Cercopithecus*, Chl = *C. aethiops*, Din = *P. (Dinopithecus)*, Ery = *Erythrocebus*, Gor = *Gorgopithecus*, Lop = *Lophocebus*; Mac = *Macaca*, Man = *Mandrillus*, Mng = *Lophocebus* sp. nov. from Koobi Fora, Mio = *Miopithecus*, Pap = *Papio (Papio)*, Pdo = *Paradolichopithecus*, Par = *Parapapio*, Pli = *Pliopapio*, The = *Theropitehcus*.



As is typical for cercopithecins, the canines of the females are similar to males of other cercopithecids. The uppers have a large mesial groove that extends to the root. The lowers are prominent above the incisors and premolars. They do, however, differ in size between the sexes, with the male canines being larger than those of the females.

Figure 4.2. Length of the I^2 / I^1. Boxes and whiskers as for figure 4.1. X-Axis shows species as follows: aethiops = *Cercopithecus aethiops*; andalee = *C. sp.* Andalee; ascanius = *C. ascanius*; mitis = *C. mitis*; nigrovir = *Allenopithecus nigroviridis*; patas = *Erythrocebus patas*; sylvanus = *Macaca sylvanus*; talapoin = *Miopithecus talapoin*.



The upper premolars are of the typical bicuspid morphology. The protocone of the P^3 is small relative to the paracone, being significantly shorter and smaller in area. The P^4 is much more quadrate in occlusal view, and occasionally develops a third distal cuspule in the position of a hypocone. The P_3 is sexually dimorphic as in most cercopithecids. As is typical of the tribe, the mesiobuccal flange is relatively long in the females when compared to that of papionins. The mesiobuccal flange is also more inferiorly oriented than it is in most papionins. The talonid is small relative to the large protoconid. The P_4 is relatively narrow, and more molariform with a well-developed talonid.

The molars are bilophodont as is typical of the family. They crowns are only modestly flaring, and relatively elongate. The M^3 is relatively small in comparison to the others, and is strongly reduced distally. On some specimens (e.g. KL191-174) all four cusps wear evenly, in a manner similar to *Cercocebus* and *Mandrillus*. As is typical for the tribe, the M_3 lacks a hypoconulid, and is relatively small in comparison to the M_2. Of the deciduous dentition, only the upper premolars are known. They are similar to the molars, but are relatively narrower, more flaring, and have weakly developed cross-lophs. The dP^3 has a well-developed paracone, and the distal lophid is significantly wider than the mesial. The dP^4 is similar to the M^1, but has a relatively wider distal lophid.

Postcrania

There is a sizeable sample of postcranial material from Andalee and Issie. *Colobus* sp. from these sites is larger than the species of *Cercopithecus*, but they are close enough in size to make many elements difficult to identify on this basis. As a result, out of the postcranial sample, only two distal humeri, and more tentatively one proximal femur, can be allocated to *Cercopithecus*. This is possible, because there do appear to be morphological differences in some elements. There is a set of slightly smaller, but more (semi-) terrestrially adapted material, that is here tentatively allocated to *Cercopithecus*. Only these elements are discussed below.

Humerus

There are two distal humeral fragments that probably represent this species. KL191-83 is the distal end of a right humerus, and KL191-469 is a trochlear fragment of a right humerus. They are both within the size range of modern *C. aethiops* and significantly smaller than the humeri assigned to *Colobus*. They are morphologically distinctive as well. The medial epicondyle is relatively short, and more retroflexed than in *Colobus*. As a result, the articular area is wide relative to biepicondylar breadth. The capitulum is prominent and relatively spherical. The zona conoidea is not pronounced. The medial trochlear flange is relatively long and sharply delimited.

Femur

KL188-45 the fragmentary proximal end of a left femur. While the head and neck are preserved, the greater trochanter is broken immediately superior to the lesser trochanter. The head is substantially smaller than other femora from Andalee (see section for *Colobus*). The fovea capitis is more elongate and oval in outline than those of the other femora which are more circular, a feature more common in *Cercopithecus* than *Colobus* (Krentz, 1993). The neck appears to be longer and less superiorly oriented than are those of other femora from this sample assigned to *Colobus* (unfortunately measurement of KL188-45 was not possible due to damage). The lesser trochanter is more prominent than in the other femora from this site.

Remarks

The species of *Cercopithecus* are well known for their homogeneity of cranial and dental form, making diagnosis of fossil material exceptionally difficult. In several features, however, the series from Andalee and Issie show features consistent with *C. aethiops* and distinct from other species. None of these are diagnostic alone, but together they form a pattern that strongly suggests this series is *C. aethiops*. These include the I^1 being smaller relative to the molars and the I^2 being larger relative to the I^1 than in other species of *Cercopithecus*. Also the even wear pattern on the upper molars occurs in *C. aethiops*, but not in other species. Finally, if the postcrania are correctly allocated, they show a degree of terrestrial habitats found only in *C. aethiops* and the *C. lhoesti* group (Gebo and Sargis, 1994). However, the presence of cranial differences from *C. lhoesti* such as the lack of maxillary ridges or fossae in the Andalee males, and the relatively large I^2, implies that the Andalee species is not *C. lhoesti*.

Cercopithecins are comparatively rare in the fossil record (Szalay and Delson, 1979; Leakey, 1988) with only 12 specimens described from the Omo, and 3 from Koobi Fora (Eck, 1987; Leakey, 1976; 1988). Fossil *Cercopithecus* is also known from Kanam East (Harrison and Harris, 1996), Late Pleistocene deposits at Olduvai and Loboi (Leakey, 1988), and an apparently Late Pleistocene level at Taung . They are also known within the Afar basin from the site of Asbole (Alemseged and Geraads, 2001). The sample from Andalee is important as it is the largest known to date from the Pleistocene and perhaps documents the occurrence of an extant species.

Tribe Papionini Burnett, 1828

Genus *Pliopapio* Frost, 2001

(= or including *Parapapio* Jones, 1937: WoldeGabriel et al., 1994, in part)

Type species: *Pliopapio alemui* Frost, 2001

Generic diagnosis:

A genus of African papionin, distinguished from *Parapapio, Lophocebus,* and *Cercocebus* by the presence of a clear anteorbital drop, though this is not as distinct as in most *Papio* and *Mandrillus*. In this aspect, its profile is most similar to that of *Macaca*, but *Pliopapio* has a relatively longer muzzle. It is different from *Papio (Papio), Gorgopithecus*, *Lophocebus*, *Cercocebus* and *Mandrillus* in that the muzzle lacks postcanine and suborbital fossae. The absence of maxillary ridges distinguishes it from *Papio, Theropithecus (Omopithecus)* and *Mandrillus*. The muzzle dorsum is saddle-shaped, and rounded in paracoronal section. In these aspects it is similar to *Theropithecus oswaldi* (*sensu* Leakey, 1993, as will be used throughout this analysis), but unlike the flattened dorsum and squared paracoronal section found in *Papio* (including *Dinopithecus*) and *Mandrillus*. Relative to neurocranial breadth, the rostrum is narrow in comparison with those of all known African papionins, though it is in the lowest end of variation for *Papio, Mandrillus* and *Macaca*. Crushing in the anterior portion may contribute to this impression, but cannot account for it entirely.

Unlike the case in *Parapapio*, *Cercocebus*, and *Lophocebus*, the cranial vault is separated from the brow ridges by a distinct ophryonic groove. The temporal lines in the holotype male remain widely separated and do not form a sagittal crest as opposed to the situation in *Theropithecus*, *Gorgopithecus, Papio (Dinopithecus)*, and *Paradolichopithecus*.

While the mandibular symphysis is shallower and more sloping in profile than that of most papionins, it is shorter and more rounded than that of *Parapapio ado* (from Laetoli and Kanapoi) or the small papionin from the Nowata Formation at Lothagam. In these latter taxa the symphysis is even longer and more sloping with the incisive alveolar process projecting more anteriorly, producing a more procumbent incisor row. Corpus fossae are absent, distinguishing it from most *Papio (Papio)* (*P. h. kindae* females have very slight fossae, and some *P. izodi* lack them), *Gorgopithecus, Theropithecus (Omopithecus)*, *Mandrillus*, *Lophocebus* and *Cercocebus*.

The molars are higher-crowned, more straight-sided, and less flaring on average than those of *Papio*, *Macaca* and *Lophocebus*, and far less so than those of *Mandrillus* or *Cercocebus*. As in most papionins, but unlike *Mandrillus* and *Cercocebus,* the premolars are not particularly large relative to the molars. The mandibular incisors are nearly vertically implanted, whereas those of *Parapapio ado* from Laetoli and Kanapoi are more procumbent.

Pliopapio alemui Type species

(= or including cf. *Parapapio* sp.: WoldeGabriel et al., 1994)

Holotype: NME ARA-VP-6/933 from the Aramis Member of the Sagantole Formation between the DABT and GATC tuffs.

Afar specimens included: See appendix 2.

Range: 4.4 - 4.2 Ma (4.4 – 3.75 Ma)

Distribution: <u>Aramis, Adgantole Mbs., Sagantole Fm</u>.

Specific Diagnosis: As for genus.

Description:

The most complete specimen is the holotype male skull ARA-VP-6/933 (see plates 2-3). The mandible is attached to the cranium by a thin layer of matrix that prevents the two from being safely separated. Therefore, the palate and much of the cranial base are not available for observation. Of the main cranial regions, only the left zygomatic is completely missing. The right orbit is damaged and lacks much of the right half, except for one triangular portion around the zygoma. The right zygomatic arch is mostly present, but crushed, missing only the region around the temporojugal suture. The right maxilla and mandible are weathered, revealing the roots of the teeth. The other cranial specimens are all considerably more fragmentary. ARA-VP-6/437 (see plate 4) is a partial right male maxillary fragment with the dorsal surface up to the piriform aperture, the roots of the canine and fourth premolar, and complete central incisor and third premolar. ARA-VP-1/1723 (plate 4) is a partial right female maxilla preserving the canine through third molar. ARA-VP-1/1007 (plate 4), is a slightly crushed left female premaxillomaxillary fragment with the rostral surface preserved nearly to the lateral border of the piriform aperture, a damaged lateral incisor, and complete canine through first molar.

Pliopapio alemui is smaller in cranial size than all known *Theropithecus* and *Papio*, other than *P. hamadryas kindae*, *P. izodi* and *P. angusticeps* to which it is similar in size. It is slightly larger than all but the largest *Macaca*, such as *M. thibetana* and *M. nemestrina*. In dental size, it is marginally smaller than *Parapapio ado* from Laetoli and Kanapoi, and similar to specimens from Ekora, the Lomekwi Member of the Nachukui

Formation, the Tulu Bor Member of the Koobi Fora Formation, and Unit 2A of the Chiwondo beds. Dental dimensions for *P. alemui* are listed in table 4.2.

Rostrum

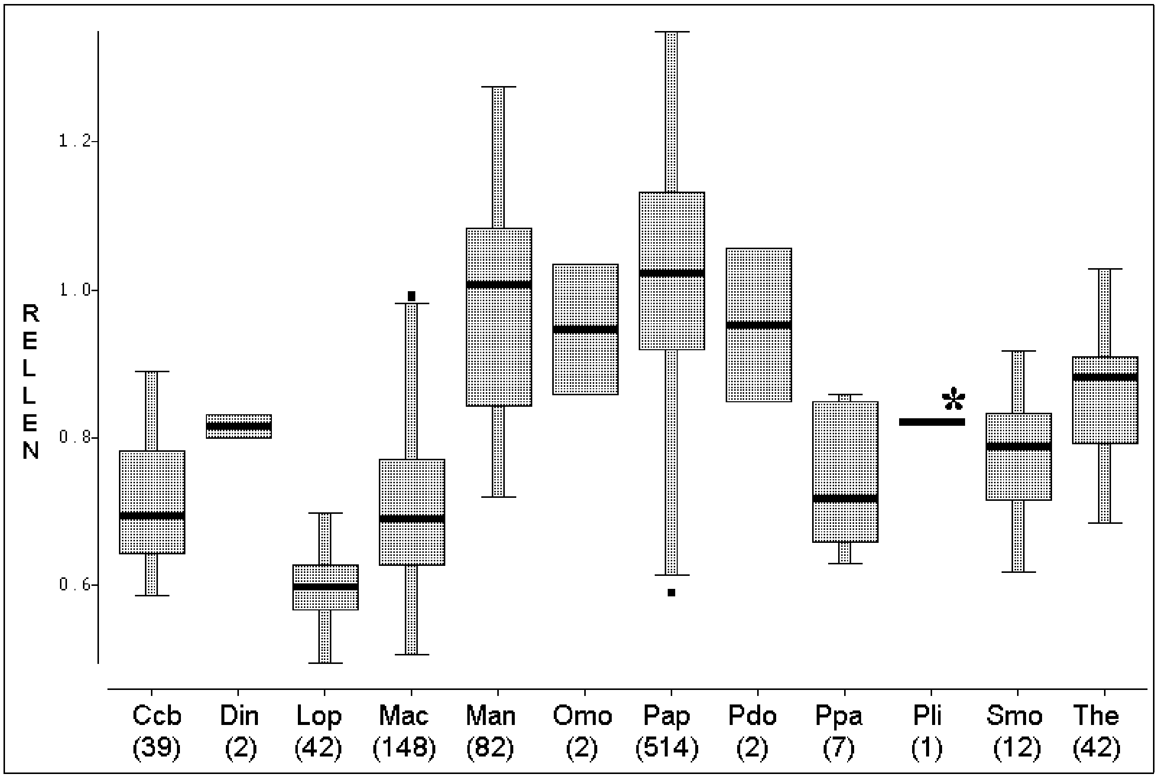
The infraorbital foramina are only preserved on the left side of ARA-VP-6/933. They are four in number and are arranged in a superolaterally concave arc as in *Theropithecus* (Eck and Jablonski, 1987). Relative to the orbit they lie roughly in mid-mediolateral position and are placed more closely to its inferior rim than in *Theropithecus*.

In ARA-VP-6/933 and ARA-VP-6/437 there is little to no development of maxillary ridges, similar to *Parapapio* (Freedman, 1957), *Theropithecus* (*Theropithecus*) (*sensu* Delson, 1993) and most *Macaca*, but distinct from *Papio* and *Mandrillus*. The maxillary fossae are also extremely shallow. Once again, this is similar to the above genera and to *Papio (Dinopithecus)* (see Delson and Dean, 1993). From what is preserved in ARA-VP-1/1007 and ARA-VP-1/1723 the females seem to lack these structures as well.

The muzzle dorsum of ARA-VP-6/933 is largely smooth and saddle-shaped as it is in *Theropithecus oswaldi*. It is concave in the sagittal plane and forms a convex arc in paracoronal cross-section at the level of the second molar. Its cross-section is sharper, however, with the nasals forming a more acute angle than they do in *T. oswaldi*. This is closer to the cross-section of *Macaca mulatta*, *M. nemestrina*, or *M. thibetana*, but with a relatively longer muzzle. When viewed laterally the muzzle profile is concave up from glabella to rhinion, displaying an ante-orbital drop, and is also concave up from rhinion to nasospinale, and finally convex up from nasospinale to prosthion. While the entire muzzle is quite long and not unlike that of *Papio*, the length of the segment from glabella to rhinion makes up less of the total muzzle length than it does in *Papio* (see figure 4.3). Rhinion is also considerably more prominent than in *Papio* or *Theropithecus*.

The sutures of the muzzle are well preserved on the left side of ARA-VP-6/933 and on ARA-VP-6/437. The premaxillomaxillary suture follows the superior portion of the nasal aperture at a margin of approximately 4mm, as it does in most larger papionins. Unlike *T. gelada*, it does not enter the piriform aperture. The nasal process of the premaxilla projects further posteriorly than it does in *Papio*, approaching to within 1.5 cm of the orbits. The premaxillomaxillary suture is therefore largely an anterolaterally

Figure 4.3. Y-Axis shows the distance from glabella to prosthion / distance from glabella to inion. Abbreviations: Ccb = *Cercocebus*; Din = *Papio (Dinopithecus)*; Lop = *Lophocebus*; Mac = *Macaca*; Man = *Mandrillus*; Omo = *Theropithecus (Omopithecus)*; Pap = *P. (Papio)*; Ppa = *Parapapio*; Pli = *Pliopapio*; Smo = *Theropithecus oswaldi*; The = *T. gelada*. Sample sizes are given in parentheses.

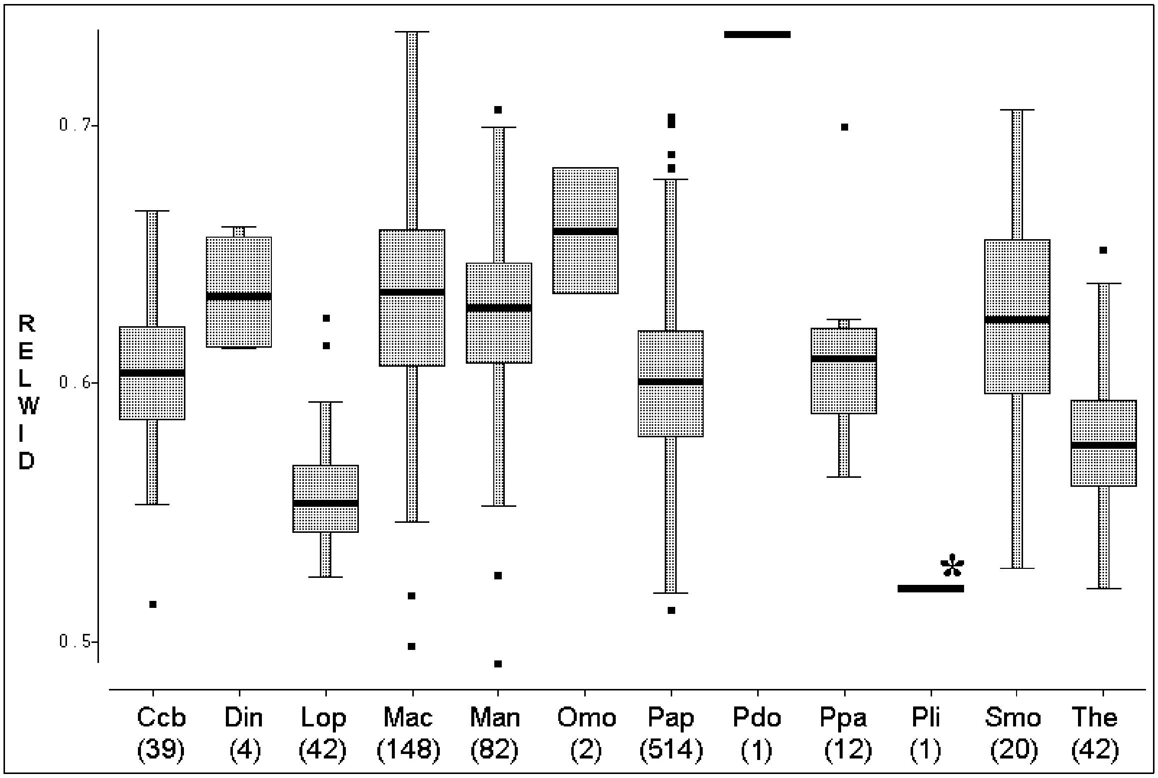


smoothly curving arc. The premaxillae project relatively far anteriorly beyond the canine, and there is a modest diastema separating the canine from the incisors (6.5 mm on the left side of ARA-VP-6/933).

When viewed superiorly, the muzzle is much narrower than the neurocranium (see figure 4.4). In comparison to the length of the neurocranium, the muzzle is longer than in most *Macaca* or *Parapapio*, and shorter than in *Papio* (*Papio*) and *Mandrillus* (see figure 4.5). The muzzle of the female ARA-VP-1/1007 is considerably shorter than that of the male ARA-VP-6/933. When they are lined up at the first molar, the mesial edge of the lateral incisor of ARA-VP-1/1007 is even with the middle of the canine of ARA-VP-6/933.

The piriform aperture is preserved in ARA-VP-6/933, partially in ARA-VP-6/437, and very partially in the female ARA-VP-1/1007. The outline of the piriform aperture is typically papionin, being roughly ovoid, but forming a "V" at its inferior pole. In breadth it is slightly narrower than that of *Papio*. The nasals of ARA-VP-6/933 are distorted, but probably would have formed a straight superior margin. The premaxillae then bow gently laterally to the apertures widest point just above the roots of the incisors, then curving convexly up to meet at nasospinale in a relatively acute inferior angle at nasospinale. There is no evidence of anterior nasal tubercles.

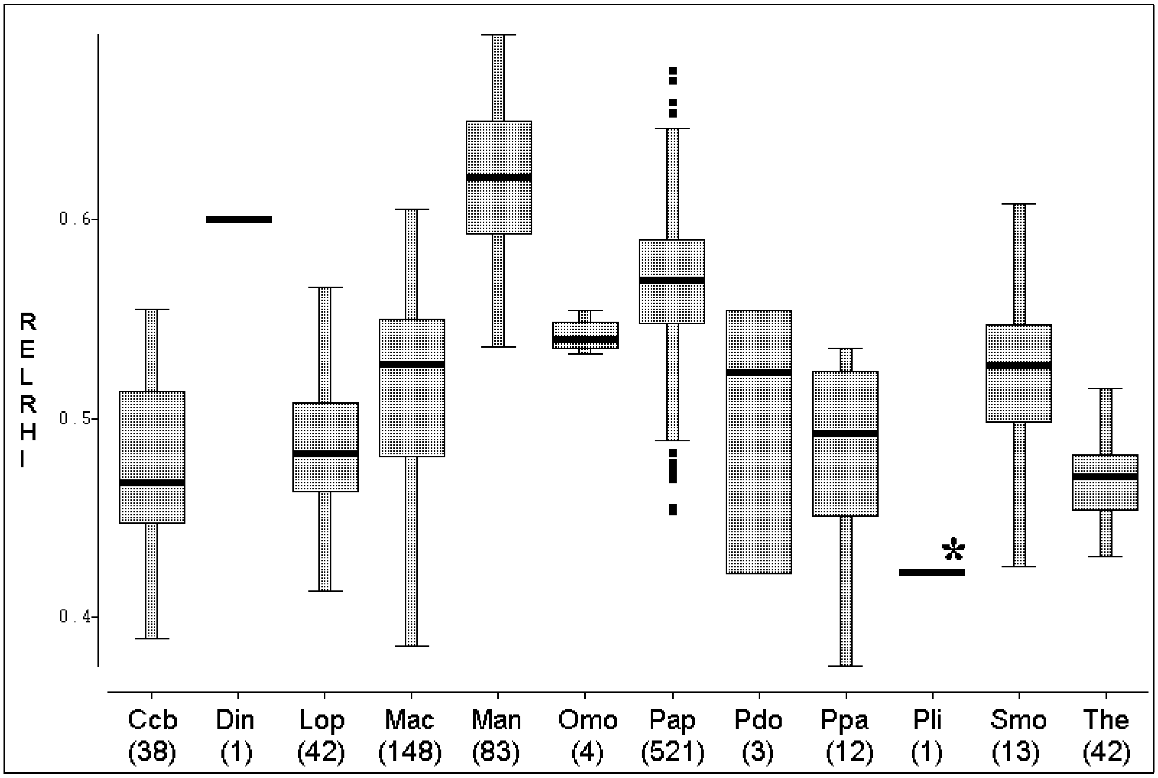
Figure 4.4. Relative width of the rostrum. Y-Axis shows distance from left to right M1/M2 contact / distance from left to right Porion. Boxes as for figure 4.1. Abbreviations as for 4.3.



The maxillary dental arcade is preserved in ARA-VP-6/933, it is preserved from C-M^3 in ARA-VP-1/1723, and from I^2 to M^1 in ARA-VP-1/1007. The dental arcade is somewhat distorted in ARA-VP-6/933, but appears to have been largely "U" shaped, with the canines marking the bases of an anterior arc composed of the incisors. The alveolar margins appear to be gently bowed laterally with their widest point at the mesial loph of M^2, and narrowest at P^3, bulging laterally again at the canine, though less so in the females ARA-VP-1/1007 and ARA-VP-1/1723. The molar series forms a short arc, but with the M^2 oriented slightly obliquely. The premolars are set in a straight line from M^1 to C^1.

When viewed laterally, the maxillary dentition in ARA-VP-6/933 or ARA-VP-1/1723 is basically straight to very slightly concave up as in most cercopithecines. The palate is preserved in ARA-VP-6/933, but it is covered in matrix (which cannot be removed without causing damage to the specimen). ARA-VP-1/1723 preserves a small piece of the palatal process, which is about 0.5 cm in depth anteriorly, and deepens slightly posteriorly.

Figure 4.5. Relative length of the nasals. Distance from glablla to rhinion / glabella to prosthion. Abbreviations as for figure 4.3.



Zygomatic arch

The maxillary root of the zygomatic arch arises from above the distal loph of M^2 in the male ARA-VP-6/933 and above the mesial loph of M^2 in the female ARA-VP-1/1723. This is further anterior than in *Papio*, *Gorgopithecus*, and *Theropithecus* other than *T. gelada* and *T. oswaldi leakeyi*. ARA-VP-6/933 is the only specimen to preserve the zygomatic arches. The anterior surface of its zygoma curves gradually and smoothly superoposteriorly with only a very slight depression in the region of the infraorbital foramina and maxillozygomatic suture. This depression is unrelated to any maxillary fossae and is the only feature to interrupt the otherwise smoothly curving surface. The inferior margin of the anterior portion of the zygomatic arch is a smooth semi-circular curve interrupted by a small pyramidal process where the maxillozygomatic suture intersects. The superior most point of the inferior margin lies below the lateral edge of the orbit, at which point the zygoma curves inferiorly again. The temporal surfaces do not appear strongly excavated as in *Theropithecus*, but there is some damage and distortion here.

In superior view, the zygomatic arches are no more laterally flared than in most *Macaca* or *Papio*, but are more smoothly curved. This is particularly notable anteriorly where they are more posteriorly angled than in *Papio*. The zygomata of the latter genus jut out more sharply, perhaps due to greater maxillary fossa development. The scar for the origin of the masseter muscle is visible in ARA-VP-6/933 and terminates anteriorly close to the maxillozygomatic suture. The posterior termination is not preserved, but must have been anterior to the zygomaticotemporal suture as there is no scar on the zygomatic process of the temporal.

Orbital region

The orbital region is only preserved in ARA-VP-6/933. Internally both orbits are occupied by matrix. The supraorbital torus is relatively prominent, but thin superoinferiorly. It is mildly "V" shaped in superior view and separated from the neurocranium by a broad ophryonic groove. Unlike *Papio, T. oswaldi*, and larger *Macaca*, there are no bulges above the torus at the midpoints of the orbits. In frontal view, the superior orbital rim and torus rise only slightly lateral to the sagittal plane then curve inferiorly, giving the torus a mildly superiorly bowed surface, and the orbits a slightly laterally "drooping" appearance. There are no supraorbital notches.

The interorbital breadth is narrow, and glabella is not prominent. There is some damage in this area, but nasion was probably the most anterior point on the frontal. The orbits themselves are largely mediolaterally oval in outline, being relatively short and broad. The lacrimomaxillary suture seems to lie just at the orbital rim, and the lacrimal fossa was likely contained entirely in the lacrimal bone.

Calvaria

The calvaria is only preserved in ARA-VP-6/933. It is relatively globular in overall shape with its greatest width at the external auditory meatus. It is generally lacking in superstructures, and considerably broader than the muzzle. When viewed in Frankfurt horizontal, the frontal bone rises above the supraorbital torus, and achieves its maximum height about 1-cm anterior to bregma. The cranial vault remains at this height until about 2.5 to 3-cm posterior to bregma. The temporal lines are faint and widely separated, curving posteriorly less than 1-cm medial to the lateral orbital margins. Posterior to this they remain subparallel, approximating only slightly posteriorly. In conjunction with the light temporalis development, postorbital constriction is slight and the temporal fossae are shallow. The nuchal crests are slight to nonexistent at inion, but become rather large laterally, having their greatest width behind the external auditory meatus. Viewed posteriorly, the vault is taller than that of *Theropithecus*, which is broad and low, but is similar to that of *Papio* or *Macaca*.

Basicranium

The basicranium of ARA-VP-6/933 is largely covered in matrix and the foramen magnum is obscured by an articulated atlas. The occipital plane is probably inclined at about 45º in Frankfurt orientation. The mastoid processes do not appear to be prominent. The postglenoid processes may be closely approximated to the glenoid fossae, but this is difficult to tell, and it is impossible to see whether they were separated by a sulcus as in *T. oswaldi darti*. The external auditory meatus are basically normal to the sagittal plane, and appear nearly round in cross-section.

Facial hafting

The only specimen where the relationship between the face and neurocranium can be assessed is ARA-VP-6/933. The glenoid fossa lies closely in line with the alveolar plane. The glenoid fossa is only slightly more elevated than in *Papio*, but less so than in *Theropithecus*. Its position is not unlike that in *Parapapio* cf. *jonesi* from Hadar (see Szalay and Delson, 1979 p.345). The face is less klynorhynch than that of *Papio* (*Papio*), but also less airorhynchous than that of *Theropithecus gelada*.

Mandible

ARA-VP-6/933 preserves most of the mandible, with considerable damage to the right side. ARA-VP-1/73 (see plate 5) is a male mandible with most of the corpora and symphysis. The inferior margin is missing posterior to the symphysis. The complete dentition is present other than the left canine through right I_1. ARA-VP-1/133 (plate 5) is a considerably distorted and crushed female mandible lacking the left ramus, but preserving most of the right. The inferior margins are largely intact and the left and right P_4-M_3 are present. ARA-VP-1/1006 (plate 5) preserves separate and partially crushed female right and left corpora with all of the dentition other than the right central incisor through the left canine. ARA-VP-1/563 (plate 5) is a female symphysis with some of the left corpus and the dentition from the right I_1 through the left M_2, and the right P_3. ARA-VP-1/740 (plate 5) is a juvenile mandible with most of the corpus and the right dP_3 through M_1 and the left dC_1 through M_1. ARA-VP-1/548 (plate 5) is a right juvenile corpus with dP_4 and M_1 in place, and the tips of the crowns of I_1 through C_1 just beginning to emerge from their crypts.

The symphysis slopes at an angle similar to that of *Macaca fascicularis*. This is more sloping than in many papionins when viewed in profile, but less so than the symphysis of *Parapapio ado* from Laetoli (Leakey and Delson, 1987) and Kanapoi (Patterson, 1968), and considerably less so than in the small papionin from Lothagam (Leakey, in press). The incisive alveolar plane is oriented nearly vertically, whereas it projects more anteriorly in the above-mentioned taxa. The incisor row is thus nearly vertical in *Pliopapio alemui* whereas the incisors of the others are more procumbent, with the central incisor projecting well beyond the lateral. The projecting alveolar process of *Pp. ado* produces a symphysis that is quite different in profile from the *Pl. alemui*. The symphysis is pierced by a median mental foramen. There appear to have been faint, triangular mental ridges. The superior transverse tori in ARA-VP-1/73 and ARA-VP-1/133 extend posteriorly to the middle of P_4 in superior view. Both superior and inferior transverse tori are well developed.

The Middle Awash mandibles show only slight or no development of corpus fossae. Although there is some damage to the inferior margin in ARA-VP-6/933, it appears that the deepest point was relatively anterior, perhaps under P_4, and that the inferior margin curved gently convex down. The inferior margin is thus anteriorly divergent. The oblique line emerges near the level of the mesial lophid of M_3 or the distal lophid of M_2. The extramolar sulcus is smooth and weakly developed. The gonial region is unexpanded. If present at all, the mylohyoid line is poorly developed.

Viewed superiorly, the tooth rows are nearly parallel along their lingual surfaces, from M_3 to P_3 with the canine slightly medial and the incisors curving sharply medially. In lateral view there is a normal curve of Spee (i.e., the tooth row is concave upward).

The ramus is well preserved only in ARA-VP-6/933. It is back-tilted, although less so than in *Papio*, but more than in *Macaca* or *Theropithecus* (*Theropithecus*). The coronoid process is equal to or slightly higher than the condyle, from which it is separated by a shallow semi-circular mandibular notch. There is a deep triangular fossa below the coronoid process on an otherwise relatively smooth lateral surface. The masseteric tuberosity is faint, and the whole area of its attachment is not heavily scarred.

Dentition

The incisors are fairly large relative to the molars, which is typical for most papionins. The I^1 is broad, flaring and spatulate in anterior view. The I^2 is more asymmetrical and not as broad, with a small lateral tubercle. The lower incisors have straight mesial and distal borders in anterior view, so that they are less flaring than the uppers. The lateral border of the I_2 is more laterally curved than that of the I_1. As is

---

Table 4.2 Summary dental dimesnions for *Pliopapio alemui*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.19. For descriptions of measurements see chapter 3.

	Pliopapio alemui												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^1	6	5.2	0.4	4.6	5.5	9.6	1.6	6.5	11.3	6.4	0.9	5.8	8.2
I^2	5	5.7	0.4	5.2	6.0	8.1	2.4	4.1	10.1	4.0	0.2	3.8	4.2
C^1 (?)	2	5.1				9.7	0.6	9.3	10.9	5.7	0.1	5.6	5.8
C^1 (?)	1					32.1				11.1			
P^3	3	6.0	0.7	5.6	6.5					5.1	0.6	4.7	5.8
P^4	3	6.2	0.4	5.9	6.5					5.1	0.2	4.9	5.3
M^1	3	7.6	0.3	7.4	7.8	7.0	0.2	6.9	7.2	8.2	0.4	7.8	8.6
M^2	2	9.0				7.9				9.7	0.7	9.2	10.2
M^3	4	8.4	0.6	8.0	9.1	6.6	0.7	6.1	7.4	8.9	0.7	8.1	9.5
M^x	30	8.6	0.8	7.0	9.9	7.7	0.8	6.4	9.0	9.0	0.8	7.9	10.9
dP^4	4	6.4	0.3	6.1	6.7	5.8	0.4	5.4	6.3	7.1	0.3	6.7	7.3
I_1	5	4.5	0.8	3.5	5.2	7.6	3.0	4.4	11.2	4.5	1.2	3.3	5.8
I_2	6	4.8	0.7	3.8	5.5	8.6	2.9	4.7	11.1	4.0	0.9	3.3	5.5
C_1 (?)	2	5.8	0.2	5.7	6.0	3.9	0.7	3.4	4.3	8.0	1.6	6.9	9.1
C_1 (?)	2	9.3				21.2	5.3	17.4	24.9	5.4			
P_3 (?)	2	3.7	0.1	3.6	3.8	7.2				6.4	1.4	5.5	7.4
P_3 (?)	1	3.7				15.6				9.2			
P_4	11	5.5	0.6	4.6	6.7					6.3	0.7	4.8	7.2
M_1	9	5.9	0.4	5.3	6.5	6.2	0.4	5.7	6.6	7.8	0.5	7.2	8.6
M_2	7	7.2	0.7	6.4	7.9	7.3	0.5	6.7	7.8	9.4	0.6	8.7	10.4
M_3	32	7.6	0.6	6.5	8.7	6.9	0.5	6.0	8.0	11.5	0.9	9.7	13.2
M_x	30	7.1	0.9	5.9	8.9	6.8	0.6	5.9	8.0	9.1	0.8	7.2	10.5
dC_1	1	4.6				5.3				3.0			
dP_3	1	4.0				4.4				6.8			
dP_4	5	4.7	0.2	4.5	5.0	5.1	0.2	4.9	5.3	7.1	0.4	6.5	7.5

typical of cercopithecines, they lack lingual enamel. As the tooth wears, this causes the enamel on the labial surface to form sharp edge. The labial surface is often "squared" in occlusal view. The canines are highly sexually dimorphic, and typical for cercopithecids with a mesial groove on the uppers that extends onto the surface of the root.

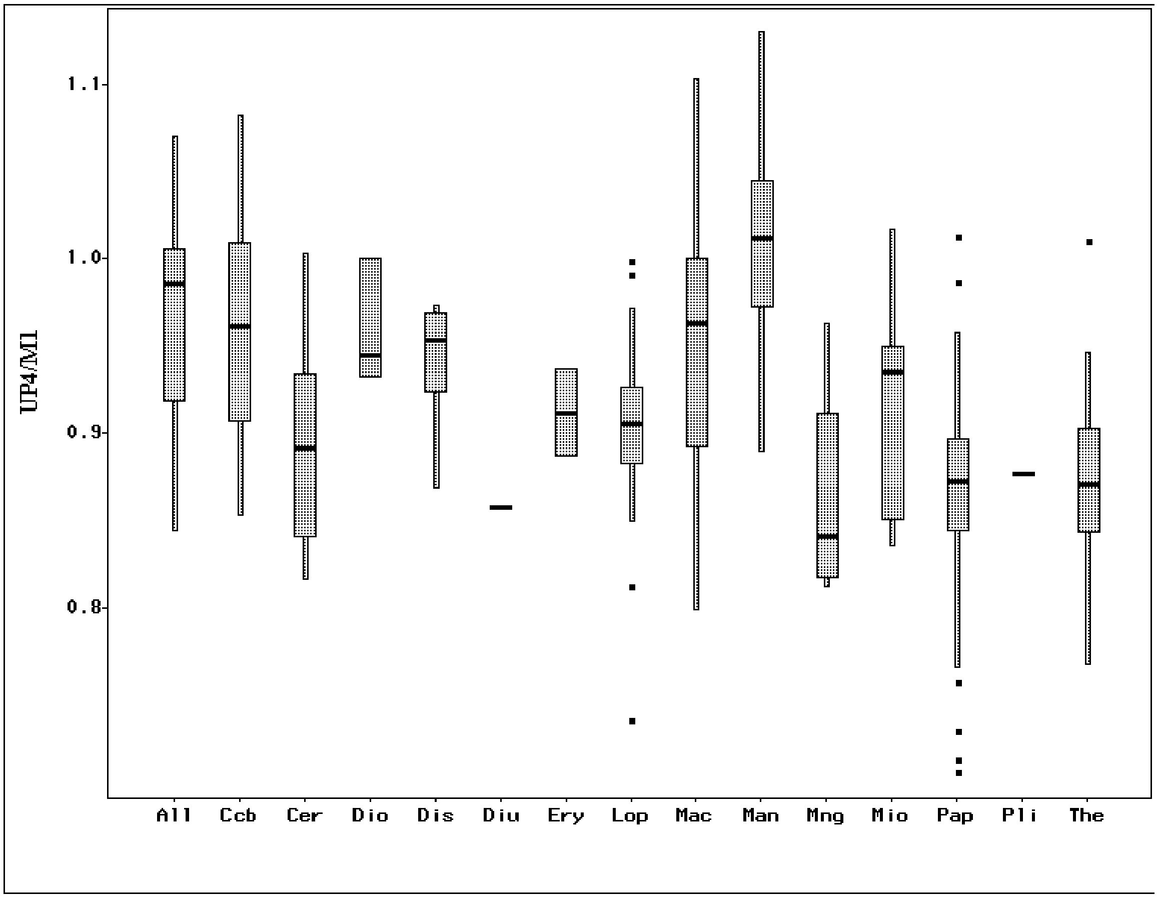
The upper premolars are typical bicuspid papionin teeth. The P^4 is not broad relative to the M^1 as it is in *Allenopithecus*, *Mandrillus*, and *Cercocebus* (see figure 4.6).

The P_3 is a highly sexually dimorphic tooth. The paraconid is not well developed and the male mesiobuccal flange is significantly longer than that of the females. It is also longer and more inferiorly directed than in the male colobine. The P_4 develops a small mesiobuccal flange in some males (e.g. ARA-VP 6/933), has more of a talonid than the P_3, and has a fairly high lingual notch.

The molars in general are high-crowned for a papionin, with relatively little flare (see figures 4.7-4.8). Cusp relief above the lower lingual/upper buccal notch is high for a papionin, but lower than in colobines. Accessory cuspules are often present in the lingual notch. In the upper molars, the lingual cusps are elevated relative to the central basin and seem to be connected by continuous, well-developed postproto- and prehypocristae. The mesial loph is wider than the distal. The M^2 is often the largest of the upper molars. The lower molars have normal low relief and higher lingual notch. The buccal cusps tend to be fairly columnar, with the mesial and distal foveae being pinched, though not to the extent of those of *Theropithecus*. The floor of the buccal notch seems to slope downward distally. On the M_{1-2}, the distal cingula develop a very small hypoconulid 6-10% of the time depending on scoring. In the M_3, the hypoconulid is generally tightly pressed against the hypoconid, so that the distal buccal notch is very constricted compared to the mesial. Additionally, the distal buccal notch rarely preserves any "shelf" at the base.

The dI_2 has a crown that is basically spatulate, low in height, broad, and angles mesially. The root is broad and labiolingually flattened. The dC^1 is a mesiodistally elongate tooth with a crown that is approximately triangular in labial view. The dC_1 crown has a prominent central cusp that is labiolingually compressed and a crest extending mesially form its apex. Distally there is a small accessory cuspule. In general, the deciduous premolars are similar to adult molars, but narrower, with more lateral flare, and loph(id)s that are more weakly developed than the adult teeth. In addition, the upper dP's have relatively larger mesial and distal foveae. The mesial fovea is particularly large and elongate on the dP^3. The dP_3 protolophid is much narrower than the hypolophid. There is also a well-developed preprotocristid, and what may be a paraconid, yielding a mesial fovea that is triangular in shape. The dP_4 is more similar to an adult M_1, but narrower with a relatively longer mesial fovea.

Figure 4.6 P^4 Width / M^1 Mesial Width. Abbreviations as for figure 4.1.



Genus *Parapapio* Jones, 1937

(= or including: *Papio* Erxleben, 1777: Houghton, 1925; Gear, 1926, in part; Leakey and Leakey, 1976, in part. *Cercocebus* Geoffroy, 1812: Hopwood, 1936, in part. *Papio (Simopithecus)* (Andrews, 1916): Dietrich, 1942. *Brachygnathopithecus* Kitching, 1952, in part. *Papio (Parapapio)*: Delson, 1975. Papionini gen. et. sp. indet. B. Leakey and Leakey, 1976.)

Type species: *Parapapio broomi* Jones, 1937

Other included species: *Pp. antiquus* (Haughton, 1925); *Pp. ado* (Hopwood, 1936)[1]; *Pp. jonesi* Broom, 1940; *Pp. whitei* Broom, 1940; *Pp. species nova* Leakey et al., in press.

Generic Diagnosis:

This diagnosis largely follows those of Freedman (1957), Eisenhart (1974), and Szalay and Delson (1979). *Parapapio* is an extinct genus of medium sized African papionins, thought to be conservative relative to other known African papionin genera. When viewed in lateral profile, *Parapapio* is distinguished from *Papio, Pliopapio, Theropithecus*, *Mandrillus, Gorgopithecus, Paradolichopithecus,* and some *Macaca* by the lack of an anteorbital drop, a relatively thin brow ridge, and lack of an ophryonic groove. It is also different from *Papio (Papio), Gorgopithecus*, *Lophocebus*, *Cercocebus* and *Mandrillus* in that it generally lacks postcanine and suborbital fossae, though shallow fossae are present in some individuals, especially in *Pp. jonesi* and *Pp. antiquus*.

---

[1] Parapapio is best diagnosed in the face, as no facial material of Parapapio ado is complete enough to observe the diagnostic features of the genus, it is only tentatively included Parapapio.

Maxillary ridges in the males are also absent or only poorly developed, unlike *Papio (Papio)*, *Theropithecus (Omopithecus)*, and *Mandrillus*. The mandible is distinct from those of *Papio (Papio)*, *Mandrillus, Lophocebus, Theropithecus (Omopithecus)* and *Gorgopithecus* in its lack of corpus fossae. The dentition is indistinguishable from that of *Papio*.

Parapapio sp. cf. *Pp. jonesi* Broom, 1940

(= or including *Parapapio* cf. *jonesi* Szalay and Delson, 1979)

Afar specimens included: AL217-8, AL363-1a-l, 10, 12, 15a-b, AL465-1, AL100-348, 354, 355, 365, 381; MAK-VP-1/49, 112.

Range: 3.4 - ~2.5 Ma

Afar range: 3.4 – 2.92 Ma

Distribution: Hadar Fm. Sidi Hakoma, Kada Hadar Mbs., Maka Fm. "W" sub SHT (cf.), *Pp. jonesi* known from: Makapansgat Mbs 2-4.; Sterkfontein Mbr. 4

Specific Diagnosis:

The different species of *Parapapio* have not been well diagnosed relative to one another, particularly the three that are generally recognized at Makapansgat and Sterkfontein: *Pp. broomi*, *Pp. jonesi* and *Pp. whitei*. Freedman (1957) essentially divided them into dental size categories with *Pp. jonesi* the smallest, and *Pp. whitei* the largest. This diagnosis follows those of Maier (1970), Eisenhart (1974) and Szalay and Delson (1979).

Pp. jonesi is a small papionin, smaller than other members of the genus, in molar and cranial size. It is significantly smaller than *Pp. whitei* (Delson et al., 2000). Maxillary fossae are generally better developed than in other species of the genus, as are the maxillary ridges. These two features yield a muzzle dorsum that is more squared in cross-section than that of *Pp. broomi*, but similar to *Pp. whitei*. The rostrum is relatively tall and deep, and shorter in comparison to the neurocranium than that of *Pp. whitei*. The premaxillae project further anteriorly beyond the canine than do those of *Pp. broomi*. This produces an incisive arc that is more rounded in *Pp. jonesi* than in *Pp. broomi*, which tends to have a more flattened incisive arc. The M^3 is not reduced distally, distinguishing it from *Pp. antiquus*.

Description:

The majority of specimens and all of the diagnostic material of this taxon comes from a single locality, AL363, in Unit 3U to S of the Kada Hadar Member of the Hadar Formation. The best specimen is a nearly complete male skull with a supposedly associated partial skeleton, AL363-1a-l (plates 6, 9). The cranium is nearly complete and from an older adult individual, as the molars are very worn. Most of the right side, including the zygomatic arch is preserved, but the left zygomatic arch, temporal squama, occipital, and inferior parietal, as well as the region around inion are absent. All of the cheek teeth are present, but are so highly worn as to preserve almost no crown morphology. The right canine is also preserved, but is heavily damaged. The alveoli for the other teeth are present. There is also a partly distorted female face and mandibular corpus, AL363-15 (plate 8-9), with nearly complete dentition, lacking only the upper right lateral incisor, upper left canine and lower right central incisor. The surface bone of the whole specimen is expanded and heavily cracked. The right side is better preserved, however, with the zygomatic arch present, and the orbital rim. The orbit and zygoma are totally lacking on the left side. Other than the right temporal, the neurocranium is lacking. The palate is completely preserved. From the same locality there is also a left mandibular corpus fragment with M_{2-3} (AL363-10), and a distal fragment of a right humerus (AL363-12) is tentatively assigned to this taxon (Delson, 1984; Delson et al., 2000). Two other Hadar specimens are included from other localities, but they are less securely placed in this taxon. They are diagnosed by being papionins other than *Theropithecus* of the same dental size as the AL363 crania, and a lack of any contradictory morphological evidence. AL217-8 is a right mandibular corpus with M_{2-3}, and AL465-1 is a left corpus, also with M_{2-3}. Finally, five isolated teeth and tooth fragments from Ahmado (AL100) are tentatively included, as are two specimens from Maka. The Maka specimens are slightly older than those from Hadar, being from below the Sidi Hakoma Tuff. These are all assigned to this taxon on the same criteria as the last two Hadar specimens.

Compared to other species of *Parapapio*, that from Hadar falls within the dental size range of *P. jonesi* as it is known in South Africa. It is larger than *Pliopapio alemui* and *Parapapio ado* from Kanapoi, but significantly smaller than *Papio (Dinopithecus) quadratirostris*. Dental dimensions for *Pp*. cf. *jonesi* are given in table 4.3. It is also similar in cranial size, as measured by centroid size, to South African *P. jonesi*, and smaller than *P. broomi* and *P. whitei*. It is in a size range smaller than male *Papio hamadryas*, other than *P. h. kindae*, but larger than all but the largest individuals of *Macaca*.

Table 4.3 Summary dental dimesnions for *Parapapio* cf. *jonesi*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.20. For descriptions of measurements see chapter 3.

	Parapapio cf. *jonesi*												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^1	1	5.9				10.0				7.7			
I^2	1	6.7								4.9			
C^1 (?)	1	5.4				12.8				7.4			
C^1 (?)	1	7.6								9.9			
P^3	2	7.1	0.2	6.9	7.2					5.7	0.2	5.5	5.8
P^4	2	8.3	1.8	7.0	9.5					5.6	0.3	5.4	5.8
M^1	2	9.2	1.4	8.2	10.2	9.1	1.1	8.3	9.8	8.1	0.1	8.0	8.2
M^2	2	11.9				10.5				10.6	0.0	10.6	10.6
M^3	2	10.5	0.1	10.4	10.6	9.1	0.2	8.9	9.2	10.9	0.9	10.2	11.5
M^x	1	7.4				7.2							
I_1	1	4.7				8.8				5.5			
I_2	1	3.9				7.5				4.7			
C_1 (?)	1	6.5				10.5				3.8			
C_1 (?)	1	10.5				17.6				6.2			
P_3 (?)	1	5.1				8.4				5.6			
P_3 (?)	1	4.8				12.6				9.0			
P_4	3	6.3	0.3	6.0	6.5					6.7	0.5	6.3	7.3
M_1	3	7.4	0.3	7.2	7.6	7.5	0.2	7.4	7.7	8.5	1.3	7.6	10.0
M_2	5	9.2	0.0	9.2	9.2	8.9	0.8	7.8	9.8	10.5	0.7	9.7	11.2
M_3	6	9.3	0.7	8.2	9.7	8.3	0.6	7.6	9.2	13.6	1.0	11.6	14.3
M_x	1	6.6				6.5				9.3			

Rostrum

The complete rostrum is preserved, but slightly distorted in AL363-1a, and largely present, though highly damaged and distorted in AL363-15a. The area around the infraorbital foramina is damaged bilaterally on AL363-1a, obscuring most of the morphology in this area, but it can be seen that they were multiple and arranged roughly linearly parallel to the zygomaticomaxillary suture. On the rostrum there is no development of maxillary ridges on either specimen, much as in *Pliopapio*, *Theropithecus (Theropithecus),* and most *Macaca*. On the male AL363-1a the maxillae entirely lack facial fossae. This specimen may lack maxillary ridges, in part, because its nasals are so prominent above the maxillae that any ridges are incorporated into the slope of the maxilla. Interestingly, in spite of the damage, there appear~~s~~ to be clear, but shallow maxillary fossae on the female AL363-15a. This is somewhat unexpected as typically males show more extreme expressions of these features. The variable presence of shallow maxillary fossae seems to occur more often in *Pp. jonesi* than it does in *Pp. broomi*.

The most striking feature about the male muzzle dorsum is the prominence of the nasal bones. They form a high peaked ridge along the superior surface of the maxillae. In paracoronal cross-section, the muzzle is very tall, and almost triangular with the nasals forming the apex. The nasals form an even sharper apex than they do in *Pliopapio*. In this feature, AL363-1a is most similar to some specimens of *Pp. whitei* from Makapansgat (*e.g*. BPI-M3072, M3065; UWMA-MP221 and MP223 [figured in Maier (1970) and Freedman (1976) respectively]). The shape of the muzzle dorsum and the prominence of the nasals are difficult to gauge in the female AL363-15a, but they were probably not as tall relative to the surface of the maxilla and the cross-section was more rounded and less peaked than it is in the male. The muzzle profile of the male is most similar to that of other *Parapapio*, but is also unique due to the prominent nasals and the robust brow ridge. Its profile from nasion to rhinion is actually sigmoidal in shape, being concave from nasion to the middle of the nasals, then becomes convex through rhinion. The dorsal convexity is so great that the dorsum of the distal end of the nasals is actually vertical just above rhinion for approximately 0.5 cm. While this nasal morphology is quite distinctive, it is actually similar to *Pp. whitei* (*e.g.* M3072 and MP221) which possesses a less extreme version of the sigmoidal profile. Although there is extensive damage to the nasals, the female specimen clearly lacks anteorbital drop and has a profile that is typical of *Parapapio*, being relatively linear from nasion to prosthion, and lacking anteorbital drop.

In the male specimen, the premaxillomaxillary suture follows the lateral rim of the piriform aperture at a margin of less than 2 mm before curving laterally anterior to the canine. Unlike *T. gelada* it never enters the piriform aperture. The nasal process of the premaxilla projects posteriorly to approximately the midpoint of the nasals before it is covered by the maxilla. The premaxillomaxillary suture is complexly curved in lateral view. Initially it arcs inferiorly following the curvature of the nasals, but then becomes concave-up along the lateral margin of the piriform aperture before curving inferiorly again anterior to the canine root. Once again, for the female most of the morphology is obscured, but the premaxillomaxillary suture is somewhat preserved on the left side. It appears that it was considerably straighter in its course than that of the male. The premaxillae project relatively far anteriorly beyond the canine, and there is a modest diastema separating the canine from the incisors. In these features, AL363-1a is similar to *Pp. whitei* (BPI-M3065, M3072, UWMA-MP221, and MP223) and *Pp. jonesi* (TMP STS 565, holotype). Known specimens of *Pp. broomi* seem to lack this area, except for a large male from Bolt's Farm, UWMA BF 43, which is only tentatively assigned to this species (and was designated *Pp. whitei* by Freedman [1965]). This specimen has premaxillae that do not project nearly as far beyond the canine, forming a straighter line between the canines.

The piriform aperture of the male AL363-1a is basically oval in outline, as are those of most papionins, but its inferior limit is not “V”-shaped, instead being more rounded. The unique nasal morphology of this specimen gives the superior part of the aperture a somewhat distinctive shape. The nasals form a semicircular arch that projects perpendicularly over the superior limit of the piriform aperture. While the breadth across both nasals is only about 1 cm, rhinion projects approximately 0.5 cm above and anterior to the lateral edge of the nasals. The widest portion of the piriform aperture is inferior to midheight. The piriform aperture of the female is heavily damaged and distorted, but what is preserved appears to be similar to the male, except for the area around the nasals. Viewed laterally, the plane defined by the rim of the piriform aperture is concave-up, and inclined at an angle of approximately 40º to the occlusal plane, in both the male AL363-1a and the female AL363-15a.

The maxillary dental arcade is typical of most papionins. The male arcade is “U”-shaped in outline, whereas that of the female, as far as can be determined, is more parabolic. The postcanine tooth rows of the male are fairly straight and parallel. The M^2 is the most laterally positioned tooth, so that there is a slight arc to the tooth row. The canines are positioned laterally relative to the other teeth, particularly the P^3. The incisors form a smoothly bowing arch between the canines, projecting more anteriorly than they do in *Theropithecus*. There is also a short diastema between the canine and I^2. The female maxillary dental arcade is not as well preserved, but allowing for this it appears to be similar to that of the male, except that the canines do not project laterally beyond the P^3 and the cheek tooth rows converge more anteriorly.

In lateral view, the occlusal surface of the dentition is rather straight. The palate is similar to those of other papionins, being rectangular in outline in both the male and female. The palate is deep and deepens posteriorly in the male, reaching a maximum depth of approximately 13 mm. It is deep, but of more constant depth in the female. The absolute depth of the female specimen is difficult to judge due to distortion, but is similar to that of the male. The alveolar processes of the male are nearly perpendicular to the main floor of the palate. Those of the female are far more sloping, but their original shape is difficult to determine. Overall, the palate shape is rather unlike that of most *Parapapio*, which tends to be broader and comparatively shallow. For instance, even in the large male *Pp. whitei* UWMA MP223 from Makapansgat, the palate reaches a maximum depth of only 10 mm, even though it is a substantially larger specimen than AL363-1a.

Zygomatic Arch

The anterior surface of the zygomatic process of the maxilla arises superior to the mesial part of the M^3 in the male. Its position in the female is difficult to assess due to damage and distortion, but it is probably somewhere above the distal M^2 or mesial M^3. The anterior surface of the zygomata curve smoothly posteriorly in both the male and female specimens. The anterior surface of the male AL363-1a is smooth, lacking suborbital fossae entirely, similar to *Pp. whitei* and *Pp. broomi* from Makapansgat and Sterkfontein, but unlike *Pp. jonesi* from Makapansgat (e.g. M3051, M3054). This pattern is also similar to the anterior surface of *T. oswaldi, Papio (Dinopithecus),* and *Mandrillus*, and may be primitive for African papionins. The region of the infraorbital foramina is damaged bilaterally. The female AL363-15a preserves slight suborbital fossae (there is a chance this is due to distortion, however). The inferior edge of the zygoma arches sharply laterally away from the maxilla. The alveolar process extends fairly far below the zygomatic root, i.e. the maxilla is comparatively deep in the male, but less so in the female.

In superior view, the zygomatic arches of both specimens curve sharply posteriorly, and are not widely flaring. The anterior portion does not jut out laterally as it does in *Papio*, *Cercocebus*, *Theropithecus*, and *Lophocebus*, but slopes more posteriorly as in *T. oswaldi, P. (Dinopithecus)*, and *Mandrillus*. In this morphology it is the same as other known specimens of *Parapapio*. In both AL363-1a and AL363-15a the most lateral portion of the zygomatic arch is in its posterior portion near to where it attaches to the neurocranium. In overall morphology the zygomatic arch is thin and lightly built.

Orbital region

Both orbits are well preserved in AL363-1a, and the right orbit is present, but distorted in AL363-15a. The supraorbital torus of the male is one of the most robust known for such a small cercopithecid. It is considerably thicker than in all known South African *Parapapio*. In superoinferior thickness it approaches 12 mm, whereas the thickest brow ridge for any South African *Parapapio* is that of UWMA BF 43 which is approximately 7 mm. Most other specimens have brow ridges that are considerably more gracile than this. In frontal view, the supraorbital torus of AL363-1a forms separate arches over each orbit, so that it is lowest in the sagittal plane, then reaches maximum height over the midpoints of the orbits. This is in part due to bulging over the midpoints of the orbits as in robust specimens of *Papio, T. oswaldi*, and *Mandrillus*. The supraorbital notches are distinct and cut deeply into the torus. The supraorbital rim of the female is considerably more gracile, but shows a similar morphology. The supraorbital rim is approximately 7 mm in thickness and has distinct supraorbital notches.

The interorbital region is narrow in both specimens. Glabella is not prominent in either specimen, so that nasion is the most anterior point on the midline of the frontal. Like other known *Parapapio*, the profile in this region clearly lacks anteorbital drop. The lacrimal fossa lies within the orbit on AL363-1a, and its anterior border seems to be at the lacrimal-maxilla suture. Due to damage, its position on AL363-15a is not clear. The lateral orbital rim of the male is robust. The frontozygomatic suture is the most posterior point of the orbital rim, it curves anteriorly both superior and inferior to this point. Frontal process of the zygomatic slopes anteriorly and increases in breadth inferiorly as it approaches the zygomatic arch. The orbits themselves are circular in outline in AL363-1a. The orbit of the female is too distorted to be sure of its original shape. Their internal morphology is largely obscured by matrix.

Calvaria

The calvaria is only preserved in AL363-1a. It is slightly crushed in the vicinity of bregma, and the vault is missing on the left side superior to the auditory meatus. It is oval in shape, being widest above the auditory meatus. Postorbital constriction is modest, being more mild than that of *Theropithecus* and *P. (Dinopithecus)*. The supraorbital torus is separated from the calvaria by an ophryonic groove. The frontal rises superiorly over 1 cm above the supraorbital rim, reaching its maximum height anterior to bregma, before flattening to a point midway between bregma and lambda. This morphology is similar to that of other known specimens of *Parapapio* (Freedman, 1957). The temporal lines are strongly marked anteriorly, curving sharply medially posterior to the orbital rim. At approximately the midpoints of the orbits, the temporal lines curve sharply posteriorly, and do not meet in the midline until about 1-cm anterior to lambda. At this point they form a short and low sagittal crest. The region around inion is absent, but just lateral to this, there is a well-developed nuchal crest that reaches its maximum height of about 5-mm just posterior to the auditory meatus.

Basicranium

The basicranium is well preserved in AL363-1a, except for the portions near and between inion and the left mastoid. The occipital plane is relatively flat and inclined at an angle of 45^o relative to the Frankfurt horizontal. The mastoid processes are low and the digastric groove nearly imperceptible. The auditory meatus are angled posteriorly at an angle of approximately 30^o to the coronal plane. The inferior surface of the meatus is distinctive. It is pinched up into a sharp crest that follows the length of the tube. The tips of the postglenoid processes are broken, but their bases are preserved. They are relatively small and gracile in comparison to those of *Theropithecus*. The articular surface for the mandibular condyle is sellar in shape, being convex anteroposteriorly, and concave mediolaterally. The eminence is not as prominent as that of *Theropithecus*. The choanae are clearly narrow, but they are largely obscured by matrix making it impossible to determine their height. The basioccipital has a sharp break in slope. Immediately anterior to the foramen magnum it is nearly parallel with the Frankfurt Horizontal, but approximately 1 cm anterior to this, the slope of the clivus increases by about 60^o.

Facial hafting

The only specimen in which the relationship between the face and neurocranium can be studied is AL363-1a. The glenoid fossa is only slightly elevated above the level of the occlusal plane. The frontal elevates significantly above the orbits. The angulation of the face on the neurocranium is similar to that of most papionins, but is less klinorhynch than *Papio hamadryas ursinus* and *Paradolichopithecus*. It is less airorhynch than *Theropithecus gelada*.

Mandible

AL363-1b (plate 9) is a mandible associated with the male cranium. It preserves the entire left side of the corpus and the right side from the symphysis through the M_2. The left ramus is also present, except for the coronoid process. It preserves the left C-M_3 and the right C-M_2. AL363-15b (plate 9) is a nearly complete but damaged corpus associated with the female face. It preserves the entire dentition except for the right I_1. AL363-10 is a right corpus fragment with the $M_{2\text{-}3}$, preserving the margin and anterior portion of the ramus. Although the overall shape is probably true to the original form, the damage is such that the overall size and proportions are likely to be slightly distorted and the surface detail erased. AL217-8 is a small corpus fragment with right $M_{2\text{-}3}$, and AL465-1 a left corpus fragment with the $M_{2\text{-}3}$. Both of these latter specimens lack the margin, and preserve little of the corpus depth. MAK-VP-1/112 is a left mandibular fragment with P_4-M_1, but little of the corpus.

Overall, the mandible is very similar to other well-preserved specimens of *Parapapio broomi* (BPI M3067) and *P. jonesi* (BPI M3061) from South Africa. The symphysis of the male, AL363-1b, slopes at an angle of approximately 50º to the occlusal plane. In the female specimen AL363-15b the symphysis appears more vertical, but this may be due to the damage. This angle is similar to that of *Papio*, *Mandrillus* and most species of *Theropithecus*. The symphysis is pierced by a median mental foramen. There appear to have been faint, triangular mental ridges. The superior transverse tori of AL363-1b and AL363-15b extend posteriorly to the middle of P_3 in superior view. The inferior torus extends only a small amount further to the mesial P_4.

The lateral surface of the corpus of the male shows only a shallow corpus fossa. The female specimen also seems to lack corpus fossae, although it is too damaged to be certain. In both specimens, the deepest portion of the corpus is positioned relatively far anteriorly. In AL363-1b the deepest part of the corpus is approximately under the M_1/M_2 contact. In AL363-15b it is difficult to be certain, but was probably in a similar position. The inferior margin is thus anteriorly divergent. The oblique line emerges near the level of the mesial lophid of M_3 or the distal lophid of M_2, and is weakly developed. The extramolar sulcus is smooth and weakly developed. The gonial area is not expanded, and curves smoothly to the ramus. If present at all, the mylohyoid line is poorly developed. In superior view, the cheek teeth are parallel with one another. The canine projects laterally in the male AL363-1b, whereas in the female they are in line with the incisors. The incisors form a short arc anterior to the canines. In lateral view the tooth rows are slightly concave-up.

The ramus is nearly complete in AL363-1b, its anterior portion is preserved in AL363-15a and AL363-10. The ramus is short, as would be expected given the shallow elevation of the glenoid fossa. It is relatively deep in the anteroposterior direction and is back-tilted, similar to that of *Papio, T. (Omopithecus)* and *Mandrillus* and significantly less so than in *T. (Theropithecus)*. On AL363-1b the inferior limit of a deep triangular fossa is preserved, and the lateral surface of the ramus is otherwise relatively smooth.

Dentition

Every element of the adult dentition is represented in this sample. There is also an isolated right lower dP_4 of a small papionin, from the nearby site of Ahmado, which may represent this species as well. The incisors are only preserved in the female AL363-15, and they are typically papionin in morphology. The upper incisors lack lingual cingula. The upper central incisors are broad and spatulate with a vertical lingual groove. In anterior view, the crown flares considerably from cervix to apex, although more medially than laterally. The lateral incisor is generally similar but has a narrower crown. Its lingual surface is more tightly curved than in the central incisor. The crown is also less flaring in anterior view, more asymmetrical, and angled medially. The lower incisors clearly lack lingual enamel. They are “squared” anteriorly in occlusal view. In anterior view, the crowns are less flaring than those of the uppers. The distal margin of the lateral incisor is tightly curved, and angles mesially.

The canines are typical cercopithecid teeth, being highly sexually dimorphic. The upper canines of AL363-1a are heavily broken and damaged. What is preserved shows a tooth that was much larger in caliber than the female. It is triangular in cross-section, with a sharp distal border. Mesially, there is a deep sulcus. The upper female canines, are relatively compressed labiolingually. The crown is low, and roughly triangular in labial view. The distal edge is slightly sigmoidal. There is a slight mesial groove on the root. They are low, and otherwise substantially smaller than those of the male.

The upper premolars are typical bicuspid teeth. The P^3 is smaller than the P^4, but neither has well developed mesial or distal foveae. The P^3 crown is also more triangular in outline in occlusal view. The P_3 has a tall protoconid, and on AL363-15b there is a large metaconid. Both specimens preserve a paraconid that is better developed than that of *Pliopapio*, *T. (Theropithecus)*, and *Papio*. The mesiobuccal flange is relatively short. In the male AL363-1b it is significantly longer than that of the female, but is shorter than those of most papionins. The P_4 is more molariform, with a clear lingual notch, and comparatively large talonid. That of AL363-15b has a small hypoconid. The P_4 of AL363-1b has a slight mesiobuccal extension.

The molars are similar to those of most papionins. The crowns are low, with a large amount of basal flare (see figures 4.7-4.8), although less than is present in *Mandrillus*, *Cercocebus* or *Lophocebus*. The cusps are low and bunodont, and the notches between shallow. The cusp tips are closely approximated due to the flaring crown. The upper molars sometimes develop small cuspules in the lingual clefts. The cross-loph(id)s uniting the cusps are poorly developed. Of the upper molars the M^2 is the largest, although the M^3 is the longest and similar in size. The lower molars increase in size from anterior to posterior.

Figure 4.7. M^2 basal flare, Mesial Width / Mesial Notch Width. Abbreviations as in figure 4.6.

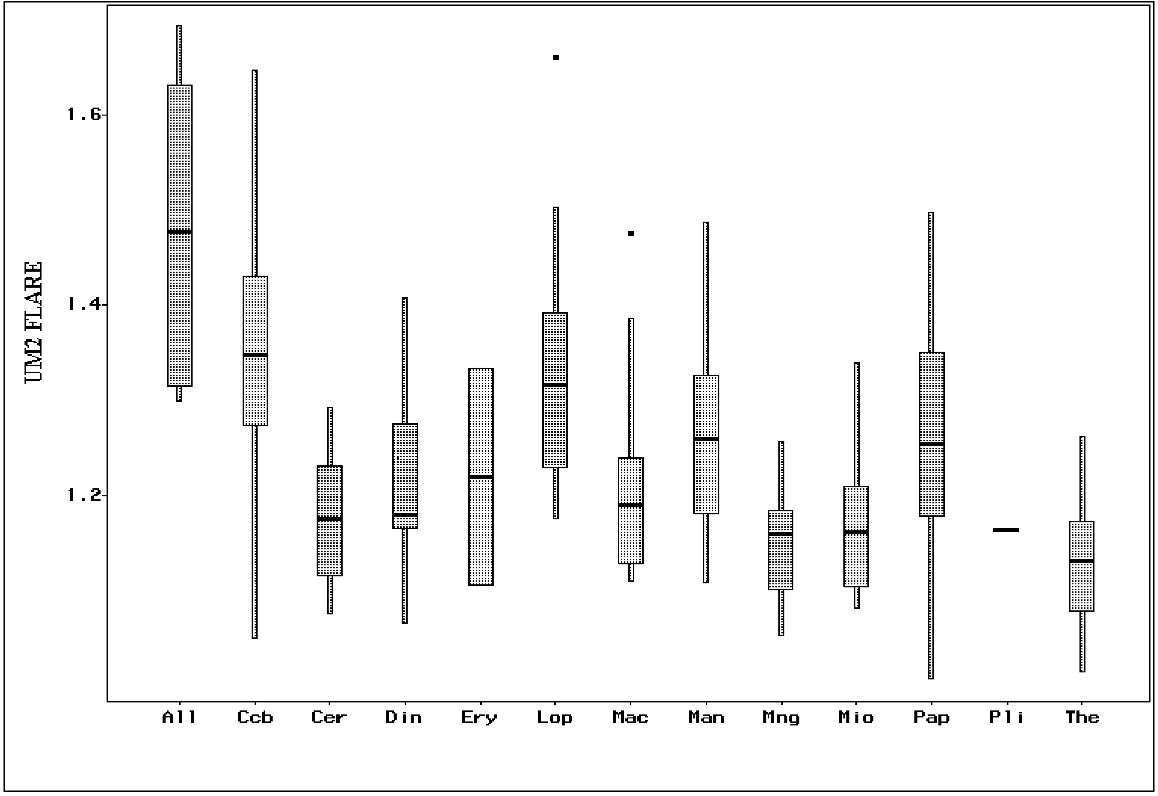
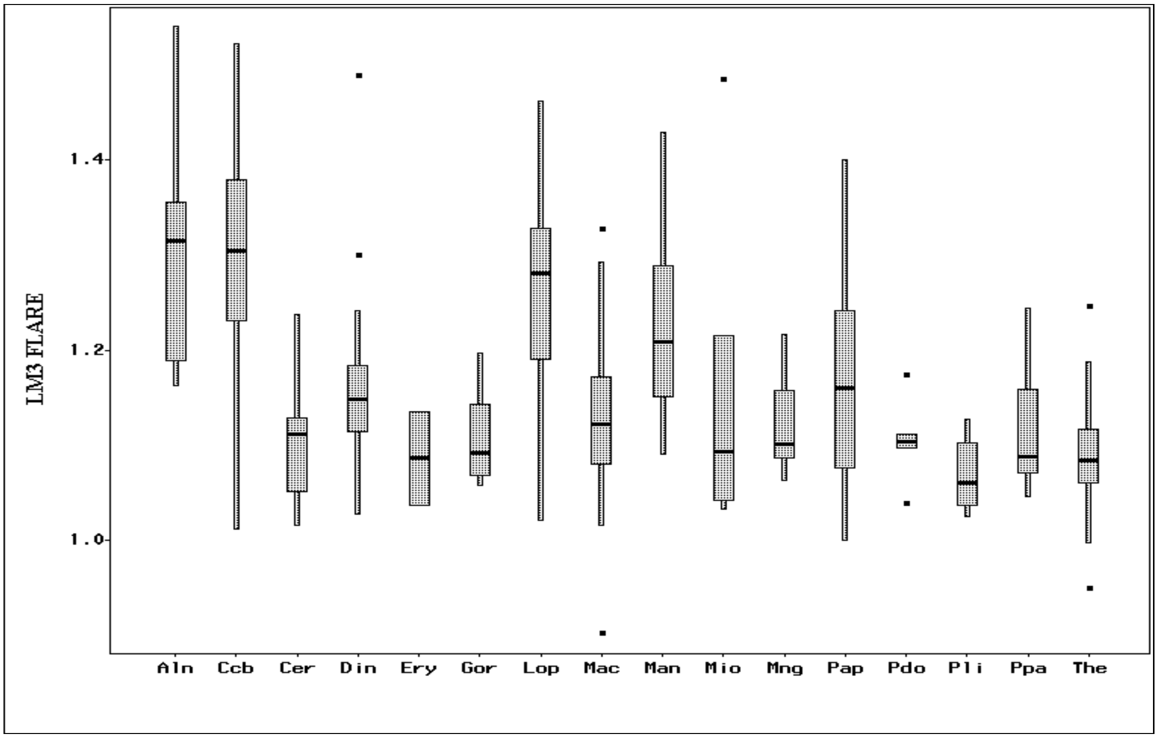


Figure 4.8 M_3 basal flare, Mesial Width / Mesial Notch Width. Abbreviations as in figure 4.6.



Postcrania

There are several postcranial elements associated with the male skull AL363-1a-b. These are discussed below under the different anatomical regions. AL363-12 is a distal fragment of a right humerus that may also represent *Parapapio*. In spite of the large samples from South Africa, this collection is the only postcranial sample known that is directly associated with diagnostic cranial remains.

Axial skeleton

AL363-1g preserves all three sacral vertebrae. It is slightly larger than the sacrum associated with the female *T. darti* partial skeleton AL193-6. In morphology it appears to be typical for the family, with a well-developed distal body and zygapophyses for articulation with the first caudal vertebra. The neural canal is also large and patent distally. AL363-1k is a thoracic vertebra, which appears typical for cercopithecids. AL363-1h/8 is a fragment of a right rib.

Forelimb

AL363-12 is a right distal humerus, preserving the distal ½ of the shaft, although there is considerable damage, so that only the distal 3 cm are well preserved. This specimen is not associated with the cranial material, and almost certainly represents a different individual from AL363-1. It is morphologically distinct from the humeri associated with *T. darti* and those identified as *T. darti* by Krentz (1992; Delson et al., 1993). In size it is slightly larger than the *T. darti* sample from Hadar. The medial epicondyle is long, large, and projects medially. The capitulum is round and projecting, and the zona conoidea is flat. The medial trochlear flange is short, and does not come to a sharp angle, unlike those of the *T. darti*. The supraulnar fossa is very deep and rounded. The supraradial is quite shallow and low. This specimen has a *m. brachioradialis* flange that is less prominent than *T. darti*, and is significantly shorter proximodistally. Posteriorly, the olecranon fossa is broad and deep. There is a small foramen on its superior surface. Ciochon (1993) identified this specimen as *Rhinocolobus turkanaensis*, but Delson (1984; Delson et al., 2000) considered it more likely to be *Parapapio*. The latter view is followed here as the supraulnar fossa is deeper than the supraradial. Furthermore it is from the same locality as several other specimens of *Pp.* cf. *jonesi*. One feature that may argue for its being *Rhinocolobus* is its comparatively large size, and Ciochon's identification remains a reasonable possibility.

Hindlimb

Proximal and distal ends of the right femur are preserved. AL363-1c preserves the entire proximal end including the greater trochanter, head and shaft to approximately 1-cm distal to the lesser trochanter. It has a relatively long neck in comparison to the other proximal femora from Hadar and the sub-Sidi Hakoma Tuff strata in the Middle Awash. The head is not at cranially oriented, the greater trochanter is approximately 9 mm taller than the head and hooks sharply medially. The lesser trochanter is long and medially oriented. The gluteal fossa extends inferior to the *m. quadratus femoris* insertion. The fovea capitis is short and oval. AL363-1d is the distal end of the same femur. It is very similar to the other distal femora from the same horizons (most of these presumably represent *T. o. darti*) except that the patellar groove may be deeper and narrower than the others. It also has higher medial and lateral margins.

AL363-1f/l is a right fifth metatarsal. In size it is quite large, being similar to those of large male Chacma baboons, but smaller than those of male Mandrills. It is considerably smaller than the fifth metatarsal of *Paracolobus chemeroni* (KNM-BC 3aa). It is similar in overall morphology to fifth metatarsals of other cercopithecids. An interesting feature is the proximal articulation for the cuboid. It is triangular in outline and is continuous with the articular surface for the fourth metatarsal medially. Inferiorly and laterally, there is a small sulcus between the cuboidal articular surface and the edge of the basal tubercle. This sulcus is larger than in modern *Papio*, but not as deep or strongly rimmed as it is in *Mandrillus*. There is also a small articular facet on the inferior surface of the tubercle for a sesamoid bone.

Remarks

While the most completely preserved individual of this sample shows several unique features, many of these may be explained by individual variation. However, there are a number of features that may well warrant specific distinction. The most striking are the shape of the nasals, the thickness of the supraorbital torus, and the narrow and deep palate. Before it can be determined whether the Afar taxon is conspecific with any of the South African forms a comprehensive review of the large South African sample of *Parapapio* is required with more thorough diagnoses of those taxa completed. Until such a revision is complete, the Afar material is best left as *Parapapio* sp. indeterminate. It resembles *Pp. jonesi* and *Pp. whitei*, but is distinct from *Pp. broomi* in that the nasals are more prominent, facial fossae are variably present (one of two specimens have them), the premaxillae are more anteriorly projecting, and the temporal lines are more strongly marked. The Afar sample resembles *Pp. jonesi* more than it does *Pp. whitei* due its relatively shorter rostrum and considerably smaller size. Lastly, it shows none of the distal molar reduction and anterior molar lengthening of *Pp. antiquus* (Maier, 1970).

Regardless of whether this is a new species or not, the Hadar material is the only definitive evidence of *Parapapio* in East Africa in the Pliocene and Pleistocene. This is because *Parapapio* can only be diagnosed based on facial evidence. All other samples or individual specimens that have been assigned to *Parapapio* from the Pliocene or Pleistocene of East Africa lack facial material (e.g. Laetoli, Kanapoi, and Omo). These assignments, including the generic allocation of *Pp. ado*, therefore must be considered tentative.

Genus *Papio* Erxleben, 1777

(= or including *Cynocephalus* Geoffroy and Cuvier, 1795; *Chaeropithecus* Gervais, 1839; *Choiropithecus* Reichenbach, 1862; *Comopithecus* Allen, 1925; *Dinopithecus* Broom, 1937.)

Type species: *Papio hamadryas* (Linnaeus, 1758)

Other included species: *P. izodi* Gear, 1926; *P. ingens* (Broom, 1937); *P. quadratirostris* Iwamoto, 1982.

Generic Diagnosis:

This diagnosis is modified from those of Freedman (1957) and Szalay and Delson (1979). *Papio* is a genus of medium to very large sized papionins. It possesses a marked anteorbital drop, which is distinct from *Parapapio*, *Lophocebus, Cercocebus* and some *Macaca*. The muzzle is "squared" in cross-section, with a flattened dorsum and relatively vertical sides, which is shared only with *Theropithecus (Omopithecus)* and different from *T. (Theropithecus), Parapapio, Pliopapio*, and *Macaca* (other than the Sulawesi species). The molars are more straight sided and the crowns less flaring than those of *Mandrillus*, *Lophocebus*, and *Cercocebus*. The P4 is not enlarged relative to the M1 as it is in *Mandrillus* and *Cercocebus*. The postcranium is only known for the extant species, which is more terrestrially adapted than other cercopithecids besides *Theropithecus*.

Papio (Papio) Erxleben, 1777

(= or including: *Papio* Erxleben, 1777. *Cercopithecus* Erxleben, 1777, in part. *Cynocephalus* Geoffroy and Cuvier, 1795. *Simia (Chaeropithecus)* Gervais, 1839; Senechal, 1839. *Choeropithecus* Blainville, 1839. *Hamadryas* Lesson, 1840. *Cercopithecus* Linnaeus, 1758: Peters, 1853, in part. *Choiropithecus* Reichenbach, 1862. *Comopithecus* Allen, 1925. *Dinopithecus* Broom, 1937: Broom, 1940, in part. *Papio (Chaeropithecus)* Gervais, 1839: Ellerman, Morrison-Scott and Heyman, 1953; Szalay and Delson, 1979, in part. *Parapapio* Jones, 1937: Freedman, 1957, in part.)

Type species: *Papio hamadryas* (Linnaeus, 1758)

Other included species: *P. izodi* Gear, 1926

Subgeneric diagnosis:

A subgenus of *Papio* distinguished from *P. (Dinopithecus)* by the presence of well marked postcanine and suborbital fossae. The vault generally lacks a sagittal crest, or if one is present, it is found only in the vicinity of inion. The mandibular symphysis has well marked mental ridges, especially in the males. The corpora generally have extensive and deep corpus fossae.

Papio sp. A.

Afar specimens included: BOU-VP-12/9, ?136, ?BOU-VP-8/2

Range: ~ 2.5 Ma

Distribution: <u>Bouri Fm., Hatayae Mbr</u>.

Description:

There is a single cranial specimen known for this taxon, BOU-VP-12/9 (plate 10). It is a slightly crushed rostrum, preserving most of the premaxillae, maxillae, nasals and a small amount of the right zygomatic bone from a female individual and separate, but associated anterior part of the calvaria. The right P^3 through M^2 are present and well preserved. The left P^3 through M^2 are also present, but damaged. The alveoli for the canines and incisors are also preserved. The neurocranial fragment is crushed obscuring much of the morphology. It preserves parts of the frontal, sphenoid, ethmoid, and small amounts of the parietals and left temporal. The other two specimens are more tentatively assigned.

In dental size it is similar to smaller subspecies of *Papio hamadryas*, such as *P. h. papio* and *P. h. hamadryas*, as well as *Parapapio broomi*, and Papionini B from the Turkana basin. The muzzle is also similar in size to females of smaller subspecies of *P. hamadryas*. Dental measurements are given in table 4.4.

Rostrum

The infraorbital foramina are multiple bilaterally, and are not arranged in an arc as they are in *Theropithecus*. They are positioned anterior and inferior to the orbit, more distally on the muzzle than they are in *Theropithecus* or *Pliopapio*, surrounding the base of the maxillary ridge. The maxillary ridges are fairly prominent and well defined for a female individual. They are relatively thin and sharply defined in comparison to the ridges of *P. hamadryas*, but are basically rounded in cross-section. They originate near the superior end of the canine root, but do not arise directly from it as they do in most male specimens. Maxillary fossae are well defined but not deeply excavated. They are deeper and more strongly delimited than they are in *Theropithecus oswaldi, Parapapio* and *Pliopapio*, but do not approach the depth seen in extant *P. hamadryas hamadryas* or *P. h. anubis*. They are actually quite similar in depth to those of *P. hamadryas kindae* and *P. izodi*. The fossae are deepest suborbitally where they slightly undercut the inferior orbital rim and mark the anterior surface of the zygomatic bone. The maxillary ridges mark their superior limit, but the inferior border is faint. They are shallow and poorly delimited anteriorly behind the canine as well.

The dorsal surface of the rostrum is flattened, as it is in *Papio, Mandrillus*, and *T. (Omopithecus)*, and clearly distinct from *Parapapio, Pliopapio, T. (Theropithecus)*, and most *Macaca*. The nasals are prominent above the flattened muzzle surface, particularly posteriorly. They are raised fairly sharply above this surface giving them a concavo-convexo-concave cross-sectional shape as described by Eck (1993). This region is actually quite similar to that of Omo 42 ’72 1, Omo 207 ’73 1762 and L185-6 [*P. (Dinopithecus)* from the Shungura Formation]. The profile is incomplete due to damage, but based on the portion of the nasals preserved on the rostrum and on the frontal fragment, this specimen clearly possessed a distinct anteorbital drop, similar to that of other *Papio* and *Mandrillus*. Anterior to the interorbital region there is a distinct change in slope, and the profile flattens to a nearly straight line through rhinion. Rhinion is not preserved, but enough of the region is present to see that it would not have been prominent.

The premaxillae are large and project fairly far anteriorly. There is a small diastema between the canine and lateral incisor alveolus. The nasal process extends approximately 2 cm posterior to the piriform aperture before it becomes covered by the maxilla. In superior view, the premaxillomaxillary suture is straight from its appearance on the muzzle dorsum around the piriform aperture before arching laterally at about the midpoint of the piriform aperture.

The piriform aperture is reasonably well preserved, particularly on the left side. It is similar to other papionins in outline, being broad and oval with a pointed inferior limit at nasospinale. The inferior part of the outline is defined by the roots of the central incisors, which are large and prominent on the anterior surface of the premaxillae. In profile view, the outline of the aperture is inclined at an angle of approximately 30º to 35º to the occlusal plane.

The maxillary dental arcade is parabolic in outline, similar to other females of *Papio*. It is widest at the M^2. The premolars are roughly parallel and at the same width as the M^1. The canines are a bit closer together than the premolars. The incisive alveoli on the premolars project anteriorly is in an anteriorly projecting arc. In lateral view, the maxillary dentition is nearly straight or slightly concave down. The palate relatively long and narrow, and fairly deep. It is even in depth from the premolars posteriorly. The alveolar processes are nearly perpendicular to the palate.

Midface and zygoma

The anterior surface of the zygomatic process arises from the maxilla at the level of the distal most M^2. This is similar to its position in females of *Papio hamadryas sspp.* and *P. izodi*. It is anterior to the position in *Papio* males. The anterior surface of the zygoma projects laterally and slightly posteriorly, but is not as swept back as in *Pliopapio*, *P. (Dinopithecus)*, *Mandrillus* or *T. (Theropithecus)*. Also, unlike these genera, the anterior surface of the zygoma is marked by a shallow suborbital fossa. The inferior surface of the zygoma originates low on the lateral surface of the alveolar process, and curves smoothly superiorly and laterally.

Orbital region

The orbital region is only incompletely preserved. The supraorbital rim and glabellar area are preserved on the crushed neurocranium, and the inferior limit of the orbit is preserved on the right side of the muzzle. On both elements it is clear that the interorbital pillar was narrow, as it is in nearly all papionins. Glabella is prominent, the supraorbital rim thin, and typical of female *Papio*. The lacrimal fossa lies slightly anterior to the orbital rim, but it is not entirely within the lacrimal bone.

Calvaria

The calvaria is heavily damaged, but a few details can be seen. There was a distinct ophryonic groove present posterior to the supraorbital torus. The temporal lines are not strongly marked, and do not curve sharply towards the midline behind the orbits. From what is preserved, it appears most likely that there would not have been a sagittal crest present.

Mandible

There are no mandibles that can be assigned to this taxon with complete certainty, but BOU-VP-8/2 is a small edentulous mandibular corpus fragment of an adult male preserving the right half of a symphysis posteriorly to the canine alveolus. It is significantly smaller than the male mandibles of *Theropithecus oswaldi oswaldi*. The symphysis is fairly sloping in lateral view and pierced by a median mental foramen. Relatively deep corpus fossae are present, which are typical of most species and subspecies of *P. (Papio)*, but are generally not deeply excavated in *T. o. oswaldi* or *P. (Dinopithecus)*. This is also different from Papionini size B in the Turkana basin, particularly the mandible ER 6064 from the Upper Burgi Member of the Koobi Fora Formation. Therefore, this specimen is tentatively assigned to the same taxon as the rostrum based on its relatively small size and well developed corpus fossae.

Table 4.4 Dental dimensions for *Papio* sp. A, *Papio* cf. *hamadryas*, and papionini indet. size B.

Papio sp. Bouri

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
BOU-VP-12/9	3	6.6	6.6		5.2	3	7.7	6.7		6.2

BOU-VP-12/9	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
UM1	11	9.2	8.1	8.9	7.9	9.9					4.2	5.0
UM2	8	11.0	9.4	10.0	8.2	11.3					5.0	8.8
UM3	3	10.9	8.9	8.9	6.4	11.3	5.0	3.2	5.3	4.8	4.8	7.8

Papio cf. *hamadryas* from Bodo

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
KL279-1	3			12.6	5.1	9.4						

Papionin from Belohdelie Member, specimen WIL-VP-1/2

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
WIL-VP-1/2	4.4	6.7	9.5	4.6	8	6.1	6.1			

WIL-VP-1/2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
LM1	16	6.9		7.9		8.3					3.4	4.8
LM2	13	9.2				10.7					3.6	5.3
LM3	8			7.8	7.4						3.2	

Dentition

Although the upper incisor crowns are not preserved, it is apparent from the roots that they were large relative to the other teeth. Their alveoli are larger than those of the *T. o. oswaldi* male KL39-1, even though BOU-VP-12/9 is a smaller animal, and has significantly smaller molars. The canine alveoli are small, which is the basis for identifying it as female. The upper premolars are bicuspid teeth and basically typical of cercopithecids. The cusps are relatively low and bunodont. Both P^3s are damaged, but it can be seen that the protocone was smaller than the paracone giving the tooth a triangular outline in occlusal view. The P^4 is a large tooth, being longer and wider than the P^3, but not as large as those of *Allenopithecus, Mandrillus,* or *Cercocebus*. It also has a more squared outline in occlusal view, due to a larger talon than the P^3.

The molars are typical papionin teeth. The cusps are low and bunodont and the buccal notches are not deep. There is marked basal flare to the crown, and the cusp tips are closely approximated. The molars are not as flaring as those of *Mandrillus, Cercocebus* or *Lophocebus*, however (see figures 4.7-4.8). On all of the molars, the mesial loph is bucco-lingually broader than the distal, although the difference is greatest on the M^3. The preprotocristae are weakly developed. The wear pattern is the typical cercopithecid pattern with the lingual cusps wearing faster than the buccal.

There are no lower teeth definitely associated with this specimen, but there is a distal fragment of a right M_3, BOU-VP-12/136. It is clearly from a non-*Theropithecus* papionin, and is of the right size to be this taxon. The possibility that this tooth represent another small papionin taxon (such as *Parapapio*) cannot be ruled out, however. It preserves the hypoconid, entoconid, and hypoconulid. The cusps are low and bunodont, and otherwise typical of papionins.

Papio cf. hamadryas

Afar specimens included: KL279-1

Range: 2.5 Ma to Recent.

Afar range: 0.64 Ma to Recent

Distribution: Upper Bodo Sand Unit; Asbole; Olduvai, Masek Beds; Lemagrut Karongo (near Laetoli); Sterkfontein Mbr. 4, ?Mbr 5.; Bolt’s Farm; Gladysvale; Drimolen; Kromdraai A,B; Schurweburg; Swartkrans, Mbs. 1-3; Coopers.

Description:

KL279-1 is an isolated left upper molar of a medium to large-sized papionin, from the Upper Bodo Sand Unit, and was listed by Kalb and colleagues (1984). It is the buccal half of the tooth, preserving the paracone and metacone. The cusps are relatively low, and the buccal notch is not deep, and is clearly not *Theropithecus*. Although the buccal surface is not the most distinctive, it appears to be less flaring than is the case in *Mandrillus, Cercocebus* or *Lophocebus*. In length it is comparable to smaller subspecies of extant *Papio hamadryas* (see table 4.4 for dental measurements), and is considerably smaller than all known *Gorgopithecus* and *P. (Dinopithecus)*. It is 1.5 myr younger than the youngest known *Parapapio*, making it unlikely to represent this genus, although this cannot be ruled out based on morphology. Furthermore, given the presence of definite *Papio hamadryas* ssp. at the nearby site of Asbole (Alemseged and Geraads, 2001) KL279-1 most likely represents this species.

Papionini gen. et sp. indet. cf. Size B: Eck, 1976
Afar specimens included: WIL-VP-1/2

Description:

WIL-VP-1/2 (plate 12) is a left mandibular corpus fragment of a small female papionin from the Belohdelie Mbr. of the Sagantole Fm., similar in dental size to *Pp.* cf. *jonesi* and KNM-ER 6064 (dental dimension in table 4.4). It is also similar in dental size to WEE-VP-1/1, a mandible that may represent primitive *Theropithecus*. It is considerably larger than *Pliopapio alemui*. It preserves most of the left corpus and ramus, including the coronoid process, but lacking the gonial area and condyle, the symphysis is damaged as well. Of the dentition, P_3 through M_2 and the distal ¾ of the M_3 are present. The dentition is heavily worn indicating an older adult individual. The P_3 mesiobuccal flange is short identifying this individual as female. The lateral surface of the corpus lacks any indication of a fossa, and although the symphysis is damaged there do not appear to have been strongly developed mental ridges present. In lateral view, the corpus can be seen to deepen anteriorly. Not enough of the inferior margin is intact to determine exactly where the deepest point would have been, but it was likely near the M_1. The ramus was not dorsoventrally tall, but was also fairly anteroposteriorly short. There was a modest triangular depression on its lateral surface. The oblique line is not strongly marked, and the extramolar space is narrow. There is a broad retromolar gap in lateral view. The thin corpus, narrow extramolar sulcus, and low ramus are features more consistent with *Parapapio* than with *Theropithecus*. The damaged and worn condition of the dentition makes this specimen difficult to classify. It is possibly the same taxon as WEE-VP-1/1, but the preserved morphology of the M3 is less *Theropithecus*-like. In total, this specimen seems more likely to represent a small papionin other than *Theropithecus*, perhaps *Pp.* cf. *jonesi*.

Genus *Theropithecus* Geoffroy, 1843

(= or including *Macacus* Rüppell, 1835 (in part). *Gelada* Gray, 1843. *Simopithecus* Andrews, 1916. *Theropythecus* Vram, 1922 (lapsus?). *Papio* Erxleben, 1777: Broom and Jensen, 1946; Buettner-Janusch, 1966 (in part). *Dinopithecus* Broom, 1937: Arambourg, 1947; Broom and Hughes, 1949 (in part).

Brachygnathopithecus Kitching, 1952 (in part). *Gorgopithecus* Broom and Robinson, 1949: Kitching, 1953 (in part).)

Type species *Theropithecus gelada* (Rüppell, 1835)

Other included species: *T. oswaldi* (Andrews, 1916), *T. brumpti* (Arambourg, 1947)

Generic Diagnosis:

Eck and Jablonski (1987), Jablonski (1993) and Delson (1993) have all provided recent diagnoses for the genus *Theropithecus* and these are followed here. *Theropithecus* is a medium to very large size papionin. The neurocranium can be distinguished from *Papio (Papio), Parapapio, Mandrillus,* and *Pliopapio* by the presence of a well developed anteriorly positioned sagittal crest. The postorbital region is greatly constricted and the zygomatic arches are widely flaring, yielding a large infratemporal fossa. The lower portion of the face is tall, due to the posterior portion of the maxilla being deep, resulting in the temporomandibular joint being elevated relative to the occlusal plane. A steep anteorbital drop characterizes the facial profile. This is unlike the anteorbital region of *Parapapio, Cercocebus, Lophocebus,* and some *Macaca*. Furthermore, it is generally steeper and the vertical segment is longer than in *Papio* and *Pliopapio.* The premaxillae are short in comparison to the maxillae, unlike *Pliopapio, Papio, Lophocebus, Mandrillus*, *Cercocebus* and *Macaca*.

Theropithecus is most clearly distinguished from all other papionins by its dentition. The incisors are small relative to the molar teeth, particularly in comparison to *Papio, Mandrillus, Cercocebus,* and *Lophocebus*. The molar teeth are highly derived and easily diagnosed relative to all other cercopithecids. They are high crowned and straight sided with a low amount of basal flare (see figures 4.7-4.8) and large amount of cuspal relief, deeply excavated notches and foveae. The cusps themselves are columnar in form, being separated by deep basins. On the lower molars, the median cleft is flattened at its base into a "pocket", the lophids are angled mesiolingually, and there is sometimes a large distal accessory cuspule present on M_{1-2}.

While *T. gelada* has several known autapomorphies in the postcranium relative to other papionins, only a few are known for the fossil species. One of the most important is the presence of elongate first and short second metacarpals. This feature gives *Theropithecus* the highest opposability index of any cercopithecid and is related to “manual grazing” behavior. It is known in *T. brumpti* from the Omo (Jablonski, 1986). The femur shows a reverse carrying angle, possibly related to “bottom shuffling” locomotor behavior (Krentz, 1993).

Theropithecus (Theropithecus) Geoffroy, 1843

(= or including *Macacus* Rüppell, 1835 (in part). *Gelada* Gray, 1843. *Simopithecus* Andrews, 1916. *Theropythecus* Vram, 1922 (lapsus?). *Papio* Erxleben, 1777: Broom and Jensen, 1946; Buettner-Janusch, 1966 (in part). *Dinopithecus* Broom, 1937: Broom and Hughes, 1949 (in part). *Brachygnathopithecus* Kitching, 1952 (in part). *Gorgopithecus* Broom and Robinson, 1949: Kitching, 1953 (in part).)

Type species *Theropithecus gelada* (Rüppell, 1835)

Other included species: *T. oswaldi* (Andrews, 1916)

Subgeneric diagnosis:

Delson (1993) divided *Theropithecus* into two subgenera, which are recognized here. His diagnoses are followed, along with descriptions by Eck and Jablonski (1987) and Leakey (1993). *T. (Theropithecus)* are medium to very large members of *Theropithecus* distinguished from *T. (Omopithecus)* in all of the following features. The muzzle is shorter and the face more airorhynch. The maxillary ridges are either weakly developed or absent. When they are present, they are rounded in cross-section, unlike those of *T. brumpti* that are more triangular. The dorsal surface of the muzzle is sellar. It is rounded and convex in parasigittal cross-section and concave in profile. The zygomatic arch is robust, but not greatly expanded and flared. The greater tuberosity of the humerus projects proximally above the head (Krentz, 1993).

Theropithecus oswaldi (Andrews, 1916)

(See subspecies for synonymy.)

Holotype: BMNH-M11539 (lectotype) from Kanjera, Kenya

Subspecies included: *T. o. oswaldi* (Andrews, 1916), *T. o. leakeyi* (Hopwood, 1934), *T. o. darti* (Broom and Jensen, 1946).

Afar specimens included: see subspecific descriptions below.

Range: 3.4 – ~0.4 Ma (3.85 – ~0.4).

Distribution: see subspecific descriptions below, plus ?Mirzapur, India; ?Cueva Victoria, Spain.

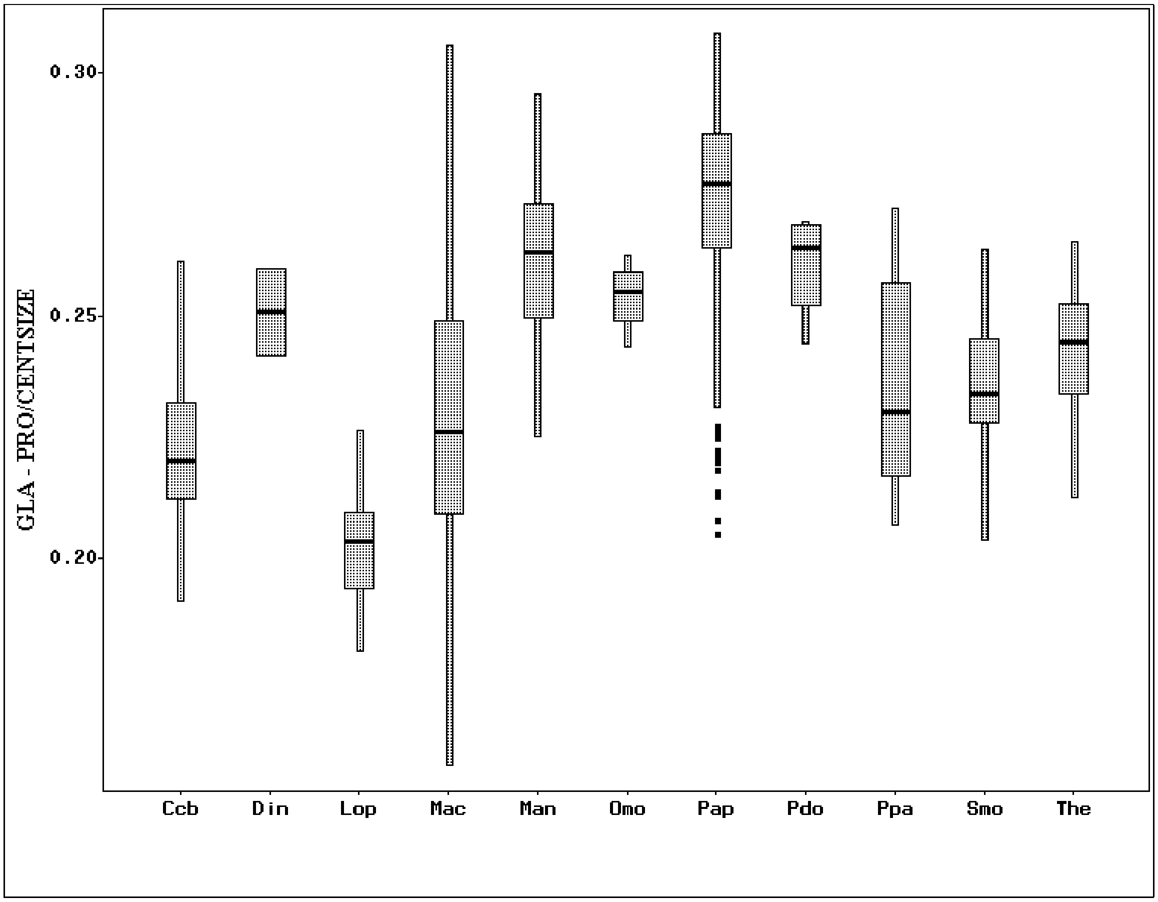
Specific diagnosis:

The concept of *Theropithecus oswaldi* used here follows that of Leakey (1993). Three chronologically sequential subspecies are recognized within Africa, each of which spans a large geographic area. This species is distinguished from the other undisputed members of the genus *Theropithecus*, *T. gelada* and *T. brumpti* largely on the basis of characters in the cranium and anterior dentition.

There are several morphological trends displayed by the subspecies of *T. oswaldi*, which show their origins in *T. o. darti* and their most extreme expressions in *T. o. leakeyi*. These trends are also features that distinguish this species from *T. brumpti* and to a lesser extent *T. gelada*.

Through time there is a general increase in body size from early *T. o. darti* (similar in size to *T. gelada*) to the largest *T. o. leakeyi* (similar in size to *Gorilla* females) (e.g. Jolly, 1972; Eck, 1987; Krentz, 1993; Delson et al., 2000). Thus, early members of this species can be separated from *T. brumpti* partly because they are smaller, and later members can be distinguished from *T. gelada* because they are larger. At the same time, there is a decrease in the length of the rostrum relative to overall cranial size (see figure 4.9), and a decrease in the size of the premaxillae relative to the rostrum. There is also a trend towards increased facial depth and airorhynchy. Finally, there is an increase in the size of the sagittal and nuchal crests. Some of these features are simply aspects of allometric scaling that are common to most papionins. Others, such as the decreasing rostral length, are in fact opposite to general papionin scaling patterns.

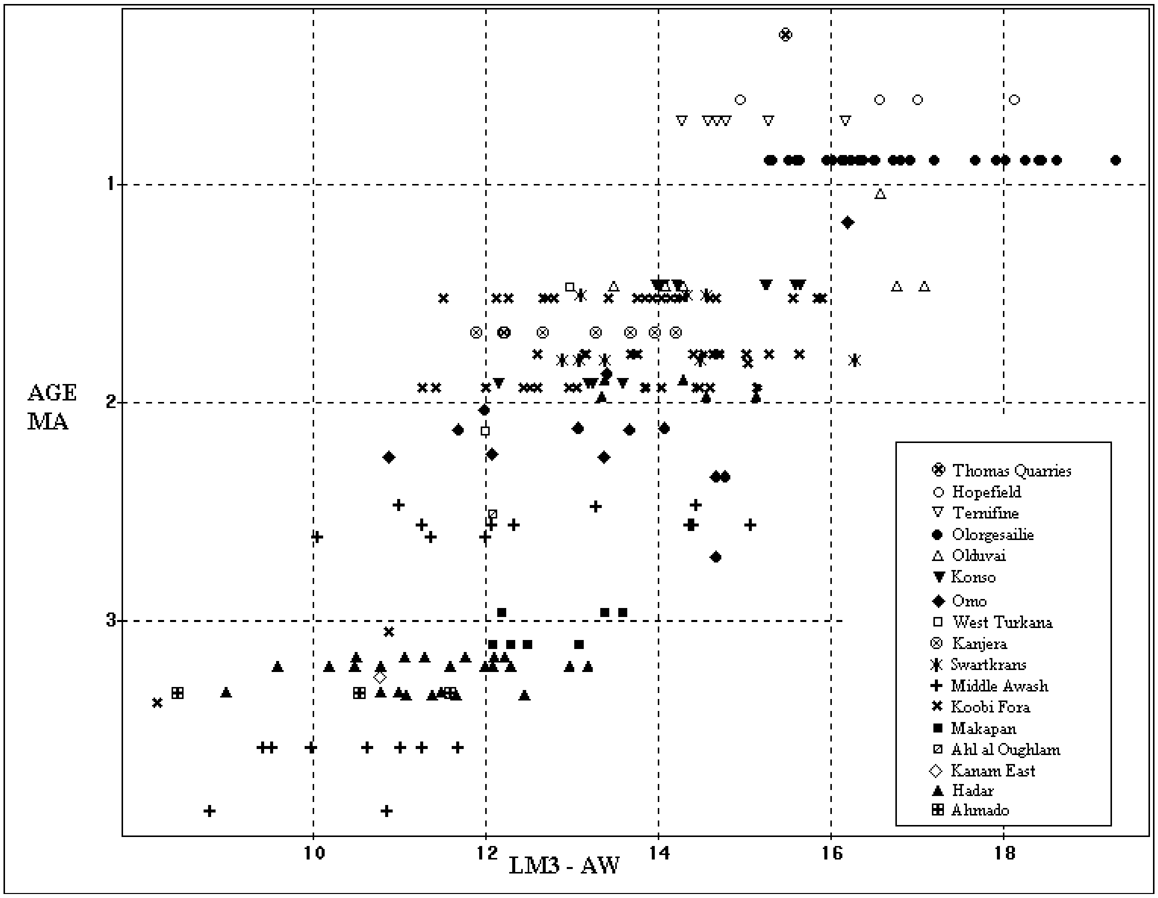
Figure 4.9 Glabella to prosthion / Centroid size. Abbreviations as for figure 4.3.



The symphysis has only weakly marked mental ridges, and in early *T. o. darti*, is more sloping than that of *T. brumpti* or *T. gelada*. The mandible either entirely lacks corpus fossae, or they are only lightly developed (except for some early *T. o. darti* that may have larger fossae). This is distinct from both *T. brumpti* and *T. gelada*, which typically have well developed corpus fossae.

Related to the decrease in premaxillary size through time, there is a progressive decrease in incisor size, and a decrease in canine height, if not caliber (Leakey, 1993). The reduction in canine size leads to a shortening of the P_3 mesiobuccal flange, particularly in males. Both of these features separate *T. oswaldi* from *T. brumpti* and *T. gelada* and may be atypical of size trends in other papionins. Finally, there is a substantial increase in dental size, particularly of the distal molars, through time (see figure 4.10). Along with the increased size, there is an increase in crown complexity, which makes *T. o. leakeyi* molars distinct from those of *T. gelada*.

Figure 4.10. M_3 Mesial width vs. age in Ma.



Theropithecus oswaldi darti (Broom and Jensen, 1946)

(= or including *Papio darti* Broom and Jensen, 1946; *Simopithecus darti* Freedman, 1957; *S. oswaldi darti* Singer, 1962; *T. (S.) darti darti*, Jolly, 1972; *T. (S.) darti* Szalay and Delson, 1979; *T. darti* Eck, 1993, Delson, 1993)

Holotype: UWMA MP1 (=M201, 1326/1)

Afar specimens included: see appendix 3.

Range: 3.4 - 2.6 Ma

Afar range: 3.4 – 2.92 Ma

Distribution: Hadar Fm. Sidi Hakoma - Kada Hadar Lower; Ahmado, Leadu; Maka; Bunketo; Matabaietu; Wee-ee; ?Shungura Fm., C-6; Koobi Fora Fm. Tulu Bor; ?Kanam East; Makapansgat.

Subspecific diagnosis:

An early subspecies of *T. oswaldi* smaller in cranial, dental, and postcranial size than *T. o. oswaldi* and *T. o. leakeyi*. Rostrum is long relative to overall cranial size. Maxillary and mandibular fossae are variable, but often more pronounced than later subspecies of *T. oswaldi*. The incisors are relatively large, although smaller than those of *Papio*. The male canines are long, being similar in size to those of *T. gelada* and *Papio*. The P_3 mesiobuccal honing flange is also relatively long. The molar teeth show the specializations of the genus, but they are weakly developed in comparison to later subgenera.

Description:

The collection of *T. o. darti* from the Afar region is the largest of this taxon to date. Eck (1993) has thoroughly described all of the *T. o. darti* cranial material from the Hadar Formation that was available at the time. Krentz (1993) has also described the long bones of the forelimb and hindlimb catalogued in Delson et al. (1993). Some additional material has been collected at Hadar since these studies were published. Additionally, specimens from Leadu and Ahmado near Hadar are not yet described. Samples of

Theropithecus from below the Sidi Hakoma Tuff at Maka, Bunketo, Matabaietu and Wee-ee are undescribed, although they were mentioned in the faunal list of White *et al.* (1993). This section will largely follow Eck's description, but where possible it will emphasize the new material that was not available for his analysis, particularly where it includes an anatomical region not previously known.

Relatively complete crania and more fragmentary cranial material is well represented in the Afar sample. AL205-1a-c is a male cranium with most of the rostrum, zygomatic arches, and neurocranium, and damaged left and right C-M_3 (and an associated mandibular fragment). It is lacking most of the interorbital area and the lateral orbital margins, with some damage to the dorsal part of the rostrum, and basicranium. AL412-1 (plate 13) is a male partial cranium that largely preserves the neurocranium and rostrum, but the premaxillae and zygomata are missing and the palate and neurocranium are covered in matrix. MAK-VP-1/100 (plate 12) is a fragmentary partial cranium of a young adult male. The neurocranium, supraorbital torus, interorbital pillar, and right maxilla with C^1-M^3 are all represented. AL321-12 is a nearly complete female cranium lacking only the zygomatic arches, incisors, canines, and right P^3. AL185-5/AL154-95 (plate 14) are the left and right maxillae and neurocranium of a subadult female (associated with a mandible) with the right I^2, left and right P^4 through M^2, and the crypts of the M^3's opening (AL185-5 was described by Eck [1993] AL154-95 is new, but fits across two contacts with AL185-5). AL187-10 is a well-preserved neurocranium and supraorbital torus, probably of a male. AL319-10 is the posterior and inferior portion of a neurocranium, most likely that of a male. It preserves most of the basicranium, the temporal bones, and the area around inion, which is marked by a tall sagittal crest. There are also 22 additional more maxillary fragments, which are listed in appendix 3.

In overall cranial size, this material is similar to *T. gelada*, and medium-sized *Papio hamadryas* subspecies, such as *P. h. cynocephalus*. Both sexes are smaller than in *T. brumpti*, *T. o. oswaldi* and *T. o. leakeyi*, as well as *Dinopithecus* and *Paradolichopithecus.* The dentition of *T. o. darti* from the Afar region is slightly smaller than that from Makapan, and similar to that of most subspecies of *Papio hamadryas* in size. It is smaller in dental size than younger subspecies of *T. oswaldi*. Dental dimensions of *T. o. darti* are given in table 4.5.

Rostrum

The rostrum is shorter in length relative to cranial size than is that of most *Papio* and *Mandrillus*, and similar in length to that of *T. gelada* and *T. o. oswaldi* (see figure 4.9). It is longer than that of *T. o. leakeyi*. The maxillary ridges are poorly expressed. They range from totally absent in AL321-12 and AL412-1 to weakly developed in AL205-1 and MAK-VP-1/100. When present, they are low and rounded in cross-section. They originate at the bulge around the canine root, and extend to the zygomatic process of the maxilla. The maxillary fossae are shallow and poorly developed in all specimens, but there is some variability. When present, they are more distinct anteriorly, below the canine root.

The dorsal surface is well preserved in AL321-12, and less completely in AL205-1, AL134-5, MAK-VP-1/100, AL185-1 and AL412-1. It is basically parabolic in paracoronal cross-section, although it is more “squared” in outline than those of many *T.*

o. oswaldi. The nasals are variably prominent above the dorsal surface the muzzle. In AL321-12 they are more prominent, whereas in AL134-5 and AL205-1 they are less well marked. Although they are absent in MAK-VP-1/100, it is apparent from the surface that is preserved that they probably would not have been as prominent as AL205-1 either. The rostral profile is deeply convex, and steep in the anteorbital region. Thus the surface of the muzzle dorsum is basically sellar being convex in the paracoronal plane and concave in the sagittal. This surface is sometimes interrupted a concavo-convexo-concave cross-section in the area of the nasals. The nasals are longer relative to rostral length than those of *T. gelada* (see figure 4.3). This is a reflection of the face being less airorhynch overall.

The piriform aperture is preserved in several specimens, particularly AL321-1, and AL310-19 (a juvenile male snout with left P^{3-4}, right P^{3}, and erupting canines), but also partially in AL205-1 and AL185-1/AL154-95. In outline it is typical of most papionins. It is basically oval in outline with a “V-shaped” inferior limit. It is broad in comparison to its length, although not as broad as that of *T. o. leakeyi*. The superior portion of its outline is sharply delimited, but its more inferior borders are more rounded. Viewed laterally, the piriform aperture slopes at an angle of approximately 30º to 35º relative to the occlusal plane (although this angle is larger in the juvenile AL310-19). This is similar in slope to that of *T. o. oswaldi*, but more acute than that of *T. o. leakeyi*. Perhaps this morphology reflects the larger anterior dentition of *T. o. darti*. Anterior nasal tubercles are absent.

The maxillary dental arcade of the male specimens is “U”-shaped in outline, with the canine alveoli forming the corners. The molars are typically arranged in a short arc, with the M2 positioned slightly more laterally than the others are. The molar series is

Table 4.5 Summary dental dimesnions for *Theropithecus oswaldi darti*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.21. For descriptions of measurements see chapter 3.

	Theropithecus oswaldi darti												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^2	2	6.4	0.3	6.2	6.6	11.3	0.4	11.0	11.5	5.8	0.7	5.3	6.3
C^1 (?)	1	6.4								7.0			
C^1 (?)	3	9.6	0.7	9.2	10.1	11.1	1.4	10.1	12.1	32.0			
P^3	5	7.8	0.5	7.0	8.3					7.0	0.5	6.2	7.6
P^4	9	8.5	0.5	7.7	9.3					7.3	0.7	6.0	8.1
M^1	12	9.7	1.0	8.2	12.1	9.3	1.0	8.0	11.5	11.3	0.8	10.5	12.7
M^2	9	11.6	0.7	10.7	12.9	10.7	0.7	9.9	11.7	13.5	1.0	12.3	15.2
M^3	7	11.7	1.1	10.2	13.3	10.1	1.2	7.8	11.3	13.8	1.2	12.2	15.5
M^x	13	11.5	1.5	8.3	13.7	10.7	1.5	8.0	13.4	13.0	1.4	10.4	15.5
dI^1	1	3.2				6.3				3.8			
dC^1	1	4.2				6.9				5.7			
dP^3	2	6.5				7.1	0.6	6.6	7.5	8.1	0.8	7.5	8.7
dP^4	4	8.0	0.8	7.0	9.0	7.3	0.8	6.4	8.2	9.9	0.7	9.0	10.8
I_1	1	6.5				10.7				6.4			
I_2	3	5.7	1.2	4.3	6.5	5.4	0.1	5.3	5.5	11.2	0.6	10.7	11.6
C_1 (?)	3	6.7	0.3	6.5	7.0	6.5	0.9	5.8	7.1	4.0	0.3	3.8	4.3
C_1 (?)	4	11.6	1.2	10.2	13.0	27.5				7.2	0.4	6.8	7.5
P_3 (?)	4	5.3	0.4	4.7	5.7	10.2	1.9	8.5	12.3	7.5	0.4	7.2	8.0
P_3 (?)	7	6.5	0.3	6.0	6.9	17.4	2.1	13.9	20.0	11.5	1.4	9.3	13.5
P_4	22	7.1	0.7	5.6	8.8					8.1	0.8	6.9	9.5
M_1	39	8.4	0.6	7.3	9.8	8.4	0.7	7.0	9.9	10.3	1.0	8.5	12.8
M_2	42	10.4	0.8	8.7	12.2	9.9	0.9	8.4	12.6	12.9	1.1	11.1	16.3
M_3	43	11.2	1.0	8.4	13.2	9.9	0.8	8.1	11.1	17.0	1.5	14.4	20.4
M_x	15	9.8	1.1	8.1	11.5	9.1	0.8	7.5	10.4	12.3	1.1	10.9	13.9
dI_1	1	3.3				5.6				4.0			
dI_2	2	2.8	0.3	2.6	3.0	5.7	0.1	5.4	6.0	4.5	0.4	4.4	4.5
dC_1	3	5.3	0.6	4.6	5.8	5.7	1.4	4.5	7.2	3.9	1.0	3.2	5.0
dP_3	5	4.6	0.2	4.4	4.8	5.1	0.6	4.3	6.0	8.1	0.5	7.5	8.6
dP_4	5	6.2	0.4	5.7	6.7	6.5	0.4	6.0	6.9	9.0	0.5	8.5	9.7

quite straight in AL205-1, but appears slightly more parabolic in outline in MAK-VP-1/100. The premolars are generally more medially positioned than the molars. In the males, the canines tend to project more laterally than do the premolars, emphasizing the corners of the “U”. In females, the canines are smaller and more medially positioned, so that the dental arcade is more parabolic. The premaxillae then tend to form a very short flat arc between the canines. This arc tends to project relatively more anteriorly in the females, perhaps due to the smaller canines. In lateral view, the maxillary dentition appears to have neither a normal nor reverse curve of Spee, but is actually fairly straight in most specimens, including AL321-12, AL205-1, and MAK-VP-1/100 (see mandible section below for further discussion). The palate is long and rectangular, with the alveolar process forming nearly perpendicular lateral walls. It is deep, and deepens posteriorly, reaching a depth of approximately a centimeter posteriorly.

Midface and zygomatic arch

Similar to other subspecies of *T. oswaldi* the midface is deep, and anteroinferiorly sloping. The zygomatic process of the maxilla is about 3.9 and 3.7 cm deep in the larger males AL205-1 and AL134-5a respectively, to slightly more than 3.1 cm in MAK-VP-1/100. In the female AL321-12 it is 3.3. The zygomatic process of the maxilla is positioned above the middle of the M^3 in AL134-5a, above the mesial M^3 in AL205-1 and above the distal M^2 in the younger MAK-VP-1/100. In AL321-12 the zygomatic arch is at the level of the $M^{2/3}$ contact. The anterior surface of the zygoma entirely lacks suborbital fossae in all specimens. In combination with the posterior orientation of the zygomata, this gives the face a rather smooth and “inflated” appearance relative to other taxa such as *Papio (Papio)*. The lower face is relatively short in anterior view. The zygomata arise from the maxillae close to the alveolar process in comparison to its position in *T. o. oswaldi*. The inferior border of the zygomatic arch curves superiorly, posteriorly and laterally, then broadly laterally in both AL205-1a and AL321-12. A pyramidal bulge at the inferior limit of the zygomaticotemporal suture interrupts the curve of inferior border of the zygomatic arch, which is near the anterior limit of the masseter muscle attachment. The temporal surface of the zygomatic bone and the zygomatic process of the frontal are deeply excavated in all specimens that preserve this surface, making the infraorbital portion of the zygoma that is thin in cross-section.

The only specimen to preserve the zygomatic arches is the older adult male AL205-1a. In superior view, their anterior origin angles sharply laterally and slightly posteriorly away from the maxilla. Then, in the region of the frontal process of the zygomatic the arch curves more posteriorly. Overall, they are nearly semicircular in outline and widely flaring. This impression may be slightly exaggerated due to the absence of much of the lateral and inferior orbital margins. The zygomatic process of the temporal forms a wide, mediolaterally flattened and triangular shelf between the cranial vault and the main body of the arch. The zygomatic arch is deep in the superoinferior plane and oval in cross-section anteriorly. This seems to be true in AL205-1a as well as specimens where more fragmentary portions are preserved. In lateral view, they are fairly straight from anterior to posterior, lacking the sigmoidal curve of most papionins. This shape may be partially due to distortion.

In inferior view, the anterior limit of the masseter muscle attachment is visible in AL321-12 and AL205-1a. In the former specimen, it reaches the distal limit of the M^2 and curves slightly onto the anterior surface of the zygoma, similar to that of BMNH-M14936 and KNM-ER 971 (from Kanjera and Koobi Fora respectively). In AL205-1a it extends to the mesial M^3. In MAK-VP-1/100 and AL134-5, the masseter scar is not preserved, but enough of the zygomatic arch is to estimate that it would have been similar to AL205-1a.

Orbit

The orbits are well preserved only in AL321-12, those of AL412-1 are preserved medially, and their outline is preserved by matrix. They are less completely preserved in MAK-VP-1/100 and AL185-1a-b/AL154-95. The superior borders are also preserved in AL187-10. In outline, the orbits are ovoid and taller than they are wide. The supraorbital rim is thinner than in later subspecies of the genus, and more similar to that of *Papio hamadryas ssp.* than to other *Theropithecus*. It is basically flat across the frontal from side to side, with bulges that occur above the supraorbital notches. The supraorbital torus does not arch superiorly as it does in KL157-1 or *T. brumpti*. There is a shallow ophryonic groove posterior to the torus between the temporal lines. The supraorbital notch is preserved in AL321-12, AL185-1a, AL187-10, AL412-1, and MAK-VP-1/100, in all of these specimens it is distinct and well developed, although less so in AL412-1. None of them have a supraorbital foramen. The temporal rim of the orbit is not very wide superiorly, but widens inferiorly, giving the midface a “visor”-like appearance. The frontozygomatic suture is only preserved in AL321-12 and MAK-VP-1/100. It lies in the horizontal plane, and runs posterolaterally. The glabellar region is not prominent in any of the specimens where it is preserved, in all the anteorbital region is vertical, and steeply concave, curving smoothly anteriorly towards rhinion. The interorbital pillar is narrow, and otherwise typical of most papionins. The lacrimal fossa lies within the lacrimal bone, whose anterior limit falls directly on the orbital rim.

Calvaria

The male specimens AL412-1, AL187-10, MAK-VP-1/100, and AL205-1a all largely preserve the calvaria, as do the females AL321-12 and AL185-1a. AL319-10 preserves some of the occipital and temporal areas. Viewed superiorly, the temporal lines converge sharply posterior to the supraorbital torus in all specimens, becoming nearly parallel with the torus in all but AL321-12. Also, in this specimen, the temporal lines remain widely separated throughout their course. In the subadult female AL185-1a, however, the temporal lines meet approximately half way between bregma and lambda, but do not form a crest. In all of the male specimens a sagittal crest is present, though generally low. It forms anterior to bregma in both AL205-1a and AL412-1, at bregma in MAK-VP-1/100, and between bregma and lambda in AL187-10. The nuchal crests are generally well developed, and often tall. In all specimens except for AL321-12 they form a compound temporonuchal crest near inion. They are most prominent about half way between inion and the external auditory meatus, giving the occipital region a somewhat squared outline when viewed superiorly.

The infratemporal fossae are large and postorbital constriction is great in all specimens. The widest part of the neurocranium is at the level of the auditory meatus, so that the calvaria is ovoid in superior view. When viewed posteriorly, the neurocranium is fairly tall and rounded in comparison to later subspecies of *T. oswaldi*, except in AL205-1 and MAK-VP-1/100 where the temporal squamae are more sloping and less vertical.

Basicranium

Several specimens preserve the basicranium. AL321-12 is the most complete, but it is also relatively well preserved in AL205-1a, AL187-10, AL319-10, AL185-1a, and partially in MAK-VP-1/100. The occipital plane varies from fairly flat in some specimens (e.g. AL321-12) to more concave in others (e.g. AL205-1a). Its inclination relative to Frankfurt horizontal is variable, from approximately 30º in AL205-1 to perhaps as high as 55º in AL187-10 and MAK-VP-1/100. In most it approximates 45º. The mastoid processes appear to be highly sexually dimorphic. In the males, it is tall and mediolaterally broad, whereas in the females it is lower and more pyramidal. The digastric groove is always strongly marked but is variable in width. In most specimens it is narrow and deep, but in AL205-1a it is comparatively broad. The auditory tube slants slightly posterolaterally, and in most specimens it slopes slightly superiorly as well. The postglenoid is generally broad and tall, and unlike later subspecies of *T. oswaldi* it is separated from the glenoid fossa by a narrow sulcus (Eck, 1993). The glenoid fossa is similar to that of *T. gelada* in its sellar shape, being concave mediolaterally and convex anteroposteriorly, although not as strongly so as in *T. o. leakeyi*. In the only specimen where they are clearly visible, AL321-12, the choanae are tall and narrow.

Facial hafting

The glenoid fossa and temporal region are positioned relative to the occlusal plane in a manner similar to that of *Papio*, and less elevated than in *T. gelada* and to a lesser extent *T. o. oswaldi* and *T. o. leakeyi*. The face is deep, although it is not as deep as it is in *T. gelada* or *T. o. leakeyi*. It is relatively klinorhynch in comparison to other members of the genus, although not to the extent of larger specimens of *Papio* or *Paradolichopithecus*. As discussed above, the glabellar region is not projecting, nor is the ophryonic groove deep.

Mandible

There is a very large sample of mandibles of this subspecies from both Hadar and Maka; all of these are listed in appendix 3. The anterior surface of the symphysis is marked by a median mental canal. Mental ridges are present and vary in their degree of rugosity and prominence. They are generally similar to those of *T. gelada*, more prominent than those of *T. o. oswaldi* and *T. o. leakeyi*, but generally less rugose than those of *T. brumpti*. Males seem to have more strongly marked mental ridges than the females. In lateral view, the symphysis slopes at a relatively shallow angle to the occlusal plane. Lingually, both transverse tori are well developed. The superior torus extends posteriorly to the middle of the P_3 or P_4, and the inferior torus to the P_4 or M_1. The plenum alveolare varies in its morphology from a concave basin to a more planar, but posteriorly sloping surface.

The corpus is thick, robust, and generally even in depth from the posterior end of the symphysis to the gonial area. The lateral surface is often marked by a corpus fossa of variable depth. Some are shallow but clearly present (e.g. AL186-17 and AL205-1c), whereas others seem to lack corpus fossae entirely (e.g. AL135-14a). None of them are nearly as deep as the corpus fossa on TMP-MP 44 (=M621, M626 in Freedman, 1957) from Makapan. In general the corpus fossae are not as deep as those of *T. gelada*, T.

brumpti, *Papio (Papio)*, and *Mandrillus*. In superior view, the corpus is quite “V”-shaped, particularly the females. There is also a wide extramolar sulcus and well-marked oblique line.

The ramus is only incompletely preserved, with the best specimens being AL 135-14a, AL196-3a and MAK-VP-1/17. It can be seen that ramus varied in its orientation relative to the corpus, at least anteriorly. In most where there is even a small amount preserved, it can be seen to be relatively vertically oriented. It is more posteriorly angled in AL135-14a, however. The lateral surface has a deep triangular fossa.

Dentition

Every element from both the permanent and deciduous dentition is represented except for the dI^2. The upper incisors are typical of papionins in morphology, but relatively small in size, particularly in comparison to those of *Papio*. They are similar in size to the incisors of *T. gelada*. The I^1 has a crown that is flaring and tilts slightly mesially. The lingual surface is spatulate and lacks a lingual cingulum. The I^2 is narrower, and its crown is not flaring, but more asymmetrical and tilting towards the midline. The lower incisors lack enamel on their lingual surface and have narrower crowns than the uppers. The labial surface of the I^2 crown is more tightly curved than that of the I^1, and the lateral occlusal edge has a sigmoidal shape in occlusal view. The canines are typical of cercopithecids in morphology, and are highly sexually dimorphic. They are similar in size to the canines of *T. gelada* or smaller *Papio*, and are not as reduced as those of *T. o. oswaldi* or *T. o. leakeyi*.

The upper premolars are relatively molariform with well-developed mesial and distal foveae and tall cingula. The P^4 is larger than the P^3 and has a strong preprotocrista. They are otherwise typical bicuspid teeth. The P_3 is basically like that of other papionins, being dimorphic, with a mesiobuccal flange that is significantly longer in the males than the females. The male P_3 mesiobuccal flange is similar in length to those of *Papio*, *T. brumpti* and *T. gelada*, but significantly longer than that of *T. o. oswaldi* and *T. o. leakeyi*. The female mesiobuccal flange is quite variable in length, from almost non-existent (e.g. AL129-8) to fairly long (e.g. AL185-5c). The P_4 is a more molariform tooth with a large talonid basin. The protoconid is columnar in form and similar to those of *Theropithecus* molars.

The molars generally show the diagnostic features of the genus, but vary in the degree of their expression. Some specimens of *T. o. darti* such as AL135-4a and AL129-8 are within the range of variation of *Papio*, in their crown height, cuspal relief, and wear pattern. Others (e.g. AL163-11 and MAK-VP-1/43) are derived in their morphology and similar to *T. gelada*. This variability in the expression of the diagnostic features of the genus more likely reflects the primitive status of this population relative to later *T. oswaldi* than it does the presence of multiple taxa in the Afar sample.

The dI^1 is essentially a miniature version of the adult tooth. The crown is convex labially, and concave lingually. It is also slightly flaring and tilted mesially. The lingual surface lacks a cingulum. It is relatively labiolingually deep in comparison to its adult counterpart. The lower incisors are significantly mesiodistally broader than the adult lower incisors. Their lingual surface is covered by enamel, unlike their permanent counterparts. The labial surface of the crown is also more convex than in the permanent lower incisors. The dI_2 is substantially more asymmetrical than the dI_1. Its crown is very mesiodistally elongate and blade-like. This is largely due to the presence of a well-developed distal cuspule, not unlike that of an adult colobine I_2, although the dI_2 of *T. o. darti* is more fan-shaped.

The upper deciduous canines are similar to the adult female upper canines, but more labiolingually compressed. The crown is triangular in labial view with a slight distal prong. The wear occurs mostly on the lingual distal margin. Mesially, there is a slight vertical sulcus that extends from the crown apex onto the root. The lower deciduous canine is quite similar to the dI_2 and to colobine I_2, but with a more prominent main cusp. There is a relatively large distal cusp, separated from the primary cusp by a slight notch, giving the crown an almost “mitten-like” shape in labial view.

The deciduous premolars are similar to the molar teeth and display the unique molar morphology of the genus. They differ from the molars in the standard cercopithecid manner: they are relatively narrow, the distal lophs of the dP^{3-4} and dP^3 are relatively wider than the proximal ones, and the crowns show more basal flare. The dP_3 has a well-developed paraconid, and a metaconid that is positioned more distally than the protoconid. This makes the mesial fovea (i.e. the trigonid) more triangular in occlusal view than in the molars.

Postcrania

There is a large collection of postcrania from Hadar and Maka that most probably represents this taxon. A few specimens are directly associated with cranial remains. These include AL134-5b-c, a distal fragment of a left tibia and a left proximal femur respectively, associated with a male rostrum (AL134-5a). AL185-5d-c are a proximal fragment of a left femur and a shaft fragment a tibia, associated with a subadult female partial cranium. AL185-22a-h is a partial skeleton of a juvenile associated with a left mandibular fragment. It includes the proximal and distal ends of the right humerus, the proximal portions of the right ulna and radius, the proximal end of the right femur and the distal end of the right tibia. AL196-3b-d are the left proximal tibia, distal humerus, and proximal ulna respectively, associated with a right mandible fragment of a female individual. In addition, there is a large sample of material that is morphologically similar to the above material, but is not directly associated with diagnostic cranial material. In total, most elements of the forelimb, hindlimb and foot are represented. Some of this material has been identified by Krentz (1992, 1993) and listed in Delson et al. (1993). It is beyond the scope of this thesis to analyze all of this material. Krentz (1993) described the likely locomotor adaptation of *T. o. darti* as being similar to those of *T. gelada* and *T. o. oswaldi*, but less strongly developed than is the case in the latter taxon.

Theropithecus oswaldi oswaldi (Andrews, 1916)

(= or including *Cynocephalus atlanticus* Thomas, 1884: Alemseged and Geraads, 1998; *Simopithecus oswaldi* Andrews, 1916; *S. oswaldi oswaldi* Leakey and Witworth, 1958; *S. danieli* Freedman, 1957; *T. (S.) darti danieli* Jolly, 1972; *T. oswaldi* Eck, 1987 (in part), Harris et al., 1988)[2]

Holotype: BM(NH) M11539 (lectotype) from Kanjera, Kenya

Afar specimens included: see appendix 4.

Range: 2.52 – 1.39 Ma

Afar range: 2.52 – ~1.8 Ma

Distribution: Ain Jourdel, Ahl al Oughlam, <u>Hadar Fm., Upper Kada Hadar Mbr</u>.; ?<u>Geraru</u>; <u>Gamedah</u>, <u>Wilti Dora</u>, <u>Matabaietu</u>, <u>Halsaiya</u>; <u>Bouri Fm., Hatayae Mbr.</u>; Konso (lower); Shungura Fm. Mbs. E3 – G14 (H3 – K); ?Fejej; Nachukui Fm., Kalochoro – Nariokotome Mbs.; Koobi Fora Fm. Upper Burgi – Okote Mbs.; Kanjera; Marsabit; Kaiso, Peninj; Olduvai Bed I, Lower Bed II; ?Chiwondo Beds Unit 3A; Swartkrans Mbs. 1 (including hanging remnant)-3; Gladysvale.

Subspecific diagnosis:

A subspecies of *T. oswaldi* distinguished from *T. o. darti* by its larger overall cranial, molar and postcranial size, and from *T. o. leakeyi* by its smaller size. The incisors and canines are relatively smaller than those of *T. o. darti* and are relatively larger than

---

[2] *Theropithecus atlanticus* (Thomas, 1884) has priority over *T. oswaldi* (Andrews, 1916), but *T. oswaldi* is used here to maintain common usage. Furthermore, the type of *T. atlanticus* can only be tentatively identified as the same species as *T. oswaldi*. However, not allocating *T. atlanticus* to *T. oswaldi* is unsatifactory as this requires recognizing two species. Pending recovery of more diagnostic material from Ain Jourdel, the name *T. antlanticus* should be suppressed as its adoption would lead to confusion.

those of *T. o. leakeyi*. It is further distinguished from *T. o. leakeyi* by having a relatively longer muzzle. Mandibular corpus fossae are generally shallower than those of *T. o. darti*. The symphysis is more vertical in profile with less rugose mental ridges than that of *T. o. darti*. Relative to *T. o. leakeyi*, *T. o. oswaldi* develops mandibular corpus fossae more often, and has a more sloping symphysis. Additionally, the anterior surface of the symphysis rarely develops a triangular anterior fossa as it does in *T. o. leakeyi*. The molars are generally more complex, and are more readily identifiable to the genus, than those of *T. o. darti*, but have less enamel complexity and fewer folds than do those of *T. o. leakeyi*.

Description:

Cranial material very well represented in the sample with several nearly complete and more partial cranial elements. KL157-1 (plate 15) is a large male cranium with left M^{2-3} and right M^2, lacking only the premaxillae anterior to the middle of the piriform aperture, and the zygomatic arches. KL39-1 (plate 16) is a nearly complete cranium of an older adult male, preserved as separate neurocranium and face with the left P^4-M^3 and right P^4-M^1 and roots or alveoli for the remaining teeth. Most of the cranium is present, except for some of the distal nasals, the lateral orbital margins, the superior calvaria, and parts of the basicranium. The dentition is heavily worn with most of the enamel lacking from the occlusal surface molars. KL38-1 (plate 17) is nearly complete subadult female cranium with the left P^3 through M^2 and right C^1-M^2. The M^2 is erupted and worn and the M^3 crypt is just opening. The P^{3-4} are in wear, and the adult canines are erupted. The left and right orbits are missing their lateral margins, the right zygomatic arch is absent, as is the basicranium around the foramen magnum. AL571-1a-c is a crushed male cranium with the median areas of the frontal, parietals and occipital, left and right maxillae, left P^4-M^3, and part of the right zygomatic bone. KL235-1 (plate 18) is a left maxilla and premaxilla with I^2-M^3, preserving the zygomatic process, much of the rostrum including the left 1/3 of the piriform aperture, much of the nasal cavity and maxillary sinus, and the palatal process to the midline. KL18-1 is a small fragment of a right maxilla with very heavily worn P^3-M^1. KL74-2c is a series of associated cranial fragments from an old adult male, including a right facial fragment with C^1-M^3, the left maxilla and premaxilla with roots of M^{2-3}, left and right temporal fragments, sphenoid and occipital fragments that fit together to form a large portion of the cranial base. BOU-VP-12/132 (plate 18) is a fragment of a left temporal fragment and a left maxilla from a male individual with P^3-M^3. The maxilla preserves the alveolar process only to the ends of the roots, except superior to the premolars where approximately 4 cm are preserved. WIL-VP-2/15 (plate 18) is a left maxillary fragment with P^4-M^3, some of the base of the zygomatic process, and a small portion of the palatal process, which is tentatively allocated to this taxon (see Remarks section below for more discussion of this specimen). BOU-VP-12/179 is a crushed calvaria with the central area of the frontal and the left temporal. Lastly, KL37-1 is a right temporal fragment and occiput, that most likely is from an individual of *T. o. oswaldi*, but could conceivably be another large papionin.

In overall cranial size this material is similar to the largest specimens of extant *Papio* and *Mandrillus*. The *T. o. oswaldi* crania are generally more heavily built and robust, however. Dentally, the molars are larger than those of most extant cercopithecids, with the lower end of the size range overlapping with only the largest individuals of extant *Papio*. They are similar in size to molars of *Gorgopithecus major* and both species of *Papio (Dinopithecus)*. Dental dimensions for *T. o. oswaldi* are given in table 4.6.

Rostrum

In comparison to papionins of similar size, the rostrum is relatively shorter than it is in *Papio*, *Mandrillus*, *Paradolichopithecus*, and *T. (Omopithecus)* (see figure 4.9). It is, however, relatively longer than that of *T. o. leakeyi*. Its dorsal surface is preserved nearly completely in KL157-1, KL39-1 and KL38-1, and partially KL235-1, KL74-2c, and AL571-1. In all specimens, the maxillary ridges are very poorly developed or absent. If present, they are always low and rounded in cross-section, and never sharp as in *T. brumpti*. In general they arise anteriorly from the roots of the canine, are most distinct on the anterior portion of the rostrum, then blend in with the contour of the muzzle anterior to the orbits. For the specimens in the Afar sample, KL39-1 has the most strongly developed maxillary ridges (though still very slight), and in the subadult female KL38-1 they are completely absent. The maxillary fossae are either absent or very shallow, and are best developed in the postcanine area, extending posteriorly to the level of the mesial M^2.

The dorsal surface of the rostrum is parabolic in paracoronal cross-section, due to the lack (or near lack) of maxillary ridges and fossae. The nasals are not prominent above the muzzle dorsum, and there is a lack of the concavo-convexo-cancave shape. Both of these features are unlike *T. o. leakeyi* and *T. o. darti*. In lateral view, the rostrum is steeply concave from glabella to rhinion, with a steep anteorbital drop. Thus, the muzzle dorsum is sellar in shape, and very smoothly curving, giving the face an "inflated" appearance.

The piriform aperture is completely preserved in KL38-1, and partially preserved in KL39-1, AL571-1a-c, KL235-1, and a bit of its superior rim is present in KL157-1. The superior border is sharply defined, whereas the borders of the inferior portion are thicker and more rounded. It is generally oval in outline, but its inferior tip is more "V"-shaped. In lateral view the aperture is inclined at an angle of approximately 30 – 45º relative to the occlusal plane, and slightly concave-up from rhinion to prosthion. There are no anterior nasal tubercles.

The maxillary dental arcade is "U" shaped in outline with relatively long and straight molar rows and a short incisive arc. In KL39-1 the molar rows converge anteriorly, and in KL157-1 they diverge slightly anteriorly. The canine alveoli are prominent in the males, as the canines are still fairly large in caliber. In lateral view, the dentition tends to develop a marked concave-down profile, or reverse curve of Spee in older individuals (Eck and Jablonski, 1984; 1987). KL39-1, KL74-2c and AL571-1 all show strongly developed reverse curves, and all have heavily worn dentition. In the younger adult male KL157-1, and the female KL235-1 it is only very slightly developed, and in the juvenile KL38-1 it is absent.

The palate is similar in shape to that of *T. o. darti*, other species of the genus, and *Papio*. It is long and rectangular in outline. It is deep and increases in depth posteriorly and its surface is basically flat and uncurved anterior to posterior. The alveolar processes are tall and form nearly vertical walls laterally. The incisive and greater palatine foramina are similar to those of other papionins.

Table 4.6 Summary dental dimesnions for *Theropithecus oswaldi oswaldi*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.22. For descriptions of measurements see chapter 3.

	Theropithecus oswaldi oswaldi												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^2	1	6.1								6.2			
C^1 (?)	3	7.3	0.3	7.0	7.5	9.4				9.5	0.7	8.7	10.0
C^1 (?)	3	12.1	4.0	9.2	14.9	31.1				13.2	3.9	10.6	17.7
P^3	5	9.1	0.8	8.0	10.1					7.4	0.7	6.4	8.0
P^4	6	9.5	0.6	8.8	10.2					7.9	0.6	7.1	8.7
M^1	7	11.2	0.7	10.1	12.1	10.8	0.9	9.3	11.6	12.3	1.7	10.0	14.2
M^2	8	13.4	0.8	12.6	14.9	12.6	0.6	11.8	13.3	15.0	1.2	13.0	16.8
M^3	8	13.6	1.0	12.4	15.2	12.1	1.1	10.9	14.2	15.7	1.3	13.9	17.7
M^x	7	12.5	1.8	9.5	14.4	11.8	1.6	8.9	13.1	14.4	2.4	11.0	17.8
dP^4													
I_1	2	6.4	0.9	5.8	7.0	7.2				5.2	0.0	5.1	5.2
I_2	1	5.6				7.4				5.6			
C_1 (?)	2	7.7	1.3	6.7	8.6	10.6				5.4	1.0	4.7	6.2
P_3 (?)	2	5.8	0.4	5.5	6.1	9.2				8.0	1.3	7.0	8.9
P_3 (?)	2	6.8	2.4	5.1	8.5	17.1	3.2	14.9	19.4	10.4	2.9	8.3	12.5
P_4	7	7.8	0.7	7.1	8.8					9.4	1.0	7.4	10.3
M_1	10	9.8	0.8	8.7	11.0	10.2	0.9	9.4	11.8	12.1	0.8	10.3	13.0
M_2	13	11.8	1.7	8.9	14.4	11.3	1.3	9.5	13.4	15.1	1.4	13.2	17.4
M_3	17	13.1	1.7	10.1	15.2	11.4	1.2	8.6	13.0	19.9	1.8	16.8	22.3
M_x	4	11.0	1.9	8.4	12.6	10.5	1.1	9.1	11.8	14.1	1.8	11.9	16.4
dC_1	1	8.1				13.9				4.5			
dP_3	1									9.8			
dP_4	1									11.3			

Midface and Zygomatic Arch

The midface is deep and anterioinferiorly sloping. The depth of the zygomatic process of the maxilla in the males KL39-1 and KL157-1 is approximately 3.8 and 4.5 cm respectively. The inferior border of the zygomatic process of the maxilla is positioned further posteriorly than that of *T. gelada* or *T. o. leakeyi*. It is above the middle and distal portions of the M^3 in the adult males KL39-1 and KL157-1 respectively. In the adult female KL235-1 it is above the M^2/M^3 contact. In the subadult female KL38-1 it is above the M^2, as it is in WIL-VP-2/15. The anterior surface of the zygoma arises smoothly from the maxilla and is basically uninterrupted by suborbital fossae, except that in KL39-1 there does appear to be a very faint suborbital fossa, largely related to the position of the anterior attachment of the masseter muscle. Combined with the swept-back orientation of the zygomatic arches and the deep anteriorly sloping suborbital area, this gives the zygomatic bone a very inflated appearance. In anterior view, the zygomatic process of the maxilla originates well above the alveolar plane, then arcs superiorly and posteriorly towards the zygomatic arch in a smooth and continuous curve. The temporal surface of the zygomatic and orbital cone is deeply excavated, leaving little room for the maxillary sinus to invade the zygomatic process.

The zygomatic arches are only preserved in KL39-1 and KL38-1. In the male, they are wide and flaring and very similar in overall appearance to those of the male *T. o. darti* AL205-1a. In superior view, they are nearly semicircular in outline, except that the zygomatic process of the maxilla juts out sharply, then at about the suture with the zygomatic curves more posteriorly. In the female the zygomatic arch is less flaring, with a more straight and posterior orientation. In all specimens where any portion of the arch is preserved, it is deep in the superoinferior direction and oval in cross-section. In lateral view, the zygomatic arch of KL38-1 is very deep but otherwise typical of papionins in shape. It is concave up from the anterior most point of the masseter muscle to the zygotemporal suture, where it becomes concave down, giving the arch a sigmoidal profile. In KL39-1 they are also deep, but lack the sigmoidal curve of most papionins and are in fact quite straight, much like those of AL205-1a.

In inferior view, the anterior limit of the masseter muscle scar can be made out on KL39-1. It is positioned approximately lateral to the distal loph of the M^3. It extends anterior to the inferior end of the zygomaticomaxillary suture. Thus, the inferior edge of the zygomatic arch extends further anterior lateral to the suture, causing a slight suborbital fossa to occur on its anterior surface, similar to the females KMN-ER 971 and BMNH-M14936. Although it is not visible in KL157-1, enough of the zygomatic arch is preserved to determine that it must have been posterior to the M^3. On KL38-1 the anterior limit of the masseter scar reaches the middle of the M^2.

Orbit

The orbits are well preserved in KL157-1, and partially preserved in KL39-1, and KL38-1. There is also a small amount of the superior orbital rim and inferior orbital rim preserved in KL74-2c and AL571-1. They are high and “egg-shaped” in outline, being greater in height than in breadth, as they are in other *Theropithecus* (Eck and Jablonski, 1987). The superior orbital rim is thick and heavily built, approaching 1 cm in the large male KL157-1 where the rim forms separate arches over each orbit, so that it is lower in the sagittal plane and higher around the middle of the orbit. In KL39-1 on the other hand, the supraorbital rim is much more of a single continuous curve from the right frontomaxillary suture to the left with only a slight depression in the sagittal area. This is similar to the morphology of the male from Kanjera BMNH-M32102 or to Omo 75N ’71 C24. KL38-1 and KL74-2c are basically similar to KL39-1 in this regard, although they are more fragmentary, whereas AL571-1 is more like KL157-1. The supraorbital torus is separated from the neurocranium by a wide but shallow post-toral sulcus. The supraorbital notch is weakly defined. The temporal rim of the orbit is wide. The frontozygomatic suture runs horizontally and laterally from the upper lateral angle of the orbit and then curves posteriorly to reach the temporal rim. The glabellar region is prominent in KL157-1 and KL38-1, projecting anterior to nasion when viewed in Frankfurt orientation, but not to the extent seen in *T. gelada*. Glabella is not prominent in KL39-1 being directly superior to nasion. Unlike most *T. o. leakeyi*, the interorbital pillar is relatively narrow, as is typical of most papionins, being similar in breadth to larger specimens of *Papio*. The lacrimal fossa lies within the lacrimal bone and its anterior limit is inside the orbital rim.

Calvaria

The calvaria is essentially complete on KL157-1 and KL38-1, lacks only the areas around bregma and inion on KL39-1, preserves the entire dorsal aspect in AL537-1, and KL37-1 preserves a small portion around the occiput and right temporal. The temporal lines are thick and strongly marked. In superior view, posterior to the orbits they converge sharply towards the midline in all specimens. In the subadult female KL38-1 they do not meet, but are quite close to the midline throughout their length. In all of the remaining specimens, which are all adult males, they form prominent sagittal crests. In KL157-1, AL571-1, and probably KL39-1 the sagittal crest form anterior to bregma. In all of these specimens the sagittal crest is prominent throughout its length, but tallest at inion where it is over 1 cm in height in KL157-1 and AL571-1. Additionally, all of the adult specimens have equally tall nuchal crests that form a compound crest at inion. The nuchal crest extends as a large semicircle starting at the auditory meatus.

As would be expected given the large area for attachment of the temporal muscles, postorbital constriction is great in all specimens. Thus, in superior view the neurocranium is ovoid in outline, with its maximum width occurring at the level of the auditory meatus. Viewed posteriorly, the neurocranium is low and broad. It is widest inferiorly, just above the zygomatic process of the temporal, and slopes sharply towards the midline.

Basicranium

The basicranium is present in KL39-1, in KL74-2c it is mostly present other than the occiput, that of KL38-1 is preserved except for the median section from the basisphenoid to the occiput, and in KL157-1 most of the basicranial detail is either damaged or obscured by matrix. The occipital plane is broad and flat, and inclined at an angle of about 45° to the Frankfurt horizontal. The mastoid processes of the males are prominent and pyramidal, while those of KL38-1 are similarly shaped, but smaller. The digastric groove is generally well marked but of variable breadth. The postglenoid processes are wide and tall, and positioned immediately posterior to the tympanic bone, and are not separated from it by a sulcus as in *T. o. darti*. The tympanic is nearly perpendicular to the sagittal plane, but angles slightly posteriolaterally. The glenoid fossa is deep and the articular eminence is prominent. The articular surface is sellar in shape, being convex anteroposteriorly and concave mediolaterally.

Facial hafting

The glenoid fossa and temporal region are elevated well above the occlusal plane, but less so than in *T. gelada*. This is in part related to the depth of the face, in particular the posterior part of the maxilla. The facial depth is evident in many factors: the tall orbits, the steep anteorbital region, the deep zygomata, and the tall alveolar processes. The face is klynorhynch, being oriented more like that of *Papio (Papio)* than *T. gelada* or even *T. o. leakeyi*. The frontal is receding, being relatively flat posterior to the supraorbital torus, except for the sagittal crest. In KL38-1 the frontal does rise a little higher above the supraorbital torus than in the other specimens.

Mandible

There are several mandibular specimens represented. KL74-2a is a nearly complete mandibular corpus from a male individual, with the left P_3-M_3 and the right P_3-M_1, but lacking both rami. The margin is intact on the right side from the symphysis to just behind the M_3, but is missing on the left. KL74-2b is a right corpus fragment in two pieces, one from the symphysis to the M_1, and the other from the M_3 to the anterior part of the ramus. It is from an individual of unknown sex as the C_1-P_3 area is damaged. It preserves the P_4-M_1 and M_3. BOU-VP-12/135 (plate 19) is a fairly complete, though damaged, right corpus, with the roots of I_1-M_3, probably of a male individual, given the fairly long flange on the P_3 and the size of the canine alveolus. MAT-VP-2/12 is a left fragment preserving with an M_3, a small bit of the corpus and the ramus. KL44-3a (plate 19) is a left corpus fragment with $M^{1\text{-}3}$, but little of the depth of the corpus is present. KL46-1 is a left corpus fragment of a female with C_1-M_3. The margin is present posteriorly to M_2. KL16-5 is a large right corpus fragment, probably male, with $M_{2\text{-}3}$. KL22-1 is a right corpus fragment with P_4 to M_3. KL65-1 is a young adult left corpus with $M_{2\text{-}3}$ and the margin is present from M_2 to gonion. KL64-3c is a right corpus fragment lacking the margin, put preserving the roots of P_4-M_2. MAT-VP 3/3 is an edentulous female symphysis, but with well preserved empty alveoli of the canines and incisors. GAM-VP-1/8 (plate 19) is a left corpus fragment of a juvenile individual with dp_3-M_1, and an M_2 crown in the crypt. MAT-VP-4/14 (plate 19) is a right corpus fragment of a subadult male with the margin, and I_1, dc, P_4-M_2 and an erupting M_3.

In lateral view, the symphysis is deep and sloping, extending posteriorly as far as the mesial M_1. Its anterior surface is pierced by a median mental foramen. The mental ridges vary in their expression, being fairly well marked in some individuals (e.g. KL74-2a) to absent in others (e.g. MAT 3/3). In general, they are more pronounced in the male specimens. In all specimens, however, they are far less prominent and rugose than those of *T. brumpti*. On the posterior surface both transverse tori are well-developed, with the superior extending posteriorly to approximately the middle of P_3, and the inferior extending to P_4 or M_1.

The corpus is thick and relatively shallow. In superior view, the corpora are distinctly “V”-shaped. It is deepest in the region of the M_1 at approximately the distal end of the symphysis, and shallows posteriorly. The lateral surface of the corpus is marked by fossae of variable depth. These range from nearly absent in some specimens (e.g. KL74-2b, KL22-1) to shallow, but distinctly present in others (KL74-2a). The oblique line is strongly marked, and there is a wide extramolar sulcus. The anterior portion of the ramus is preserved in MAT-VP-4/14 and MAT-VP-5/30. The ramus was relatively more vertical in orientation than that of *Papio* and *T. brumpti*.

Dentition

The incisors are small relative to the other teeth, but are otherwise typical of papionins in morphology. The only upper incisor preserved is an I^2 on KL235-1. The crown is spatulate in shape, lacks a lingual cingulum, and is basically slightly flaring. When viewed anteriorly, it tilts slightly mesially. The lower incisors are well preserved on AL596-1 and MAT-VP-4/14. The lingual surface lacks enamel. In labial view the crown is not flaring, but is basically parallel-sided. The distal border of the I_2 slopes slightly mesially and the labial surface is more tightly curved than that of the I^1.

Canine morphology is typical of cercopithecids. The female C^1 crown is triangular in labial view, and has a sulcus on its mesial face and root. The crown is relatively short, thick and robust. They also seem to wear apically. That of the male is substantially larger in caliber and height, with a deeper mesial sulcus that extends from the root to the crown. They are triangular in cross-section with the distal margin being quite sharp due in part to honing by the P^3. The lower canines are also typical of cercopithecids, being more labiolingually compressed than the uppers and have a larger distal margin. The male lower canine is substantially larger than that of the females, and may develop a small cuspule on its distal margin.

The upper premolars are standard bicuspid cercopithecid teeth. They are relatively molariform, with the protocone being columnar and otherwise similar to the lingual cusps of the upper molars. The P^4 is larger than the P^3, more quadrate in outline, with larger mesial and distal foveae. The P_3 is also typical of papionins: the protoconid is tall and pointed, the metaconid is small. The male mesiobuccal flange is short in comparison to most papionins. It is shorter than in *T. brumpti* and *T. o. darti*, but still longer than that of *T. o. leakeyi*. The P_4 has a large and well-developed talonid and is very molariform with much of the unique morphology of *Theropithecus* molar teeth.

The molars show all of the specializations that are diagnostic for the genus. They are high crowned, lack basal flare, and have a large amount of cuspal relief. The buccal/lingual clefts are deep and have flat floors. The upper molars are often slightly less developed in this regard, however, than are the lowers. The molars are relatively large and broad in comparison to the other teeth. The lower molars increase in size from anterior to posterior. The M^2 and M^3 are approximately equal in size and the M^1 is smaller.

All of the deciduous dentition preserved for *T. o. oswaldi* is mandibular. Along with much of the adult dentition, a single deciduous lower canine is preserved on the juvenile male mandible MAT-VP-4/14. It is a small and incisiform tooth. Its labial surface is convex and pointed at the apex. Its lingual surface is concave and has a crest connecting the apex to the lingual margin.

Three mandibular fossils preserve both deciduous lower premolars: GAM-VP-1/8, AL537-5, and AL593-1. In all of these specimens they are damaged. They are essentially similar to the molars, but have relatively narrow crowns. On both dP_3 and dP_4, the distal lophid is broader than the mesial, but to a greater degree on the dP_3. The mesial and distal foveae of both are relatively long. A paraconid is present on the dP_3 and connected to the protoconid by a well-developed preprotocristid. Thus the mesial fovea is triangular.

Postcrania

There is a comparatively large amount of postcranial material from the ca. 2.5 Ma Matabaietu Formation, the Hata Member of the Bouri Formation, the upper part of the Kada Hadar Member, and from the site of Pinnacle near Hadar. The only postcranial elements directly associated with cranial remains are KL64-3a-e, which preserves a scapular fragment, a left distal humerus, proximal ulna and radius, along with several shaft fragments associated with a right mandibular corpus fragment. Given that most of the isolated material is of a size expected for *T. o. oswaldi*, and that over 85% of the identifiable craniodental material from this these strata is *Theropithecus*, most of these postcrania probably represent *Theropithecus*. These elements include all of the long bones of the limbs, some tarsal elements, as well as partial scapulae and pelvic bones. It is beyond the scope of this thesis to analyze all of this material in detail. However, the postcranial morphology of *T. o. oswaldi* from Kanjera and Olduvai has been thoroughly described by Jolly (1972). Krentz has discussed the forelimb material from the Shungura Formation (Krentz, 1992). He has also briefly described the forelimb and hindlimb of *Theropithecus* from several East African localities, including Kanjera, Koobi Fora, Omo, and Olduvai (Krentz, 1993). These authors have generally concluded that *T. o. oswaldi* was a highly terrestrial cercopithecid, similar in many respects to *T. gelada*, but perhaps showing slightly more arboreal ability than the modern species. Pending a thorough analysis, the material from the Afar region appears to be similar in most preserved morphological details.

Theropithecus oswaldi leakeyi (Hopwood, 1934)

(= or including *S. leakeyi* Hopwood, 1934; *S. oswaldi olduvaiensis* Leakey and Whitworth, 1958; *S. jonathani* Leakey and Whitworth, 1958; *S. oswaldi mariae* Leakey and Whitworth (nomen nudum), 1958; *S. oswaldi hopefieldensis* Singer, 1962; *S. oswaldi leakeyi*: Leakey, 1965; *T. (S.) oswaldi leakeyi*: Jolly, 1972; *T. (S.) oswaldi mariae* Jolly, 1972; *T. (S.) oswaldi* cf. *oswaldi*: Jolly, 1972; *T. (S.) aff. oswaldi* ssp. indet A, Szalay and Delson, 1979; *T. (S.) oswaldi hopefieldensis*: Szalay and Delson, 1979; *T. o. leakeyi*: M.G. Leakey, 1993)

Holotype: BM(NH) M14680 from Olduvai BED IV, Tanzania

Afar specimens included: NME BOD-VP-1/4, DAW-VP-1/1, HAR-VP 1/1, KL6-8, KL188-218, KL189-34, 57, 58, 60, 62, 64, 69, KL281-1, 3, KL286-1, KL337-1

Range: 1.65 - ~0.4 Ma

Afar range: 0.64 – ~0.4 Ma

Distribution: Ternifine; Thomas Quarries; Asbole, Andalee, Bodo, Dawaitoli, Hargufia; Konso (upper); Shungura Fm., Mbr. L; ?Nachukui Fm., Nariokotome Mbr.; Olorgesailie; Kapthurin; Olduvai Beds Upper II – IV, Masek; ?Nyeri; Hopefield; Gladysvale.

Subspecific diagnosis:

This subspecies is distinguished from both *T. o. darti* and *T. o. oswaldi* by its larger cranial, molar, and postcranial size. The rostrum is shorter relative to cranial size and the zygomatic is positioned more anteriorly (typically near M_2). Cranial superstructures are larger than in any other known cercopithecid. The posterior maxilla is deeper. The mandibular symphysis lacks mental ridges, and often has a triangular fossa on the anterior surface between the roots of the canines. The area for the incisors is very small, and the canine roots converge inferiorly. The mandible completely lacks corpus fossae, the ramus is tall and vertical. The molar teeth are larger than those of other subspecies. The M_3 is larger relative to the M_2, which is in turn larger relative to the M_1 than in other subspecies. Molar enamel complexity is also greater in this subspecies than in the older subspecies. The incisors are relatively smaller. The canines are relatively shorter, though are often still very broad. The P_3 mesiobuccal flange is likewise short.

Description:

The sample of this subspecies is relatively small. However, most of the specimens are fairly complete so that most of the skull, other than the mandible, is represented. KL337-1 (plates 20-21) is a nearly complete adult male cranium from Bodo (figured in Kalb et al., 1984; Delson, et al., 2000). HAR-VP-1/1 (plate 22) is an adult male cranium from Hargufia, lacking only the posterior neurocranium, but with significant damage to the right side of the face, zygomatic arch and neurocranium. KL281-1a/3 is a muzzle fragment and neurocranium respectively from the Upper Bodo Sand Unit, probably of an adult male. DAW-VP-1/1 (plate 23) from Dawaitoli, is the only identifiably female specimen. It is a well-preserved neurocranium along with the interorbital pillar, a fragment of the left maxilla, the right maxilla from M^3 through the M^1, superiorly up to the frontal and lateral to the orbit, and a fragment of the right maxilla preserving the C and P^3. BOD-VP-1/4 (plate 24) is a left maxillary fragment of unknown sex with M^{2-3} and part of the palatal, and base of the zygomatic processes. KL6-8 (plate 24) is a left maxillary fragment preserving M^3 and part of M^2, the root of the zygomatic process, and a small part of the palate with the greater palatine foramen. KL189-34 (plate 24) is a right maxillary fragment with P^3-M^2, part of the palate and inferior concha. This specimen is probably male as the base of the canine root is preserved in the area of the inferior concha, which is large in caliber. KL188-218 preserves the middle ½ of the supraorbital torus, and the median 5 cm of the calvaria from glabella to about 3-cm posterior to bregma. It is of unknown sex, but closest in size to the female DAW-VP-1/1. Most of the above specimens are probably roughly contemporaneous, and are derived from above and below the unnamed tuff at Bodo, Hargufia and Dawaitoli which has been dated to 0.64 Ma (Clark et al., 1994). The exceptions are KL188-218 and KL189-34, which are from the lower Andalee Member of the Wehaietu Formation. They are likely to date to somewhere between about 0.5 and 0.25 Ma based on faunal, archaeological, and stratigraphic grounds (Kalb et al., 1982).

In overall size the male crania are similar to that of a female gorilla, but with a relatively smaller neurocranium and larger face. The female neurocranium is slightly smaller than those of the males, but the face is too poorly preserved to accurately gauge its size. It does appear that the overall facial length would have been shorter relative to the neurocranium than that of the males. It is impossible to be certain of this, but given that this is almost universally true among all known cercopithecines, this statement appears likely.

In spite of the fact that *T. o. leakeyi* is well known from sizable samples of material from widely dispersed sites in the Middle Pleistocene (Delson et al., 1993) the Afar material includes the only relatively complete crania. Interestingly no mandibular material is preserved. In general morphology it is quite similar to both *T. o. oswaldi* and *T. o. darti*, with the main difference being its far greater size. In some aspects, it actually appears more similar to *T. o. darti* from Hadar than to *T. o. oswaldi*, in most aspects, however, it shows extensions of several trends that distinguish *T. o. oswaldi* from *T. o. darti*.

Rostrum

All of the specimens that preserve the muzzle dorsum are from the upper Bodo stratigraphic level, and are relatively uniform in their morphology. The maxillary ridges are weakly developed, but more prominent than in KL157-1, KL39-1, and BMNH-M32102 from Kanjera, but are similar to those of Omo 75N ’71 C24, at least as best as can be told. They are low and rounded but do not appear to arise from the canine alveoli. This may be due to the fact that the canine roots are relatively small and only faintly present. This is in contrast to AL205-1a where the canine roots are relatively long and large in caliber. The maxillary ridges of the Afar *T. o. leakeyi* males appear to arise posterior to the canine alveoli and broaden posteriorly to form a bulge between the infraorbital foramina and the nasals. The female does not preserve this area. The maxillary fossae are shallow and poorly defined, but slightly more so than those of most

Table 4.7 Dental dimensions for *T. o. leakeyi*.

	UI1			UC		
	W	L	H	W	L	H
Females						
DAW-VP-1/1				9.4	9.7	9.2
Males						
HAR-VP-1/1	6.1	7.1	8.9	12.8	14.9	24.8
KL337-1				11.0	14.5	

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
DAW-VP-1/1	8	10.4	8.3		6.5					
Males										
HAR-VP-1/1	5	10.3	7.7		7.8	5	11.2	9.4		7.5
KL337-1	6	9.5	7.5		7.8	8	11.9	10.1		11.7
Sex Unknown										
KL189-34	8	12.0	8.3							

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
KL337-1	16	13.1		13.4		14.7						
Sex Unknown												
KL189-34	16	14.3		(15.5)		15.5						

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
DAW-VP 1/1	16	15.9	14.0	15.3	12.2	18.5					6.1	8.4
Males												
HAR-VP 1/1	16	15.5	14.5	13.7	11.5	19.9					6.9	8.2
KL337-1	16	16.5		15.0		18.5					6.2	8.2
Sex Unknown												
BOD-VP 1/4	16	16.9		15.8		18.3						
KL189-34	16	(18.3)				17.8						

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
DAW-VP 1/1	12	16.1	13.2	14.1	11.1	19.5					5.6	9.7
Males												
HAR-VP 1/1	2	17.2	11.9	14.3	10.8	22.5					6.8	12.1
KL337-1	12	16.1	14.4	14.4	12.5	19.9					8.1	8.6
Sex Unknown												
BOD-VP 1/4	14	18.2		17.3		21.0					6.8	7.7
KL6-8	16	17.1		16.3		21.3						

T. o. oswaldi. Adding to the impression of faint, but present, maxillary fossae are the single large infraorbital foramina. These are positioned approximately 3cm inferior to the middle of the inferior orbital rim. From the infraorbital foramen two weakly defined lines diverge anteriorly giving the faint impression of a "V" shaped maxillary fossae with the infraorbital foramen at its apex. From what is preserved, the female DAW-VP-1/1 appears to lack maxillary fossae entirely.

The morphology of the muzzle dorsum is in some ways more similar to that of *T. o. darti* than that of *T. o. oswaldi* in the presence of distinct sulci on either side of the nasal bones giving the muzzle dorsum a concavo-convexo-concave curvature as described by Eck (1993). Further, these sulci are anteriorly divergent forming a wedge shape in superior view, following the border of the nasal bones, which are elevated above them. These sulci continue posteriorly onto the interorbital pillar and practically converge just inferior to nasion in KL337-1 and HAR-VP-1/1 and appear to be on a similar course in KL281-1a which is broken just at the level of the inferior most orbital rim. There also appear to be slight paranasal grooves preserved on the interorbital pillar of DAW-VP-1/1.

The piriform aperture is partially preserved in HAR-VP 1/1, completely but poorly preserved in KL337-1, and only just the upper right corner in KL281-1a is present. As in other *T. oswaldi ssp.* specimens, the superior portion of the rim is sharply defined and the inferior portion is more broadly rounded and comes together in a double concave-up "V" towards nasospinale. The aperture is oval in general shape, but appears relatively broader in proportion and larger in overall size relative to other subspecies of *T. oswaldi*. Anterior nasal tubercles are absent on all specimens and there is a shallow midline groove from nasospinale to prosthion. The surface formed by the outline of the piriform aperture is roughly planar and inclined at an angle close to 45° to the occlusal plane.

In relative length, the muzzles are shorter than geologically older specimens (see figure 4.9). The length of the nasals relative to total rostral length is similar to other *T.*

oswaldi, relatively shorter than in *Papio* and *Mandrillus*, thought not as short as in *T. gelada* (see figure 4.3). The face is also relatively deeper.

The maxillary dental arcade is "U"-shaped in outline, similar to other *T. oswaldi*, but with a relatively smaller incisive arc. The second incisors are only very slightly separated from the canine alveoli, which are less pronounced in the dental arcade than in earlier *T. oswaldi*. There is at most a mild reverse curve of Spee in KL337-1 and DAW-VP-1/1, but HAR-VP 1/1 has a normal convex down alveolar margin. This may be due to the younger age of the latter specimen and to the only recently erupted M^3. KL189-34 appears to have a reverse curve of Spee, but is too incomplete to be certain.

The palate is relatively shallow anteriorly and deepens substantially posteriorly. It is over 2 cm deep between the third molars in KL337-1 and HAR-VP-1/1. The lateral walls of the palate are subperpendicular to the palatal plane and nearly parallel from the third premolar to the third molar. In DAW-VP-1/1 a small bit of the palatal process of the maxilla is preserved from M^3 to M^1 and on from P^3 to C, and it appears to be similar to that of the males, deepening posteriorly, with the alveolar process forming a subperpendicular wall. The incisive and palatine foramina are typical of cercopithecines.

Midface and Zygomatic Arch

Below the orbit the midfacial area is steep and tall, with the inferior border of the zygomatic arch being 4.5 cm below the inferior margin of the orbit in KL337-1, over 5 cm in HAR-VP-1/1, and an estimated 4-cm in DAW-VP-1/1. When viewed in Frankfurt horizontal, the inferior portion of the zygomatic process of the maxilla arises from above the distal half of the M^2 in KL337-1, HAR-VP-1/1, and DAW-VP-1/1. The anterior surface of the zygomatic arch arises smoothly from the maxilla as in *T. o. oswaldi*, but is interrupted by the large infraorbital foramen giving it a slightly less "inflated" appearance. The inferior border of the zygomatic arch forms a concave down arc superiorly, posteriorly, and laterally away from the second molar and terminates in a sharp lateral bend at the anterior most point of origin of the masseter. The posterior surface of the zygoma, in all specimens where it is preserved, is marked by deep fossae.

The zygomatic arches are wide, but appear less flaring than in KL39-1 and AL205-1a, possibly due to relatively greater overall width of the whole face. The zygomatic arch is deep in the superoinferior direction and oval in cross-section. Viewed laterally, the zygomatic arch is very deep but otherwise typical of cercopithecids in shape. It is concave up from the anterior most point of the masseter muscle to the zygomaticotemporal suture, where it becomes concave down. In some specimens of the *T. oswaldi* lineage, such as KL39-1 and AL205-1a, they are quite straight in lateral view.

Both KL337-1 and HAR-VP 1/1 have masseter muscle scars that terminate anterior to the M^3, when viewed in Frankfurt orientation. In KL337-1 it is just lateral to the lateral edge of the orbit and in HAR-VP-1/1 it is directly inferior to the lateral edge of the orbit.

Orbit

The orbits are well preserved in KL337-1, the left is reasonably so in HAR-VP-1/1 and although the rim is damaged, the basic outline is visible, particularly on the right side in DAW-VP-1/1. The orbits are high and “egg shaped” as in *T. o. darti* and *T. o. oswaldi*. The superior orbital rim is thick and heavily built, approaching 1.5 cm in the

Hargufia specimen, but is thinner in DAW-VP-1/1 and KL188-218. In KL337-1 it forms separate arches over each orbit so that it is lower in the sagittal plane and higher laterally around the middle of the orbit. In HAR-VP-1/1 and KL188-218 on the other hand, the supraorbital rim is much more of a continuous curve from the right fronto-temporal suture to the left with only a slight depression in the sagittal area. This is more like the morphology of the male from Kanjera (BMNH M32102) or Omo 75N ’71 C24. In DAW-VP-1/1, the superior orbital rim is absent bilaterally in the middle of each orbit, but preserved medially and laterally. From what is preserved, it would not have formed separate well-developed arches as in KL337-1, but would have been more similar to HAR-VP-1/1. The supraorbital notches are well defined in HAR-VP-1/1, but only weakly so in KL337-1 and KL188-218. The temporal rim of the orbit is wide in all of the middle awash fossils, exceeding 2 cm in the Hargufia specimen. The frontozygomatic suture is approximately horizontal in inclination, with its medial limit forming in upper lateral corner of the orbit (as is normal in cercopithecids). It trends laterally, then posteriorly before reaching the temporal rim. The interorbital pillar is broad, being widest in HAR-VP-1/1 and narrowest in the female DAW-VP-1/1 and in KL188-218. In all three of the Middle Awash Crania, the lacrimal fossa is within the lacrimal bone, the anterior edge of which forms the orbital rim. The medial rim of the lacrimal fossa forms the lateral border of the paranasal sulcus, medial to which the nasals bulge slightly. The interorbital pillar is both absolutely and relatively quite broad in the Middle Awash specimens. The glabella projects slightly anterior to nasion, when the skull is viewed in the Frankfurt orientation, with the female DAW-VP-1/1 being the most prominent in the sample, but less so than in *T. gelada* and some *Papio hamadryas anubis*.

Calvaria

The cranial vault is well preserved in KL337-1, KL281-3, DAW-VP-1/1, and partially in HAR-VP-1/1 and KL188-218. The most striking feature about all of these specimens is the massive development of attachments for the temporal muscles, which must have been substantial, forming large compound sagittal and nuchal crests. In KL337-1 and KL281-3 the temporal lines are extremely prominent. Posterior the orbits they are oriented mediolaterally at an angle nearly perpendicular to the sagittal plane and they converge very far anteriorly on the calvaria to form a prominent sagittal crest. In combination with the deep excavation of the temporal fossae, this makes the superior orbital rims form what Benefit and McCrossin (1997) have called "supraorbital costae". The sagittal crest is extreme in KL337-1. It is broken anterior to bregma, but is nearly ½ cm high where the temporal lines converge, and is nearly 2 cm in height at bregma. It increases in height posteriorly from bregma to reach its maximum at inion, where it meets the nuchal crest and forms a compound crest. At inion this crest approaches 3 cm in height. The sagittal crest appears to have been similar in KL281-3, but there is significant damage making absolute values difficult to determine. Viewed superiorly, the temporal lines of DAW-VP-1/1 are strongly developed and curve sharply medially posterior to the orbits, but do not converge, instead running subparallel posteriorly from behind the supraorbital torus to form a sagittal crest only well posterior to bregma. They are 33 mm apart at the apex of the temporal fossa, 6.5-mm apart at bregma, and meet just anterior to lambda. KL188-218 has temporal lines that are more strongly marked than DAW-VP-1/1 and converge at approximately bregma to form a sagittal crest which is initially low but by the posterior limit of the specimen, a few cm behind bregma, it is about 1 cm in height.

In all specimens where the posterior portion of the calvaria is preserved, large nuchal crests are present. These are semicircular in superior view. In the male KL337-1 and probably male KL281-3, there is a slight prominence at inion, but not in DAW-VP-1/1. In all specimens, the nuchal crest is large immediately behind the auditory meatus, and remains so all the way to inion. In KL337-1 this crest is nearly 3 cm in height for much of its length, and in DAW-VP-1/1 it is nearly 2 cm. In all specimens the nuchal crest in combination with the zygomatic arch forms a continuous shelf lateral to the neurocranium, providing a very large area of muscle attachment for the m. temporalis.

Viewed superiorly, the neurocranium is egg-shaped being narrow anteriorly, widest at the level of the auditory meatus, it is then semicircular in posterior to the meatus. This egg-shape is caused by the fact that there is a very large amount of postorbital constriction. In combination with the wide zygomatic arches, this postorbital constriction produces a very large infratemporal fossa. In posterior view, the widest point of the neurocranium, not counting the nuchal crest, is low, at about the level of the auditory meatus. The temporal squamae are low and more inclined medially than in earlier *T. oswaldi*.

Basicranium

The basicranium is well preserved in KL337-1 and DAW-VP-1/1, but is somewhat obstructed by matrix in KL281-3. The occipital plane is flat, but curves inferiorly towards the margin of the nuchal crest. The mastoid region is raised only very slightly above the occipital plane, and the digastric groove is broad and shallow. In fact, if it were not for the digastric groove, it might appear as if there were no mastoid processes. There is little difference in mastoid morphology between the two males and the female. The tympanic bone is angled slightly posteriorolaterally. The postglenoid process is tall, broad and pressed directly against the tympanic. The glenoid fossa is deep and the eminence is prominent. The articular surface is distinctly sellar in morphology, being concave-down in the medio-lateral plane and convex-down in the anteroposterior plane. The rate of curvature of both seems tighter than in *T. o. darti*, and the articular surface is raised well above the surrounding bone.

Facial hafting

In KL337-1, HAR-VP-1/1 and DAW-VP-1/1 the glenoid fossa and temporal region is elevated well above the occlusal plane, perhaps even more so than in other members of the genus, save *T. gelada*. This may be related to the extremely deep and short face. The frontal is receding, being more inferior than the brow ridge, with the exception of the sagittal crest. It is difficult to tell whether there is an ophryonic groove or not in the males due to the extreme postorbital constriction and well developed temporal lines, but there does appear to be a slight, shallow and wide ophryonic groove on DAW-VP-1/1. It is difficult to tell whether the face is lower overall relative to the neurocranium when compared to other papionins or whether the lower alveolar plane is accomplished solely by deepening of the face.

Dentition

Of the dentition, only the upper permanent teeth are preserved, all of which are at least partially represented except for the lateral incisor. Dental dimensions are given in table 4.7. HAR-VP-1/1 preserves the upper central incisor. Its crown shape is typical of most papionins, being spatulate, lacking a lingual cingulum and flaring slightly from the cervix to the crown tip. Its crown flares slightly more medially than laterally. The one feature that is most striking about the tooth is its diminutive size, both relative to the molar teeth, and to the cranium overall. It is relatively even smaller than the incisors of *T. o. oswaldi*. It is similar in absolute size to upper first incisors of macaques and mangabeys. Judging from the alveoli on both KL337-1 and HAR-VP-1/1 the I^2 was smaller than the I^1.

The canines are essentially typical of cercopithecids, and sexually dimorphic. Their most obvious feature is that the canines of both sexes are relatively small in comparison to both molar size and cranial size. The male canines are relatively shorter and larger in caliber than those of most cercopithecids, and their distal edge is not as sharp.

The upper premolars are relatively large and molariform. The lingual cusps are columnar with well-developed mesial and distal foveae. The P^4 is larger than the P^3, and quadrate in occlusal view with a large talon. The P^3 is more triangular in occlusal view. The molars are large with complexly folded enamel with deep flattened buccal and lingual clefts. The M^3 is the largest tooth, being longer and broader than the M^2.

Postcrania

There are several postcranial elements, which are not directly associated with any of the cranial material, but can be confidently assigned to this taxon based on size. In total they sample the regions around the elbow, femur, and ankle. All of the postcranial elements except for KL286-1 come from Andalee and may represent a single individual (Kalb et al., 1982).

Forelimb

KL189-60 is a distal fragment of a left humerus. It is very large, being similar in size and morphology to KNM-OG 1056, a large humerus of *T. o. leakeyi* from Olorgesailie. The medial flange is somewhat short, but sharply projecting, and angled nearly perpendicular to the trochlea. The *zona conoidea* is nearly flat, and poorly developed. The olecranon fossa is fairly small and shallow, given the size of the specimen. The medial epicondyle is modest in length, but projects medially, so that the articular area is narrow relative to total biepicondylar breadth. The *m. brachioradialis* flange is short and weakly developed.

A proximal fragment of a left ulna, KL189-58, that articulates with KL189-60 is also present. The olecranon process is damaged, but it would have been strongly retroflexed. The trochlear notch is deep, and the superior border of the trochlear articulation on the anconial process is undulated with the lateral side significantly higher than the medial. The radial notch is deep, rounded and bears a double articulation.

Hindlimb

There are three femoral fragments preserved in the sample. Two are from Andalee, and the third (KL286-1) is from Bodo. KL189-57 is a nearly complete right femur except for the head, neck, and proximal tip of the greater trochanter. KL189-64 is the damaged proximal end of a right femur with approximately 4-cm of the shaft. The posterior half of the head and neck are missing, as is the greater trochanter. KL286-1 is a left proximal femur with 1/3 of the shaft, preserving the head neck and both trochanters. The morphology of all three is similar.

KL189-57 is complete enough to allow an estimate of the total length of the femur. The length to the greater trochanter would have been slightly longer than 297 mm. Judging from the other two femora, the length to the head would have been approximately 7-12 mm shorter. The articular surface of the head extends onto the posterior surface of the neck and the fovea capitis is large and oval in outline. The neck is short and very robust. In all three specimens, the greater trochanter is taller than the head and curves slightly medially. The greater trochanter of KL286-1 projects significantly above the head. That of KL189-57 would not have been as tall as that of KL286-1. Due to damage it is difficult to estimate how much taller that of KL157-64 would have been. The lesser trochanter is visible in all specimens and is short and angled medially.

The shaft is thick, robust, and strongly bowed in the anteroposterior plane. The most striking feature of the shaft is its strongly reversed valgus angle of approximately 15º relative to the sagittal plane. Related to this carrying angle, the distal morphology of the femur is also fairly distinctive. The medial epicondyle is smaller and more lightly built than the lateral, and the lateral border of the patellar groove is more pronounced than the medial.

Some of the ankle morphology is preserved in two additional specimens. KL189-62 is a distal fragment of a left tibia with a long and prominent medial malleolus. Its astragalar articular surface is highly asymmetrical. KL189-69 is a right astragalus with an equally asymmetrical trochlea, where the lateral border is much higher than the medial. The proximal margin is low and forms a continuation of the slope of the trochlea. The medial malleolar cup is deep and extends nearly to the plantar surface. The proximal calcaneal facet is convex, but not strongly so.

cf. *Theropithecus* sp. cf. *T. oswaldi*

Specimens: WEE-VP-1/1, 1/19; ?KL155-1

Description:

There are two mandibular specimens and an isolated molar included in this sample, all from Wee-ee. Dental dimensions for this material are listed in table 4.8. WEE-VP-1/1 (plate 25) is a right corpus fragment with P_4 through M_3, and the alveoli for the P_3. The inferior margin and ramus are absent, but approximately 1.5 to 2 cm of the corpus is preserved below the teeth. From the alveoli it can be seen that the P_3 had a very short mesiobuccal flange and is therefore most likely from a female individual. The molars show many features typical of *Theropithecus*, but they are not completely developed. These include relatively high and straight-sided crowns with low amount of basal flare, the cups are relatively high, the lingual notches are flattened at the base, the buccal clefts are fairly flat floored, and the buccal cusps are columnar. Furthermore, the molar proportions are also similar to *Theropithecus*, in that the molars increase in both length and breadth posteriorly. The P_4 is also quite molarized showing many of the above specializations seen in the molars. Some of the corpus morphology is visible. Laterally, it lacks fossae. Medially, the superior transverse torus extends posteriorly to the P_3 and the inferior extended further posteriorly, but it is unclear how far. WEE-VP-1/19 is an isolated lower left molar that is most likely to be an M_1 as the distal lophid is broader than the mesial. It is similar in morphology to the molars of WEE-VP-1/19.

Stratigraphically, the specimen is from the Belohdelie Member of the Sagantole Formation, which is bracketed by the VT-1 (=Moiti) and CT tuffs dated to 3.85 ± 0.03 and 3.89 ± 0.02 Ma respectively (White et al., 1993; Renne et al., 1999). If this specimen is correctly allocated to genus, then it is the oldest securely dated specimen known, being some 400 kyr older than oldest specimens from Hadar, Maka, sub-Tulu Bor, and Lothagam Lonyumun.

KL155-1 (plate 25) is a nearly complete mandible of a male with the left C_1-M_3, and right P_3-M_3. The right and left halves are separate and broken at the symphysis, but fit together. It lacks the superior portions of the rami, the gonial areas and the region of the right incisors and canines. In overall size the corpus is larger than that of either *Pliopapio alemui*, *Parapapio ado* from Laetoli, and *Pp. cf. jonesi* from Hadar. The anterior surface of the symphysis is not well preserved, but it is clear that the mental ridges were present, but not prominent or rugose. On the posterior surface, most of the morphology is damaged. It is clear that both transverse tori are well developed, with the inferior torus projecting further distally, to approximately the middle of P_4. In profile it slopes at an angle of approximately 50º to the occlusal plane. The corpus relatively deep overall, and deepens posteriorly in lateral view, unlike the corpora of *P. (Dinopithecus)* which tend to be shallower under the M_3 than under the M_1. There is also an inferior bulging of the inferior margin beneath the M_2. The lateral surface of the corpus almost completely lacks corpus fossae. In superior view the corpora are relatively narrow, similar to those of modern *Papio*. The oblique line is fairly well marked, but the extramolar sulcus is fairly narrow. Little of the rami are preserved, but enough is present to see that it was more posteriorly inclined than in most *T. (Theropithecus)*.

Dentally, it is ambiguous. The teeth are all typical of larger papionins. The incisors are absent, but the alveoli of the left I_{1-2} are preserved. They are not as small as those of geologically younger *T. oswaldi*, but are smaller than those of modern *Papio*. The canines are typical in morphology, being large and robust, but not very tall. The P_3 has a long mesiobuccal flange and the P_4 also has a very short mesiobuccal flange. The molars show some of the features of *Theropithecus*, but not completely. They are not very high-crowned, but do show a low level of flare. They also have buccal clefts with broad floors that are somewhat flattened, and buccal cusps that are fairly columnar. These features are similar to their development in some specimens of *T. o. darti*, such as AL129-8, but are also seen in some specimens of *Papio*.

Thus, the dentition is similar to primitive *T. oswaldi* and *Papio*. The mandibular morphology is, however, more consistent with *Theropithecus* given its lack of corpus fossae, and its posteriorly convergent profile. Therefore, in overall morphology this specimen is most consistent with early *Theropithecus oswaldi*. For these reasons, and that this specimen matches the expected morphology of a male specimen from the same taxon as WEE-VP-1/1, it is included with it here as tentatively assigned to primitive *T. oswaldi*. It is not known for certain whether this specimen comes from the same stratigraphic level as WEE-VP-1/1, or whether it is from the level just below the Sidi Hakoma Tuff.

Table 4.8 Dental dimensions for ?*Theropithecus* from Wee-ee.

	LC		
	W	L	H
Males			
KL155-1	11.5	8.1	

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
WEE-VP-1/1					6	4.9	6.8		2.7	4.4
Males										
KL155-1	6.1	10.2	19.0		6	7.4	7.4		3.5	4.9

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
WEE-VP-1/1	12	6.9	6.6	7.3	7.2	9.6					3.1	4.8
Males												
KL155-1	16	8.6		9.0		10.1						
Sex Unknown												
WEE-VP-1/19	10	8.6	7.7	8.3	7.3	10.2					3.9	5.0
LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
WEE-VP-1/1	8	8.4	7.9	8.7	8.1	11.2					3.6	5.6
Males												
KL155-1	14	10.7	10.1	10.5	10.2	12.3					3.0	4.5
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
WEE-VP-1/1	4	8.8	7.9	8.4	7.3	13.5					3.7	7.1
Males												
KL155-1	6	10.9	9.9	10.1	9.2	16.5					4.0	6.2

cf. Cercopithecinae gen. et sp. indet.

Afar specimens included: WEE-VP-1/6

Description:

This specimen is the distal end and ½ shaft of a left humerus. It is from a species of monkey similar in size to the *Cercopithecus* species from Andalee. The distal epiphysis is completely fused. In general it is similar morphologically as well. It is for this overall resemblance that this specimen is tentatively allocated to the Cercopithecinae. The medial epicondyle is broken, but was probably only modestly retroflexed. The articular surface has a fairly well developed medial trochlear flange, which is damaged, but the preserved length is similar to specimens from Andalee. Also the articular surface has a fairly well developed zona conoidea. The overall width of the humerus relative to the articular surface is similar to that seen in *Cercopithecus*. The brachioradialis flange is relatively prominent. The supraradial notch is larger than the supraulnar, a feature possibly associated with the Colobinae (Delson, 1973).

This specimen is from the Belohdelie Member of the Sagantole Formation, and therefore dates to between 3.85 and 3.89 Ma, making it highly unlikely to represent the same species as is present at Andalee. Additionally, it is larger than would be expected for a humerus associated with the little cercopithecin mandible from Koobi Fora (ER 396). In spite of the difficulty in diagnosing this specimen, it is important as it clearly cannot be the same species as WEE-VP-1/1, KL155-1, or WIL-VP-1/2 (regardless of whether these specimens represent one or two taxa), and therefore documents additional diversity in the Belohdelie Member.

Subfamily Colobinae Jerdon, 1867

Genus *Kuseracolobus* Frost, 2001

(= or including Colobinae sp. A. Eck, 1977: WoldeGabriel et al., 1994, in part. cf.

Paracolobus sp. R. E. F. Leakey, 1969: WoldeGabriel et al., 1994, in part)

Type species *Kuseracolobus aramisi* Frost, 2001

Generic Diagnosis:

This diagnosis follows Frost (in press). A genus of colobine monkey with a broad interorbital area, as is typical for colobines, but distinguishing it from *Libypithecus*, *Nasalis*, and *Rhinocolobus* (especially considering size). The projection of the lower face anterior to the zygomatic arches in *Kuseracolobus* is generally similar, in proportion to overall cranial size, to that of *Cercopithecoides*, *Mesopithecus*, *Trachypithecus* and the Leadu colobine (discussed below under cf. *Cercopithecoides* sp. nov.). In comparison to *Colobus*, the lower face of *K. aramisi* is less projecting, and it is distinctly less so than in the long-faced genera *Paracolobus*, *Rhinocolobus*, *Dolichopithecus* and *Nasalis*. In profile, the maxillary alveolar margin completely lacks the airorhynchous shape of *Semnopithecus*.

As is typical for most colobines, the mandibular symphysis lacks a median mental foramen. This distinguishes it from both *Rhinocolobus* (at least as known from the Shungura and Koobi Fora Formations) and some *Cercopithecoides*, which possess one. In lateral view, the symphysis is deep with a vertical profile. The corpus is quite deep and robust overall, and deepens posteriorly. In its depth and robusticity, the corpus is different from Colobinae gen. et sp. nov., *Procolobus, Cercopithecoides, Semnopithecus,* *Pygathrix* and *Presbytis*. It is more like *Colobus*, *Paracolobus* and *Rhinocolobus*, but not as deep as the corpora of the last two genera. It is further differentiated from *Paracolobus* and *Rhinocolobus* by the presence of larger *prominentia laterales*, similar to *Nasalis* (including *N. (Simias)*). The gonial region is expanded, separating it from the Leadu colobine, *Cercopithecoides,* and *Procolobus,* but far less so than in *Paracolobus mutiwa*.

In the dentition, the I^1 crown is not flaring in anterior view, so that the apex is not significantly wider than the base. This is distinct from the flaring I^1 in *Procolobus*. The P^3 protocone is not reduced as in *Cercopithecoides*, *Colobus*, and *Rhinocolobus*. The distal lophid of the M_3 is typically narrower than the mesial, as is typical for the Presbytina, and likely primitive for the Colobinae (Szalay and Delson, 1979). Three individuals out of 30 in the *K. aramisi* sample show hypolophids that are wider than their protolophids, and most are subequal. Most of the M_3 hypolophids are wider relative to their protolophids than those of *Mesopithecus*.

Kuseracolobus aramisi Frost, 2001, Type Species

(= or including Colobinae sp. A. Eck, 1977: WoldeGabriel et al., 1994, in part. cf. *Paracolobus* sp.: WoldeGabriel et al., 1994, in part)

Holotype: NME ARA-VP-1/87 from the Sagantole Fm. Aramis Mbr., between the GATC and DABT tuffs.

Afar specimens included: see appendix 5.

Range: 4.4 - 4.2 (4.4 – 3.75) Ma

Distribution: Aramis, Adgantole Mbs., Sagantole Fm. (also from Fm. “W” below VT-3 if BOD-VP-3/2 is included).

Specific Diagnosis: As for genus.

Description:

The best cranial specimens, ARA-VP-6/1686 and KUS-VP-2/70 (plate 26), are both females. ARA-VP-6/1686 preserves both maxillae and premaxillae below the middle of the zygomatic process of the maxilla, but little of the palate. The entire dentition is preserved other than the right I^2 and M^2. KUS-VP-2/70 preserves a left premaxillo-maxillary fragment with C^1-M^1, most of the root of the zygoma, part of the lateral aspect of the face and piriform aperture, and most of the palatal process. A small fragment of the right maxilla with M^{1-2} and some of the palatal process is also preserved, along with the glabellar portion of the frontal and an isolated left I^1. The holotype ARA-VP-1/87, preserves a left maxillary fragment with M^{1-3} and the roots of P4, a small part of the palatine process, and the very base of the zygomatic process (see plate 26). ARA-VP-1/6 is a male left maxilla preserving P^3-M^3, and the root of C^1 (see plate 26). It is highly damaged, however, revealing the roots of the teeth.

Kuseracolobus aramisi is larger in cranio-dental size than *Colobus, Libypithecus* and *Mesopithecus*, but smaller than *Cercopithecoides* (other than a new species from Lothagam to be described by Leakey et al., in press), *Paracolobus*, *Rhinocolobus,* and *Dolichopithecus*. It is similar in size to *Nasalis,* Colobinae gen. et sp. nov., and larger subspecies of *Semnopithecus entellus*. Colobines of similar dental size also occur in the Omo Shungura Formation in Members B, C, D and G, from the Tulu Bor Member at

Koobi Fora, and from the Upper Laetolil beds. The dental dimensions of *K. aramisi* are given in table 4.9.

Table 4.9 Summary dental dimesnions for *Kuseracolobus aramisi*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.23.

	Kuseracolobus aramisi												
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^1	6	5.2	0.3	4.9	5.8	7.1	2.1	4.0	9.0	5.9	0.3	5.5	6.1
I^2	13	4.9	0.5	4.3	6.1	7.4	1.0	5.7	8.5	5.2	0.6	4.3	6.3
C^1 (?)	2	5.0	0.2	4.8	5.1	7.9	0.4	6.8	9.1	6.7	1.6	6.4	6.9
C^1 (?)	2	7.3	0.3	7.1	7.5	21.7				10.4	0.3	10.2	10.6
P^3	9	6.4	0.5	5.9	7.4					5.7	0.6	4.9	6.7
P^4	5	6.5	0.4	6.2	7.1					5.5	0.3	5.1	5.8
M^1	10	7.1	0.4	6.4	7.9	6.9	0.3	6.4	7.4	7.9	0.5	7.3	9.0
M^2	7	8.0	0.4	7.6	8.7	7.3	0.3	7.0	7.9	8.7	0.2	8.2	9.0
M^3	6	8.2	0.4	7.8	8.7	6.8	0.1	6.7	6.9	9.0	0.3	8.6	9.5
M^x	41	8.3	0.5	7.5	9.4	7.5	0.4	6.7	8.6	8.7	0.6	7.9	10.0
dP^4	4	5.7	0.0	5.7	5.7	5.6	0.1	5.5	5.7	6.7	0.2	6.5	7.0
I_1	2	4.4	0.2	4.2	4.6	7.5				3.5			
I_2	9	4.6	0.5	3.8	5.5	6.9	1.1	5.1	8.5	3.6	0.4	3.0	4.4
C_1 (?)	1	5.7								3.7			
C_1 (?)	3	8.4	0.5	7.8	8.8	16.6				5.5	0.2	5.3	5.7
P_3 (?)	2	4.8	0.5	4.5	5.1	8.2				5.9	0.5	4.9	5.4
P_3 (?)	4	4.7	0.2	4.5	5.0	11.6	0.8	11.0	12.8	7.3	0.2	7.0	7.4
P_4	15	5.1	0.2	4.7	5.7					6.7	0.5	6.0	7.5
M_1	13	6.1	0.3	5.8	6.6	6.2	0.5	5.5	6.9	7.9	0.5	6.9	8.7
M_2	10	7.2	0.4	6.5	7.6	7.3	0.6	6.4	8.0	8.8	0.6	8.0	9.9
M_3	34	7.2	0.4	6.3	7.9	7.1	0.3	6.3	7.7	11.8	0.8	10.5	13.5
M_x	42	6.9	0.7	5.7	8.2	7.0	0.7	6.0	8.5	8.7	0.5	7.7	10.0
dP_4	4	4.5	0.2	4.3	4.7	4.8	0.3	4.4	5.0	6.7	0.3	6.3	7.0

Frontal

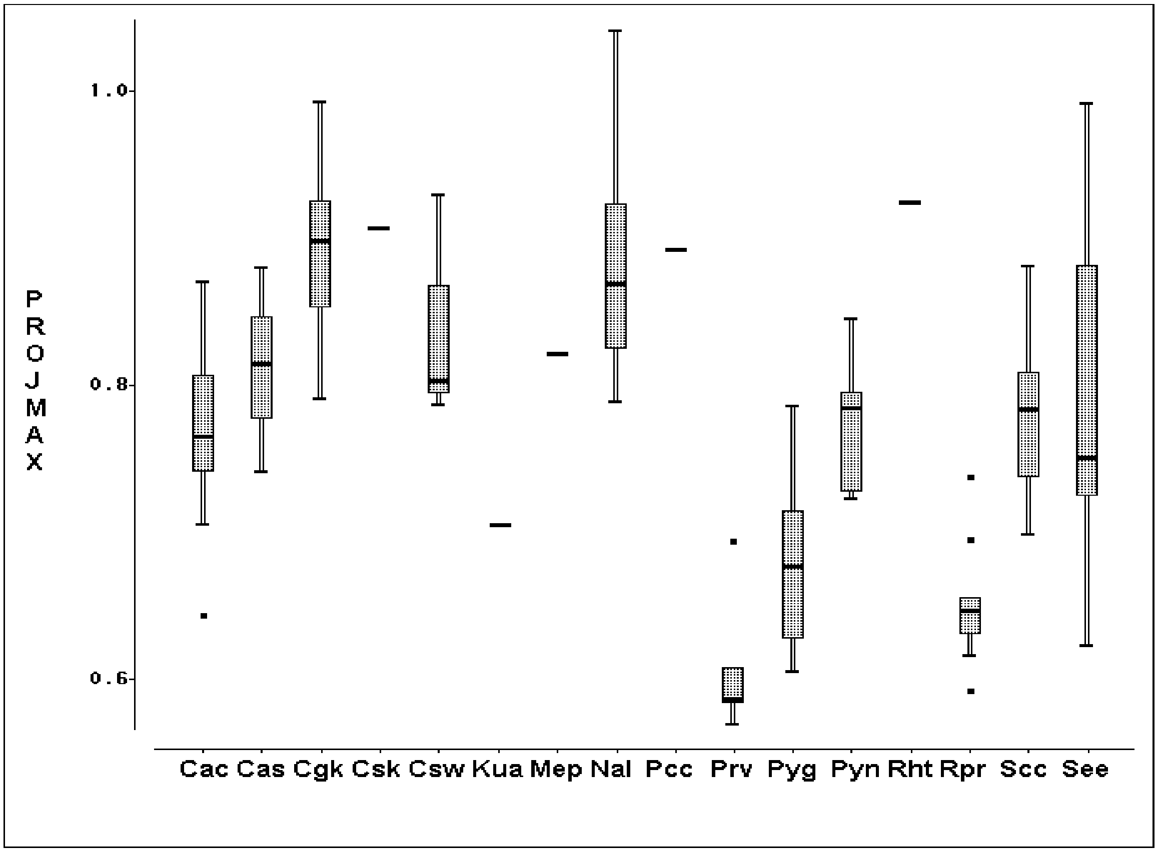
A small part of the glabellar area is preserved in KUS-VP-2/70 and ARA-VP-1/13. Both are similar in overall morphology to Colobinae gen. et sp. nov. The first specimen is a female and has an interorbital breadth of 12.1 mm, the second is of unknown sex and has an interorbital breadth of 10.8 mm, compared with 13.8 mm in the male Leadu specimen. Both Aramis specimens preserve nasals that are slightly pointed anterosuperiorly.

Maxilla

The best specimens are ARA-VP-6/1686 and KUS-VP-2/70, but the male ARA-VP-1/87 also preserves a left maxillary fragment. The root of the zygoma appears to be positioned above M^1, or the M^1/M^2 contact in both male and female specimens. This placement of the zygoma is slightly more anterior than that found in *C. williamsi* from Koobi Fora, and most *C. williamsi* from South Africa. The piriform aperture is more vertically inclined and the rostrum shorter than they are in most cercopithecines. The piriform aperture is quite narrow and tall, and the plane of its outline forms an angle slightly more than 60º with the alveolar margin in the subadult KUS-VP-2/70 and approximately 45º in ARA-VP-6/1686. The inferior portion of the piriform aperture is sharply "V"-shaped. In superior view, the premaxillae form a squared-off rostrum. The premaxillae would have been relatively short overall and generally similar in outline to those of AL32-4 and KNM-ER 4420. In total, this yields a lower face that does not project as far anterior to the zygomatic arches as it does in other colobines (see figure 4.11).

The maxillary dental arcade is best preserved in ARA-VP-6/1686, and although distorted bilaterally, it is reasonably intact on the left. KUS-VP-2/70 and ARA-VP-1/87 also preserve partial tooth rows. The dental arcade forms a gentle arc from M^3 to C^1, being widest around the M^1/M^2 contact, with no tooth deviating from this line. There is a sharp angle at the canines, and the incisors form a relatively straight, flat arc between the canines. The palate is partially preserved in KUS-VP-2/70 and appears to have been fairly shallow and flat. It is slightly deeper in the male ARA-VP-1/87, which preserves a small part of the palatal process.

Figure 4.11 Distance from prosthion to midpoint on the line connecting right and left inferior most point on zygomatico-maxillary suture.



Mandible

The mandible is best preserved in the male specimen ARA-VP-1/87 (plates 27-28), which retains much of the corpus and the majority of the rami, though the margins and gonion are damaged and the condyles are lacking. Except for the right M_1, the entire post-canine dentition is preserved. ARA-VP-1/5 (plate 29) is the symphysis of a male with the left C_1-M_1 and right P_3-M_1. ARA-VP-1/290 (plate 29) is probably a sub-adult male symphysis with the left I_{1-2} and P_4-M_1 and the crowns of the canines and P_3's erupting. ARA-VP-6/796 (plate 29) is the symphysis of a female with the left M_1 through right P_4. ARA-VP-1/1774 (plate 29) preserves the right corpus down the inferior margin under the M_{1-3}. ARA-VP-1/564 (plate 29) preserves part of the corpus below the molars, but none of the margin. Other specimens preserve more fragmentary portions.

The symphysis is quite steeply sloping, rather deep overall, and has a vertical profile. Both transverse tori are robust. The superior transverse torus extends posteriorly to the distal portion of P_3, and is fairly steeply sloping. Anteriorly the symphysis lacks a median mental foramen.

On the lateral surface of the corpus is a very slight fossa. This is largely due to the presence of lateral bulging near the inferior margin, which is the widest part of the corpus. This can be most clearly seen in the female ARA-VP-6/796, but also in ARA-VP-1/290. This morphology is unlike that of the Leadu colobine, AL231-1a (a specimen from Hadar most likely to be the same taxon as the Leadu colobine) and *Cercopithecoides* (particularly KNM-ER 4420), where the corpus is the widest at mid-height. The mental foramen seems to be single in all of the mandibles recovered, and its position varies from below the M_1/P_4 contact in ARA-VP-1/1774 to the P_3/P_4 contact in the juvenile ARA-VP-1/290. The corpus is fairly deep overall, especially compared with the Leadu colobine, AL231-1a, or *Cercopithecoides* from both East and South Africa. It is shallower but thicker than mandibles of *Paracolobus mutiwa* and *Rhinocolobus*. In ARA-VP-1/87 the right corpus deepens posteriorly from P_3 to M_3, though there is damage below the M_1 through mesial M_3. ARA-VP-1/1774 deepens from M_1 to M_3 and preserves a bulge below the M_2. The gonial area is partially preserved in ARA-VP-1/87 and is expanded, though not to the extent seen in *Paracolobus mutiwa*. This is quite distinct from the comparatively unexpanded gonial area seen in the Leadu colobine and *Cercopithecoides*.

Viewed superiorly, there is a wide extramolar sulcus, and the oblique line blends into the corpus at mesial M_2 or distal M_1, comparable to that in the Leadu colobine and AL231-1a. There is no strongly marked ridge at the anterior limit of the masseter scar. The mandibular dental arcade, though it is slightly distorted, is best preserved in ARA-VP-1/87. It forms a parabolic arch, except that the area across the incisors is flattened.

Dentition

The dentition overall is typical for colobines. The upper incisors are smaller and far less flaring than in papionins. The mesial and distal margins of the I^1 crown are roughly parallel and slant mesially, and the widest part of the crown is approximately at mid-height. Lingually, there is a cingulum around the base. The I^2 is caniniform in crown shape and also has a lingual cingulum. The lower incisors possess lingual enamel and are small, peg-like teeth compared with those of papionins. The I_1 lingual surface is shoveled, and the crown is slightly flaring in anterior view. The I_2 has a crown that is narrower overall, more of a parallelogram in outline, and possesses a distal cuspule, or "lateral prong" (Delson, 1975). The canines are typical of cercopithecids, being comparatively large teeth and highly sexually dimorphic.

The upper premolars are typical bicuspid teeth. The protocone of the P^3 is usually present and often large, but sometimes reduced. The P^3 is generally more triangular in occlusal outline, and the P^4 often has a bit more of a talon. The P_3 is sexually dimorphic as for most cercopithecids, particularly in the development of the mesiobuccal flange. It is also typical of colobines in that the paraconid is generally more pronounced than in cercopithecines. The male mesiobuccal flange is shorter than those of male cercopithecines (though longer than female cercopithecines), is more inferiorly directed, and the talonid extends more lingually. The P_4 is a more molariform tooth, but may develop a mesiobuccal flange in males. There is also a greater amount of cusp relief (*i.e.* the difference between the height of the cusps and the lowest points of the crown between them) than is the case in cercopithecines.

The molar crowns are only slightly flaring with tall, widely spaced cusps that are connected by sharp cross-lophs. On the upper molars, the paraloph is broader than the hypoloph, but less so than in cercopithecines. The buccal notch has a "crease" reaching toward the cervix from the buccal notch. A distal fifth cuspule is variably present on the M^3. The upper molars are all roughly similar in overall size, and generally arranged in a straight line. The lower molars have very deep lingual notches with high cusps. The distal cingulum of $M_{1\text{-}2}$ forms a distal cuspule 6-8% of the time, depending on scoring. On the M_3, the hypoconulid is well developed, and there is typically (62-92%, depending on scoring) a tuberculum sextum as well. This contributes to the presence of a well-developed distal lingual notch between the hypoconulid and the entoconid. There is also a well-developed distal buccal cleft. The metalophid is usually wider than the protolophid on $M_{1\text{-}2}$ but generally not on M_3 (though it is occasionally). These lophid proportions for *K. aramisi* are typical of Asian colobines (which may be the primitive state for the subfamily, see Szalay and Delson, 1979), but different from extant African colobines.

Of the deciduous dentition, the dI_2 is possibly known in ARA-VP-1/2092. It looks like a miniature of the permanent I_2, with a relatively narrow crown and a distal prong. This is distinct from normal papionin morphology, where the lower dIs are rather broad. Of the deciduous premolars, upper and lower dP4s are known. The dP^4 is much like the M^1, but far more flaring, with more approximated cusps. The mesial and distal foveae are relatively longer than in the molars. The dP_4 is similar to the M_1, but is narrower relative to its length, with a metalophid that wider in comparison to the protolophid than in M_1. The lophids are not quite as well developed as those of the molars, but are better developed than those of the deciduous premolars of cercopithecines.

Genus *Rhinocolobus* M.G. Leakey, 1982

(= or including Colobinae gen. et sp. nov. M.G. Leakey and R. E. F. Leakey, 1973; M.G. Leakey, 1976; Eck, 1976, 1977; cf. Genus et sp. nov. Omo M.G. Leakey and R. E. F. Leakey, 1973. Colobinae gen. et sp. nov. 1. Szalay and Delson, 1979)

Type species *Rhinocolobus turkanaensis* M.G. Leakey, 1982

Generic Diagnosis:

The generic diagnosis for *Rhinocolobus* has not changed since its original description by Leakey (1982). Her description will largely be followed here. The most diagnostic features of the genus are concentrated in the face, which is airorhynchous overall, compared to other large colobines. The interorbital pillar is relatively narrow, distinguishing it from most colobines other than *Nasalis*, *Dolichopithecus,* and *Libypithecus.* The rostrum is relatively long, at least sub-nasally, and different from that of *Cercopithecoides, Kuseracolobus,* the Leadu colobine, *Colobus* and *Procolobus*. The nasals are extremely short, even relative to other colobines. The piriform aperture is unique among cercopithecids. It is very long anterioposteriorly and relatively wide for a colobine. It is oriented so that its margin lies in a plane that is at a low angle relative to the alveolar plane. In profile, the piriform aperture, and face in general, is concave in outline, not unlike *Pygathrix* or *Rhinopithecus* in this one aspect, but is substantially longer. Additionally, it can be observed on some specimens that there is what appears to be a muscle scar around the superior ½ of the rim (personal observation). The supraorbital tori are prominent, projecting, and separated from the neurocranium by a deep ophryonic groove. The neurocranium is relatively long and narrow, with only a small posterior sagittal crest in the male. Nuchal crests are present in both males and females. Unfortunately, there is little facial material preserved in the sample from the Afar depression.

The mandibular symphysis is pierced by a median mental foramen (in the Turkana basin material, but see below) which distinguishes it from *Colobus, Paracolobus, Kuseracolobus*, *Paracolobus*, but not from *Procolobus(Procolobus)*. The symphysis also lacks mental ridges as do those of most colobines, but is unlike the symphysis of *P. (Procolobus)*. It is relatively sloping in profile, when compared to other large colobines such as *Paracolobus mutiwa*, or *Cercopithecoides.* The symphysis and corpus are relatively deep, narrow, and deepen posteriorly, similar to *Paracolobus*, but different from *Cercopithecoides*. The corpus lacks facial fossae or prominentia laterales, further separating it from *Cercopithecoides*. The gonial region is large, and in the males it appears to have been inferiorly expanded.

Dentally, the incisors are small relative to the molar teeth, the P^3 has a reduced protocone as appears to typify the Colobina, but the P_4 has a prominent metaconid. The distal lophid of the M_3 is typically equal to or narrower than the mesial, being wider than the mesial in only 42% of the Turkana sample.

There is a partial skeleton associated with a mandible from Koobi Fora. Based on this specimen, *Rhinocolobus* is distinguished from the other large colobines and the colobine from Leadu by possessing postcranial adaptations associated with arboreal locomotion (Birchette, 1982; Ciochon, 1993). The humeral head is broad, spherical and higher than the greater tuberosity. Distally, the humerus is characterized by being anteroposteriorly flat and mediolaterally broad. The medial trochlear keel is short, the capitulum is relatively spherical, and the *zona conoidea* is prominent in comparison to other cercopithecids. The medial epicondyle is long and projects medially. On the proximal ulna, the olecranon is shorter than that of *Paracolobus*, and less retroflexed than it is in *Paracolobus*, and significantly less so than in *Cercopithecoides williamsi* from Koobi Fora.

Rhinocolobus turkanaensis M.G. Leakey, 1982, Type Species

(= or including Colobinae gen. et sp. nov. M. G. Leakey and R. E. F. Leakey, 1973; M. G. Leakey, 1976; Eck, 1977; Colobinae gen. et sp. indet. B., Eck, 1976; Colobinae gen. et sp. nov. 1. Szalay and Delson, 1979)

Holotype: NME Omo 75 1969-1012 from Shungura Fm. Lower Mb. G.

Afar specimens included: AL318-2, AL256-1a-c, AL248-5, AL435-1, AL126-31; cf. AL300-1

Range: 3.4 - 1.88 Ma

Afar range: 3.4 – 3.18 Ma

Distribution: Shungura Fm. A - G; Usno Fm.; Koobi Fora Fm. ; Hadar Fm. Sidi Hakoma - Denen Dora Mbs.

Specific diagnosis: As for genus.

Description:

Rhinocolobus was previously only described from the Koobi Fora and Omo Shungura Formations of the Turkana Basin. The Hadar material was initially identified as *Rhinocolobus* by Delson (Szalay and Delson, 1979, as Colobinae gen. et. sp. nov.) and later in several subsequent review articles (Delson, 1984; 1994; 2000). In cranial and dental size *Rhinocolobus* is larger than all other known Colobinae except for the two named species of *Paracolobus*, and *Cercopithecoides kimeui*. Dental dimensions for *R. turkanaensis* are given in table 4.10. The material described here is similar to that from the Turkana basin in all aspects, except that the symphysis of the Afar material lacks a median mental canal.

Maxilla

The maxilla is well preserved in specimens from the Omo Shungura and Koobi Fora Formations of the Turkana basin, but from the Afar region, there is only a single maxillary fragment, AL318-2, from unit 2 or 3 of the Denen Dora Member of the Hadar Fm. It is a fragment of a left maxilla from a male with the first incisor, canine root, and P^3

to M^1. There is some distortion of this specimen so that the premolars, canine, and incisors are spread apart more than they would have been in life. On the I^1, the slanting distal margin, and lingual cingulum are visible. The P^3 crown is too damaged to see any detail, the P^4 is missing the protocone, but the paracone is tall and a sharp cross loph is preserved. The M^1 shows high cusp relief, the lophs are sharp and well developed, and cusps are widely spaced as there is only minimal basal flare. Little of the bony morphology is preserved. The zygoma is potentially at the distal M^1/anterior M^2. The curvature of the premaxilla, in its mesio-distal arc, is similar to some of the Koobi Fora material, *e.g*. KNM ER 4448. This impression may be suspect given the distortion of this specimen.

Mandible

The mandible is more completely preserved, and represented by several specimens. All of those identifiable to sex are male. The most complete, AL256-1a-c (plate 30), is that of a male reconstructed from three fragments, with left I_1-P_3, M_{2-3}, right I_1-M_3, but the right M_2 lacks its distal portion. It is very similar to the mandibles Omo 75s '70 C68 and L412-1 from the Shungura Formation, but lacks the inferior portion of the corpus. AL248-5 is an edentulous symphyseal fragment of a male, but preserves the entire depth of the symphysis. AL435-1 (plate 30) is a right corpus fragment with well preserved M_{1-3} and approximately 2.5 cm of the corpus below the alveolar process. AL126-31 is a right corpus fragment with M_{2-3} but does not preserve much of the corpus below the teeth.

Table 4.10 Dental dimensions for cf. *Rhinocolobus turkanaensis*.

	UC		
	W	L	H
Males			
AL318-2	10.0	15.2	

	UP4				
	WS	W	L	IC	H
Males					
AL318-2	2		6.8		7.1

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL318-2	7	8.2	6.9			9.8					3.1	5.8

	LI1			LI2			LC		
	W	L	H	W	L	H	W	L	H
Males									
AL256-1	5.7	4.3	5.3	6.4	4.7	6.7	11.3	7.0	

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Males										
AL256-1	6.2	9.5	13.0	6.5	5	6.1	8.5		3.9	5.5

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL256-1	15	7.1	6.7	7.6	7.2	9.4					2.7	4.4
Sex Unknown												
AL435-1	10	6.9	6.3	7.6	7.0	9.7					3.1	4.9

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL256-1	8	8.5	8.2	8.7	8.0	10.7					2.7	5.5
Sex Unknown												
AL126-31				8.8	8.4							
AL435-1	8	8.2	7.9	8.8	8.5	10.9					3.1	6.6

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL256-1	8			8.5	8.2	13.7					3.2	6.9
Sex Unknown												
AL126-31	5	8.5	8.3	8.5	8.4	13.8					3.0	6.6
AL435-1	5	8.5	8.2	8.7	8.4	14.8					2.9	6.9

The symphysis is robust, and deeper than that of *Cercopithecoides williamsi*, but is shallower than male specimens of *Rhinocolobus* from the Omo, the KL57-1 mandible, and *Paracolobus*. The incisive alveolar process is slightly proclined, inferior to which, the symphysis is quite steep in profile, then 1.5 - 2 cm below the alveoli, the there is a break in the slope, and the symphysis extends posteriorly at a shallow angle. This symphyseal shape is typical of *Rhinocolobus* and *Paracolobus*. Unlike *Rhinocolobus* from the Turkana basin, there is no median mental foramen. Both transverse tori are well developed, but the inferior one extends further posteriorly than the superior. There are distinct, but slight corpus fossae present on AL248-5, just anterior to the mental foramen, which, lies inferior to the P_4. AL256-1, AL126-31, and AL435-1 all show that the corpus was not broad, and had a narrow extramolar sulcus and weakly developed oblique line. While the margin is not preserved, AL435-1 preserves enough of the corpus to show that the fossae did not extend very far posteriorly, and that the corpus was deeper than is the case for *Cercopithecoides.* Furthermore, the portion that is preserved is already deeper than the corpus of MAK-VP-1/35 (here tentatively assigned to *Cercopithecoides*). All of this is consistent with *Rhinocolobus* from the Turkana basin, except for the lack of a median mental foramen.

Dentition

The upper dentition is only preserved on AL318-2. The upper central incisor is rather small, given the size of the molars, but its morphology is normal for colobines, and similar to others known for this species from Koobi Fora. Its crown does not flare towards the occlusal end, but is approximately the same mesiodistal length at the alveolus as at the tip. There appears to have been a lingual cingulum present. Of the upper canine, most of the crown is missing, but its cervical area and root are preserved. Its morphology is typical of male cercopithecids, being large relative to the other teeth, with a deep mesial sulcus. The P^3 is present, but its crown is damaged so that little morphology can be observed. The P^4 is damaged so that the protocone is missing, but the paracone is preserved. The paracone is tall as would be expected of a colobine, and there is what appears to be a well-developed transverse loph. The M^1 is the only upper molar preserved. The hypocone is damaged, and the distolingual corner is missing, but the tooth is otherwise intact. It is typically colobine, with a large amount of cusp relief, a low notch, and sharp transverse lophs. The crown also has only a low amount of flare.

The lower incisors, canines, and premolars are only preserved on AL256-1a, where they are heavily worn. They are typical of colobine incisors being relatively small peg-like teeth. Enamel is clearly present on the lingual surface of the teeth. The lower central incisors are small, but are too worn to determine anything else about their crown morphology. The lower lateral incisors are also quite worn, but some details can be seen. There is a small distal cuspule or "lateral prong" present. The crown would have been narrow and tilted mesially. The lower canines are typical for male cercopithecids, being very large relative to the other teeth. Though both are missing the apical parts of their crowns they would have been tall fairly conical teeth, but with a mesial groove, and distal tubercle.

The P_3 is a highly sexually dimorphic tooth in cercopithecids. The protoconid is tall and conical. The mesoibuccal honing flange is long compared to female specimens, but shorter than that of a cercopithecine male. It is also relatively anteriorly oriented. There is more of a paraconid developed than would be the case on a cercopithecine. The talonid is also large and well developed. The only preserved P_4 is relatively complete, but is missing the enamel on the lingual side. The cusps are high relative to the well-developed talonid. The metaconid is similar in size to the protoconid. There is even slight development of a paraconid. The mesiodistal axis of the tooth is basically in line with the molar row.

The lower molars are represented on a few mandibles that are assignable to this species. AL256-1 preserves the right M_{1-3} and left M_{2-3}, AL126-31 preserves the right M_{2-3}, and AL435-1 preserves the left M_{1-3}. In general the lower molars are typical of the colobines with high cuspal relief, sharp cross-lophs, and deep lingual notches. The crowns show very little basal flare, and the cusp tips are widely spaced. The teeth are very "clean" lacking extra cuspules. The M_{1-2} have the typical colobine pattern of the distal lophid being wider than the mesial. For the two measurable M_3's the distal loph is equal to the mesial on AL126-31and wider on AL435-1. This may hint at colobinan affinity for this species. The buccal cusps are relatively columnar or "pinched". This feature is fairly common among the colobines. The tuberculum sextum is very small or absent on AL126-31 and AL256-1, but larger on AL435-1.

Postcrania

No postcrania are directly associated with any of the dental material, but there is a single distal fragment of a right humerus, AL300-1 which is likely to represent this taxon. It is larger and morphologically distinct from the *T. o. darti* distal humeri, which predominate in the Hadar sample. Morphologically it is very similar to the distal humeri from Koobi Fora assigned to this taxon, and discussed by Birchette (1982) in his description of *P. chemeroni*. If the Koobi Fora allocations are correct, *Rhinocolobus* has an extended and medially oriented medial epicondyle, and an articular area that is narrow relative to biepicondylar breadth. AL300-1 is similar to the Koobi Fora material in all of these respects. Overall, the distal humerus AL300-1 is quite broad mediolaterally and flat anteroposteriorly. Also similar to the Koobi Fora humeri, the the zona conoidea is prominent and the medial trochlear flange relatively short, and not sharp, particularly when size is taken into account. Ciochon (1993), in a multivariate morphometric analysis of cercopithecid forelimbs, allocated this specimen to *T. brumpti*. This specimen, however, lacks several features typical of *T. brumpti* such as an extended medial trochlear flange and retroflexed medial epicondyle (Krentz, 1992;1993). Furthermore, this assignment seems unlikely given the absence of any cranial remains of this species outside of the Turkana basin.

There are also two humeri from Bunketo that are likely to be colobine: one proximal and one distal, BUN-VP-2/8 and BUN-VP-2/9 respectively. BUN-VP-2/9 is similar in its morphology to AL300-1, but is smaller. It is possible that AL300-1 is male and BUN-VP-2/9 is female, or they could be different taxa (e.g. one being the same species as the mandible MAK-VP-1/35). Additionally, the BUN-VP-2/8 proximal humerus is similar to KNM-ER 1542o from Koobi Fora. It has a broad, short, and spherical humeral head that projects well above the tuberosities in height. It is smaller than the Kenyan humerus.

Genus *Paracolobus* Leakey, R.E.F. 1969

(= or including Colobinae gen. et sp. indet. (C) Eck, 1977. Cf. *Paracolobus* sp. Szalay and Delson, 1979).

Type species *Paracolobus chemeroni* Leakey, R.E.F. 1969

Other included species: *P. mutiwa* Leakey, M.G. 1982

Generic Diagnosis:

The generic diagnosis used here follows that of R.E.F. Leakey (1969) and the revised diagnosis of M.G. Leakey (1982). *Paracolobus* is known from the Chemeron Fm. in the Tugen Hills of Kenya by the holotype and only specimen of *P. chemeroni*. A second, highly autapomorphic species, *P. mutiwa*, is known from the Shungura, Usno, Koobi Fora and Nachukui Formations in the northern Turkana basin.

Paracolobus is a very large colobine with a long rostrum, separating it from the shorter faced genera such as *Kuseracolobus, Procolobus, Colobus* and *Cercopithecoides*. The nasals are short relative to the length of the muzzle. The interorbital breadth is broad, but distinct from *Nasalis, Libypithecus,* and *Rhinocolobus.* In the type species, the temporal lines converge at about bregma, and presumably would have formed a sagittal crest in the males. Of the calvaria of *P. mutiwa*, only the anterior portion of the frontal is unknown on the holotype female. It does not appear that it would have had an anteriorly positioned sagittal crest. Whether males of *P. mutiwa* would have had sagittal crests, and whether females of *P. chemeroni* would have lacked them must await further material. The only other colobine genera in which the temporal lines meet this far forward as in *P. chemeroni* are *Procolobus* and *Libypithecus.* The supraorbital torus is thick, glabella is prominent, and a postglabellar sulcus is present.

The symphysis is vertical and deep and lacks a median mental foramen, distinguishing it from *Rhinocolobus, Cercopithecoides,* and *Procolobus (Procolobus).* The corpus is deep, unlike that of *Cercopithecoides* and *Procolobus*. The P^3 has a protocone, unlike *Colobus* and *Cercopithecoides*. The ramus is tall and vertically oriented, and the gonial area is expanded greatly in *P. mutiwa*, but not *P. chemeroni*.

The postcrania generally show features typical of arboreal colobines, especially the foot. Some features, on the other hand, suggest more terrestrial locomotion, such as the intermembral index, scapular, and humeral morphology (Birchette, 1982).

Paracolobus chemeroni, R. E. F. Leakey, 1969, Type Species
(= or including *Paracolobus* cf. *chemeroni* Kalb et al., 1982)
Holotype: KNM-BC 3 from Chemeron Fm. Site JM 90/91 (=BPRP #97, following Gundling and Hill, 2000).
Afar specimens included: KL57-1
Range: 3.0 (-~2.5) Ma (Chemeron date from Gundling and Hill, 2000).
Afar range: ~2.5 Ma
Distribution: Chemeron Fm. Loc JM90, ?Matabaietu Fm.

Specific diagnosis:

A species of *Paracolobus* distinguished from *P. mutiwa* by its shorter rostrum, which lacks maxillary ridges and fossae. The mandible is deep, but shallower than that of *P. mutiwa*, and further lacks the expanded gonial region of *P. mutiwa*. Also on the mandible, it lacks a ridge on the lingual surface inferior to the M_3. The limb bones are longer than those of *P. mutiwa*, in spite of similar articular end size.

Description:

There is only a single specimen tentatively assigned to this taxon from the Afar region. If this allocation is correct, it is extremely important, as this specimen represents the only material outside of the type locality in the Chemeron Formation where this species is found. This specimen, KL57-1 (plate 31), is a left mandibular corpus of a male with the symphysis, P_4, and M_3. The teeth are both moderately worn and damaged. KL57-1 is from Natoo North, and from sediments which are probably stratigraphically equivalent to the 2.5 Ma Matabaietu Formation (Kalb et al., 1982b; Kalb, 1993). KL57-1 was briefly discussed by Kalb et al. (1982b) and described as *Paracolobus* cf. *chemeroni*.

Mandible

The mandible is similar in size to *Paracolobus chemeroni* and *Rhinocolobus turkanaensis*, but significantly smaller, and especially shallower than *P. mutiwa* from the Omo, and considerably smaller than the male *P. mutiwa* KNM WT 16827. The symphysis is deep and vertically oriented. There are neither mental ridges nor a median mental foramen. The alveoli for the canines are large in caliber, indicating that the specimen was male, but the alveoli for the lateral incisors are quite small, and those for the central incisors seem to have been absent premortem. Overall, the corpus is relatively narrow and deep, and deepens posteriorly. Unlike *P. mutiwa*, there is no distinct ridge below the M_3 on the medial surface. The lateral surface is unmarked by fossae or prominentia laterales. The gonial region is absent, but there is no indication that it would have been expanded, in fact it appears that it would have been fairly small. The oblique line is not well marked and the extramolar sulcus is relatively narrow. Thus in overall corpus morphology, this mandible is most similar to the type specimen of *P. chemeroni*, and to some mandibles of *R. turkanaensis*, but the gonial region was not likely to have been expanded as it is in male *Rhinocolobus*.

Dentition

There are only two teeth preserved on the mandible. The long axis of the P_4 is in line with the molar series, and has a well developed talonid. Although the cusps of the trigonid are well worn, it can be seen that the metaconid was similar in size to the protoconid. The other preserved tooth is the M_3, on which the cusps are well worn. The crown is straight sided, and the lingual notch is low, and the buccal cleft is deep and well excavated. The crown is relatively long and narrow, and the distal loph is narrower than the mesial. The hypoconulid is large, and there is no real tuberculum sextum. In overall size the tooth is quite large, being outside of the size range for Shungura *Rhinocolobus*, but similar to the *Paracolobus chemeroni* type specimen, and just within the lower limit of *P. mutiwa* from the Shungura Formation, though well below the mean. Dental dimensions are given in table 4.11.

Table 4.11 Dental dimensions for *Paracolobus chemeroni*.

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
KL57-1	11	9.7	9.7	9.1	9.2	15.5					2.4	5.3

Genus *Cercopithecoides* Mollet, 1947

(= or including *Parapapio* Jones, 1937: Broom, 1940; Broom and Robinson, 1950; Freedman, 1957, in part. *Brachygnathopithecus* Kitching, 1952, in part. cf. Colobinae Leakey and Leakey, 1973.)

Type species: *Cercopithecoides williamsi* Mollet, 1947

Other included species: *C. kimeui* Leakey, M.G. 1982; *C.* sp. nov. Leakey et al., in press.

Generic Diagnosis:

The diagnosis for this genus is little changed from the description of Szalay and Delson (1979) and the emended diagnoses of Leakey (1982) and Freedman (1957). There are three named species of *Cercopithecoides*. The best known is the type species, *C. williamsi*, which has been collected from many Pliocene and Pleistocene sites in South Africa and Angola, and also has been recognized by Leakey (1982) at Koobi Fora. A second larger species, *C. kimeui*, is known from Olduvai Gorge, Koobi Fora (Leakey and Leakey, 1973b; Leakey, 1982), Rawi (Ditchfield et al., 1999; personal observation), and Hadar. Finally a species significantly smaller than the previous two has been recognized from Lothagam. It is of uncertain stratigraphic provenience, but may be from the Apak Member of the Nachukui Formation (Leakey et al., in press).

Medium to very large colobines with globular, rounded calvaria. The rostrum is short in comparison to neurocranial length, very different from *Paracolobus, Rhinocolobus, Dolichopithecus,* and *Nasalis*. It is not as short as that of *Rhinopithecus*, however. The frontal process of the zygomatic bone is narrow, unlike *Paracolobus* and *Rhinocolobus*. The interorbital region is broad, which is distinct from *Libypithecus*, *Rhinocolobus,* and *Nasalis*. The supraorbital tori are thick and separated from the calvaria by a deep ophryonic groove, which is distinct from *Colobus*, and most species of *Presbytis* and *Trachypithecus*. The calvaria itself lacks a sagittal crest, at least anteriorly, which separates it from *Paracolobus* and *Procolobus*. The P^3 lacks a protocone, which is similar to modern African colobines, but different from *Libypithecus, Kuseracolobus, Paracolobus* and *Rhinocolobus*.

The symphysis is steep, but shallow and pierced by a median mental foramen, which is different from all colobines other than *Procolobus (Procolobus)* and *Rhinocolobus* from the Turkana basin. The mandibular corpus is shallow and thick, which contrasts greatly with that of *Kuseracolobus, Rhinocolobus, Paracolobus,* and to some degree *Colobus,* but is not unlike that of *Procolobus (Piliocolobus)* and the Leadu colobine. The gonial region is unexpanded or expanded only a small amount. This contrasts with mandibles of *Kuseracolobus, Rhinocolobus*, *Paracolobus mutiwa,* and *Colobus*.

The only species for which significant postcrania are known is *C. williamsi,* with an associated skeleton from Koobi Fora (the morphology of which may not be typical for the South African material). It is distinguished from all other known colobines, except *Dolichopithecus,* in the degree of its adaptations for terrestrial habitus (Birchette, 1981; 1982).

Cercopithecoides kimeui, Leakey M.G. 1982

(= or including *Cercopithecoides* sp. nov.; Leakey and Leakey, 1973. cf. Colobinae Leakey and Leakey, 1973. *Cercopithecoides* sp. 2. Szalay and Delson, 1979.

?*Cercopithecoides* sp(p). Szalay and Delson, 1979, in part. *Papio/Parapapio* sp. Ditchfield et al., 1999)

Holotype: NMT 068/6514 from MLK Olduvai Gorge (Middle Bed II)

Afar specimens included: AL 603-1; cf. AL577-1; ?KL272-1

Range: ~2.4 – 0.8 (3.4 - 0.64) Ma (3.4 Ma depending on tentative assignments in the Lokochot and Tulu Bor Members of the Koobi Fora Formation, and 0.64 from Bodo--see below for the latter).

Afar range: ~1.8 (-0.64) Ma

Distribution: Olduvai Gorge, Middle Bed II, Masek Beds, Koobi Fora Formation KBS and Okote Members; Rawi Formation; Pinnacle locality, Hadar; (and possibly the Lokochot and Tulu Bor Mbs of the Koobi Fora Fm.; and Upper Bodo Sand Unit if KL272-1 is this species)

Specific diagnosis:

This diagnosis follows that of Leakey (1982). A species of *Cercopithecoides* larger than *C. williamsi* (and far larger than *C.* sp. nov. from Lothagam). The mandibular corpus is broader and more robust than that of *C. williamsi*, and has large *prominentia laterales*. The upper molars are unique among the Colobinae, in being low-crowned. They are also quite broad and quadrate in outline, and show more flare than do other colobine molars.

Description:

The best Afar specimen by far, and the only one assignable to this species with any confidence, is AL603-1a (plate 32), a partial skull of a female. It is very similar to the partial cranium KNM-ER 398 from Koobi Fora. Although badly weathered, most of the cranium and mandibular corpus are preserved, and the description below is based entirely on this specimen. The neurocranium is basically complete, but the brow ridges are damaged lateral to the interorbital pillar. The left side preserves most of the orbit, except for some of the rim on the superior half. The right zygomatic bone is largely missing, but on the left it is preserved anterior to the frontal process. The face is otherwise largely complete. The basicranium is obscured by matrix and a bit damaged as well, but some details can be discerned. The complete, but damaged and weathered, mandibular corpus is present, but both rami are lacking. Three isolated teeth are associated with this specimen, and do fit back onto their roots. These are the right M^{2-3} and the left M^3. Also from Pinnacle, a distal fragment of a large humerus was recovered, AL577-1. This specimen is from a very large cercopithecid, appears to show some colobine affinities, and is distinct in its morphology from *Theropithecus* humeri. In fact, it is slightly larger than most of the humeri assigned to this latter taxon. It is potentially from *C. kimeui*, but no humeri are known for this species with which to compare this specimen. Lastly, there is a single isolated upper molar from Bodo, KL272-1, that was assigned to *Papio* by Kalb and colleagues (1980). This specimen may represent *C. kimeui*, but this identification is much more tentative.

This is a very large cercopithecid by any measure. The female cranium from Hadar is in most measurements similar in size to the male holotype of *Rhinocolobus* *turkanaensis*, except that the face is smaller. The face is also smaller than that of the holotype of *Paracolobus chemeroni*. Overall, it is similar to the female crania of *C. kimeui* (ER 398 and ER991) from Koobi Fora. The calvaria is a bit smaller than the male from Olduvai. The face is substantially smaller than the male face from Rawi (personal observation). Dentally, it is similar in size to *Paracolobus* and *Rhinocolobus,* and substantially larger than all other colobines. Dental dimensions are listed in table 4.12

Rostrum

The infraorbital foramina are partially obscured, but appear to be two in number bilaterally. There are slight bulges over the canine roots, but otherwise maxillary ridges are absent. The maxillary fossae are shallow, but clearly present, particularly suborbitally. The anterior surface of the zygoma is excavated inferior to the middle of the orbit, and undercuts the orbit slightly. Thus, the inferior border of the zygomatic, at this point, is posterior to the inferior orbital rim. This is quite distinct from the other large colobines such as *Paracolobus* and *Rhinocolobus,* and much more like *Procolobus*.

The rostrum is short relative to neurocranial length. The nasals are short relative to overall rostral length, as is typical for most colobines other than *Nasalis*, but are longer than those of *Rhinocolobus*. In lateral view, the profile is relatively vertical and straight from glabella to prosthion, with most of the rostral length being distal to rhinion, similar to the profile of *Colobus*. Similar to the Leadu colobine, but different from most *Colobus,* rhinion is comparatively prominent. The alveolar process shows a strong normal curve of Spee, as seems to be common among most colobines.

Table 4.12 Dental dimensions for *Cercopithecoides kimeui*

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL603-1	8	11.3	10.1	10.4	8.9	11.2					3.3	5.9
UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL603-1	5	10.4	9.2	8.8	7.4	11.7					2.8	5.5
UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL272-1	11	10.2	9.3	9.5	8.3	11.2					4.0	5.45

The premaxillae are relatively small (partly because the incisor roots are quite small) being short, and rounded in superior-view. In general, females have more rounded premaxillae than do males. However, AL603-1a is different from the premaxillae of females of *Kuseracolobus,* most *Colobus,* and some *C. williamsi* which are more squared in superior view. The nasal processes of the premaxillae form the lateral borders of the piriform aperture and extend superior to its superior border, and then terminate lateral to the nasals, considerably inferior to nasion. They do not contact the frontal as in *Presbytis, Trachypithecus*, and some *Colobus* and *Procolobus*. The premaxillo-maxillary sutures follow a fairly straight course from their termination at the nasals to their inferior limit mesial to the canine. They bulge slightly laterally around the piriform aperture, maintaining a distance of about 2-3 mm from its rim.

Relative to its height, the piriform aperture is broader than those of most colobines, but narrower than those of most papionins. It is oval in outline, but its inferior pole comes to a sharp angle at nasospinale. In lateral view, the piriform aperture is inclined at an angle of approximately 45° to the occlusal plane.

While the teeth are largely absent, the alveolar process is preserved and the basic shape of the dental arcade can be observed. The cheek teeth form straight rows from M^3 to C^1, with lateral borders that bulge slightly, being widest at M^{1-2}. The alveolar processes are wide overall, to accommodate the broad molars. The incisors form a flat arc from side to side. This yields a dental arcade that is essentially “U”-shaped, being somewhat less parabolic than in many smaller colobines. This may in part be due to the relatively broad square molars. The palate is fairly long and square in outline. It is relatively deep compared to most colobines, and deepens posteriorly. The exact depth is difficult to determine as much of the palate is covered in matrix, but at least 1 cm of depth can be observed near the M^3.

Zygomatic arch

The zygomatic process of the maxilla lies superior to the M^2. This position is similar to that of the females of *C. kimeui* from Koobi Fora, and is relatively posterior compared to other colobines. It is further posterior than any specimens of *C. williamsi*, and similar to the female of *Rhinocolobus turkanaensis* KNM-ER 1485. Only *Paracolobus* and the male holotype of *Rhinocolobus* have a zygoma that is more posteriorly positioned. It is more anteriorly positioned than is the case in most of the larger papionins, such as *Papio* and *Mandrillus*.

When viewed anteriorly, the zygomata are shallow. The inferior margin curves smoothly upward from its origin and reaches a maximum height under the lateral part of the orbit, then on the same curve it continues downward again. This point of maximum height of the inferior border also corresponds with the portion of the zygoma that most undercuts the orbit. While the zygomatic arches are absent posterior to the frontal process, what can be seen of them on the left side shows them to be fairly swept-back in superior view.

Orbital region

Both brow ridges and the lateral portions of the orbits are missing. Only the medial 2cm of the supraorbital torus is present. This portion of the torus is thick, projecting and robust, and is separated from the neurocranium by a wide ophryonic groove. Although much of the orbits are damaged, they probably were broader than tall, and were likely to have been slightly laterally oriented. As is typical of the Colobinae, the interorbital region is broad, even taking the overall size of the specimen into account. Glabella is quite prominent and projects anterior to nasion.

Calvaria

The neurocranium is globular in overall appearance, and is relatively long and narrow in superior view. In Frankfurt horizontal, the frontal bone rises from the ophryonic groove, in a smooth arc, and reaches its maximum height at approximately bregma. The temporal lines do not form a sagittal crest, but remain separated by at least 2 cm. They are well marked anteriorly, but fade posteriorly. The nuchal crests are damaged bilaterally, but it can be seen that they were well developed, and reached nearly 1 cm in height on the right side. In superior view, the widest part of the neurocranium is at the level of the auditory meatus, but it is not significantly wider than the rest of the vault, in part because postorbital constriction is minimal.

Basicranium

The basicranium is reasonably well preserved, but is partially obscured by adhering matrix. The occipital plane is inclined at approximately 45º relative to Frankfurt horizontal. The mastoid processes are small and pyramidal in shape, and the digastric groove is shallow and wide. The postglenoid process is tall and broad, and separated from the glenoid fossa by a wide groove. The glenoid fossa is shallow and flat.

Facial hafting

Facial hafting is similar to that in *Colobus* and other *Cercopithecoides*. The glenoid fossa is nearly in line with the alveolar plane, being elevated only slightly, thus the face is not particularly deep as in *Theropithecus.* The face is less airorhynchous than that of *Paracolobus chemeroni*, and much less so than *Rhinocolobus*.

Mandible

The mandibular corpora are largely preserved but heavily weathered. The rami and gonial areas are totally lacking. While the mandible is edentulous, it does possess the roots for the entire dentition. The symphysis is relatively shallow, but has a nearly vertical profile. Its anterior surface is pierced by a median mental foramen. This trait is rare among colobines, but occurs in all known *Cercopithecoides*, *Rhinocolobus* from the Turkana basin, and *P.(Procolobus)*. On the genial surface, both transverse tori are present, but the inferior is partially obscured by some adhering matrix. The superior surface of the superior transverse torus extends posteriorly to the distal part of the P_3, and the inferior back to the mesial part of the P_4.

As with other mandibles allocated to *Cercopithecoides*, the corpus is shallow, being deepest under M_1 then shallowing posteriorly. Although shallow, the corpus is thick and robust. The lateral surface of the corpus has a very shallow fossa, largely due to the large *prominentia laterales* that are present. These actually form the deepest portion of the corpus in lateral view, which is below the M_1. The mental foramen is obscured by matrix.

Dentition

The only teeth preserved with AL603-1 are the right M^{2-3} and left M^3. The upper molars are distinctive from those of other colobines. They are quadrate in occlusal view, being short, broad, and low crowned. Even though the teeth are low crowned, a relatively large amount of crown height is made up by the cusps above the buccal notch, whereas in papionins most of the crown height is below the level of the buccal notch. Also, unlike papionin molars, the cusps are relatively widely spaced, and the crowns are less flaring buccally. The M^2 is larger than the M^3. KL272-1, an isolated upper right molar from the Upper Bodo Sand Unit, may also represent this species. It is low crowned, short and broad. Relative to its length it is narrower than the teeth of AL603-1, but is within the range of variation shown at Koobi Fora. The lingual cusps are more buccally placed than those of other specimens of this species. On the other hand, this specimen might instead represent a non-*Theropithecus* papionin. Dental measurements are given in table 4.12.

In addition to the three molars preserved, all of the roots are present, and a few comments can be made about the relative sizes of the other teeth. The incisors would have been small relative to the cheek teeth. The canine roots are small, which is the basis of the diagnosis of this specimen as female. The premolars are large, and the P^4 is larger than the P^3. The P_3 mesiobuccal flange is short, which is also consistent with this specimen being a female. The P_4 is broader than the P_3. The molars are large, and the M^2 is the largest of the upper molars. For the lower molars, the first is smallest, and the third is the largest.

Postcranium

There are no postcrania that are definitely associated with the cranium. There is an isolated left distal humerus, AL577-1, which is also from the Pinnacle site, and may also be assignable to this taxon. It is a very large humerus, similar to the largest specimens of *Theropithecus oswaldi oswaldi* in size. It also has a medial trochlear flange that is sharp and well developed, longer than those of all other colobines except for KNM-ER 4420, but shorter than that of *Theropithecus* or *Papio*. Unlike most distal humeri allocated to *T. o. oswaldi* it has an articular area that is narrow relative to total biepicondylar breadth, a very prominent *zona conoidea*, and a tall supraradial fossa, all of which are features that may be associated with colobines (Delson, 1973; personal observation). The medial epicondyle is stout, large and retroflexed. These features are generally associated with more use of terrestrial substrates during locomotion. In overall appearance it is similar to AL2-64, the distal humerus associated with the Leadu colobine, but much larger.

cf. *Cercopithecoides* sp. novum

(= or including Colobinae gen. et sp. indet, smaller, Szalay and Delson, 1979,in part.
Colobinae sp. A. Eck, 1977: Delson, 1984; 1994, in part.)

Afar specimens included: NME AL2-34 (and associated elements), AL231-1a, AL249-23, AL222-14, AL660-2

Range: 3.4 – 3.28 (3.4 – 2.5) Ma

Distribution: Leadu; Hadar Fm., Sidi Hakoma Mbr. (also from Matabaietu if isolated teeth listed under Genus at species indet. Medium are included).

Diagnosis:

A medium-sized species of colobine, most likely assignable to *Cercopithecoides*, similar to *Kuseracolobus aramisi* and larger individuals of *Semnopithecus entellus shistacea* in overall size. It is smaller than *C. williamsi* and substantially smaller than *C. kimeui*. The glabellar region and supraorbital torus are both prominent, but less so than is the case in *C. williamsi*. The supraorbital rim is separated from the calvaria by a sulcus, which is not as deep as that of *C. williamsi*. The mandibular symphysis lacks a median mental foramen, unlike *C. williamsi* and *C. kimeui*, but similar to the new species from Lothagam. The mandibular corpus does not have strongly developed *prominentia laterales*. Dentally, the upper molars are high crowned and with well developed lophs/lophids, unlike the molars of *C. kimeui*. The molars show none of the unusual wear pattern of *C. kimeui* and some *C. williamsi* (e.g. UWMA BF 43 and DGUNL LEBA01).

Description:

This description is based upon an associated partial skeleton from Leadu (AL2-34, and associated elements) near Hadar (plates 33-34), which represents a single adult male individual, and upon four specimens from the Sidi Hakoma Member of the Hadar Formation. These are a nearly complete mandible (AL231-1a) (plate 34), an isolated P^3 (AL249-23), a right maxillary fragment with M^{1-3} (AL660-2), and a distal fragment of a left humerus (AL222-14). The Leadu colobine is larger in size than *Colobus*, *Libypithecus* and *Mesopithecus*, but smaller than *Cercopithecoides, Paracolobus* and *Rhinocolobus*. It is similar in size to the largest *Semnopithecus*, and to *Kuseracolobus*. *Kuseracolobus* is similar to AL2-34 in those few aspects of the face that are preserved, but it is considerably different in the morphology of its mandible and postcranium. Other colobines of similar size are known from below the Sidi Hakoma Tuff at Wee-ee 5, and at Matabaietu in the Middle Awash, from the Omo Shungura Formation in Members B,C,D and G, from the Tulu Bor Member at Koobi Fora, and from the Upper Laetolil beds. These fossils are only isolated teeth, and two postcranial elements, so their specific status is indeterminate at this time. Dental dimensions for cf. *Cercopithecoides* sp. nov. are given in table 4.13.

Rostrum

Overall, the muzzle is shorter than that of *Libypithecus*, *Rhinocolobus* and *Paracolobus*, but longer than that of *Colobus*, being similar in proportion to that of *Cercopithecoides*. As is typical for the subfamily, it lacks maxillary fossae and ridges. The muzzle is high but rounded in cross-section, describing a generally smooth parabola.

Table 4.13 Dental dimensions for cf. *Cercopithecoides* sp. nov.

	UI1			**UI2**			**UC**		
	W	L	H	W	L	H	W	L	H
Males									
AL2-34	4.9	4.9	5.9	5.5	4.7	6.3	7.0	12.0	25.0

	UP3					**UP4**				
	WS	W	L	IC	H	WS	W	L	IC	H
Males										
AL2-34	2	6.8	4.9	3.7	4.4	2	7.6	5.6	3.4	5.2
Sex Unknown										
AL249-23			5.5							

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	8	7.9	7.5	7.4	6.7	8.8					1.9	4.1
Sex Unknown												
AL660-2	8	7.5		7.3	6.9	8.0					3.0	

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	5	8.6	7.9	7.8	7.0	8.6					2.8	4.7
Sex Unknown												
AL660-2	6			7.5	6.8	9.2					2.9	5.7

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	1	8.8	7.2	7.6	6.5	9.2	4.4	4.3	4.3	4.4	3.1	5.2
Sex Unknown												
AL660-2	2	7.4		7.5	6.9	9.5					3.4	

	LI1			**LI2**			**LC**		
	W	L	H	W	L	H	W	L	H
Males									
AL2-34	4.7	3.5	4.9	5.1	3.5	5.0	8.5	5.0	
AL231-1a				4.2	3.2	5.8	8.2	4.6	

	LP3				**LP4**					
	W	L	FL	H	WS	W	L	IC	NH	H
Males										
AL2-34	4.6	8.5	11.6	6.3	7	4.9	8.0		1.9	3.1
AL231-1a	4.3	7.2	12.9	3.8	3	4.9	6.6	2.2	2.1	4.6

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	8	6.5	6.1	6.8	6.4	8.3					1.9	4.4
AL231-1a	12	6.6	6.3	6.6	6.5	8.8					2.2	4.3

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	6	7.4	7.1	7.5	7.1	8.6					2.4	4.2
AL231-1a	8	7.0	6.8	7.4	7.3	9.2					2.7	5.7

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
AL2-34	2	7.8	7.0	7.9	7.4	12.2	4.0	4.2	4.4	4.4	3.1	5.7
AL231-1a	4	7.0	6.7	7.3	7.0	10.5	4.3	4.0	4.0	3.9	2.5	3.5

In lateral view, the profile is steep from glabella to nasion, with glabella being only slightly prominent, and curving in a smooth, concave-up arc to rhinion followed by a slightly concave slope from rhinion to prosthion. When viewed superiorly, the muzzle is fairly short and squared in outline, not unlike that of *Cercopithecoides*.

The nasal bones are short and considerably broader distally than superiorly, where they are quite narrow. Relative to the overall length of the muzzle, the nasals are shorter than those of *Nasalis* (including *N. (Simias)*), and longer than those of *Rhinocolobus, Paracolobus* and *Rhinopithecus*, but otherwise similar to those of most colobines. The nasal process of the premaxilla extends 1.5 cm beyond the superior limit of the piriform aperture as a thin sliver to the base of the interorbital pillar. The premaxillo-maxillary suture runs as a fairly smooth arc from this point to the alveolar process, being nearly straight in both anterior and lateral views. The inferior half of its length is on the relatively flat anterior surface of the muzzle near the canine.

The piriform aperture is narrow and tall, as is typical for the subfamily, with its superior-most point being slightly superior to the inferior limit of the orbits. Its rim defines a plane that is inclined at an angle of approximately 45º to the occlusal plane. Superiorly it is smooth and rounded, reaching its widest point about 2/3 of the way up, and then narrowing inferiorly where it comes to a sharp point.

The maxillary dental arcade is rather “horseshoe” shaped, with the small incisors lined up in a slightly curved row anteriorly, then from the canines to the third molar the tooth rows form gently bowed arcs, being only slightly off straight, with most of the curving occurring at the premolars. The palate is broad and shallow, deepening slightly posteriorly. It is generally flat and planar for most of its surface, curving slightly at the alveolar processes. The choanae are covered in matrix.

Midface

While the zygomatic bones and much of the zygomatic processes of the maxillae are lacking, a bit can be said about the midface, which is short superoinferiorly. The zygomata arise from the maxillae above the mesial M^2 and distal M^1. In anterior view, the zygomata arise immediately superior to the alveolar processes, yielding a midface that is short in overall height. This is unlike *Cercopithecoides*, *Rhinocolobus* and *Paracolobus* where they arise 1 cm or more superior to it.

Orbital Region

Relatively little of the orbital region is preserved. The orbital rim is separated from the neurocranium by a broad ophryonic groove. What is preserved of the supraorbital rim is fairly thick superoinferiorly. The interorbital pillar is broad, as is expected for a colobine, but it is relatively broader than that of *Nasalis*, *Rhinocolobus* and *Libypithecus*. The lacrimal bone makes up the posterior half of the lacrimal fossa with the maxilla forming its anterior rim, which is also the orbital rim, so that the fossa lies entirely within the orbit. Overall, the orbits themselves are rather large and tall relative to the size of the face, but their breadth is not preserved.

Endocast and Facial Hafting

The endocast, AL2-35 preserves much of the front of the brain. It fits tightly with the face, and allows an estimate of the relative sizes of the neurocranium and face. The braincase would have been relatively large compared to the face, as in *Colobus, Procolobus,* and *Cercopithecoides*. It is comparatively smaller than that of *Libypithecus, Paracolobus* and *Rhinocolobus*. There is enough preserved to tell that the neurocranium was not long and narrow as in *Cercopithecoides kimeui*, but more rounded in superior view. The occlusal plane was likely only slightly inferior to the glenoid fossa and basicranium, due to the relatively low facial height.

Mandible

There are two well-preserved mandibles. AL2-34/27b is a corpus and complete dentition. The margin is intact from the left M_3 to the right M_2. The right ramus is lacking, but the left is partially preserved. None of the gonial region remains, however. AL231-1a is a nearly complete male mandible, in left and right halves. It preserves most of the margin on the left, except for in the gonial area, and on the right it preserves from below M_1 back to gonion, except for a small piece just anterior to gonion. Both rami are largely intact. Of the dentition, the left C_1-M_3 and right I_2,P_3-M_3 are preserved.

The symphysis is squared and vertical in profile, but shallow. It is considerably more shallow than that of the *Kuseracolobus*. The incisive alveolar process forms a very slightly curving arc. As is typical of the subfamily, there is no median mental foramen. This is unlike the case in *Rhinocolobus* from the Turkana basin and *Cercopithecoides*.

Both transverse tori are represented, and the planum alveolare is short and steep, extending back only to distal P_3.

The corpus is shallow and broad, especially when compared to *Rhinocolobus*, *Paracolobus*, and *Kuseracolobus*. Corpus fossae are absent, as are *prominentia laterales*. The corpus bulges laterally in the middle of its height, like that of *Cercopithecoides*, and unlike *Paracolobus chemeroni* and *Kuseracolobus*, which are widest near the inferior margin due to large *prominentia laterales*. In lateral view, the corpus is generally shallow, and relatively even in overall depth throughout its length, but with a bulge approximately under the M_1. The mental foramen is double bilaterally in AL2-34 and single bilaterally in AL231-1a, and lies inferior to the P_3/P_4 contact and P_4 respectively. The gonial region is only minimally expanded.

In superior view, the oblique line merges in with the corpus at about M_{1-2}. The whole corpus is quite broad, with a wide extramolar sulcus present. On the medial side of the corpus, inferior to the M_3 there is no ridge. The ramus is vertical, but dorsoventrally short and deep anteroposteriorly. This is similar to mandibles of *Cercopithecoides*, but unlike those of *Rhinocolobus* and *Paracolobus*, and is what would be expected from the short midface and low glenoid fossae relative to the alveolar plane. There is only a shallow triangular fossa, and the coronoid process is higher than the condyle. Laterally on the ramus, the anterior edge of the masseteric tuberosity is not marked by a ridge, but does bulge laterally.

Dentition

The incisors are small and peg-like. The upper incisors are only preserved on AL2-34, and their crowns preserve well-developed lingual cingula. The I^1 crown is spatulate, and is not significantly larger than the I^2. Its crown is widest near the cervix, then remains nearly even in width throughout its remaining height. The I^2 is a more caniniform tooth that is substantially wider at the cervix than it is at its apex. Its crown is also angled mesially, when viewed anteriorly. The lower incisors are small, and have non-flaring crowns with enamel on their lingual aspects. The I_2 is narrower than the I_1, its crown is slightly mesially angled, and has a well developed “lateral prong”. The upper canine crowns are large as is the basis for the identification of this specimen as male. The lower canine is best preserved on AL231-1a, but also fragmentarily on AL2-34. They are typical of male individuals being large in caliber. The root has a distinct mesial sulcus in AL231-1a, but this feature is unobservable in AL2-34 due to damage. The canine seems to lack the disto-buccal tubercle of the Aramis colobine, having only a distal cingulum.

The upper premolars are bicuspid teeth, as is typical for the family. The P^3 has a slight mesiobuccal flange, and the protocone is greatly reduced, but not completely absent. The P^4 has a well-developed protocone, no flange, and a more strongly developed talon, giving a more quadrate outline in occlusal view. As is expected in a male, the P_3 has a fairly long mesiobuccal flange. The paraconid projects slightly from superior surface, much like *Kuseracolobus*. The protocone is tall, and projects above the crowns of the other teeth. Distally, the talonid bulges medially. The P_4 has a short mesiobuccal flange as well, which is longer in AL2-34 than in AL231-1a. Its crown is set in line with the molar tooth row. On both individuals, the metaconid is well developed. Laterally, there is a bit of a shelf to the buccal cleft as in the molars. The talonid is also well developed in both individuals.

The upper molars are preserved in both AL2-34 and AL660-2. As is typical of colobines, the molars have crowns with minimal basal flare, widely spaced cusps, a large amount of cuspal relief, and sharp cross-lophs. The upper molars are all similar in size, but they do increase in size distally. The lower molars have tall cusps, and low lingual notches. They are basically the same on both mandibles, except that the M_3 of AL231-1a lacks a tuberculum sextum and has a more reduced hypoconulid than is the case on AL2-34, which has a small tuberculum sextum. The molars increase in size from front to back, and the distal loph of the M_2 is wider than the mesial loph. The mesial and distal lophs of the M_3 are sub-equal, but the distal may be a bit wider. The molar rows are fairly straight, but diverge slightly distally.

Postcrania

Several elements of the axial skeleton, forelimb, and hindlimb are associated with the cranial material from Leadu. This partial skeleton is one of the better specimens in all of the African Pliocene, and is certainly the most complete single cercopithecid individual from Ethiopia. The elements from this partial skeleton are described below under the individual regions. The only postcranial element that may represent this taxon, other than the partial skeleton from Leadu, is a distal fragment of a humerus: AL222-14, from the Sidi Hakoma Member in the Hadar Formation. It is not directly associated with any cranial material, but is tentatively assigned to this taxon based on its similarity to the distal humeral fragment AL2-63, associated with the face and mandible from Leadu.

Vertebrae

One thoracic, five lumbar, and many caudal vertebrae are preserved. They are typical of cercopithecids in their morphology. The lumbar region was clearly long, but it is impossible to gauge its length relative to the other vertebral segments. It is clear that this individual possessed a long tail, as there are twelve caudal vertebrae present, which are each quite long, and they still do not represent the complete length of the tail.

Forelimb

A left scapular glenoid fragment with a small bit of the spine and coracoid process, AL2-64, is preserved. The glenoid cavity is somewhat concave, being much more curved than the larger scapula from Aramis. More striking than the curvature is the medial bulging of the distal part of the cavity, whose border curves sharply medially making a very circular posterior portion, very much like that of KNM-ER 4420.

The proximal and distal ends of the left humerus are preserved (AL2-63 and -64 respectively). The distal humerus from Hadar, AL222-14, is quite similar to AL2-64. When the proximal end is viewed laterally, the greater tuberosity is higher than the head, although this depends to some degree on how the shaft is oriented. It is impossible to tell how retroflexed the shaft would have been, as only the proximal 3 cm are preserved. The lateral surface of the greater tuberosity is marked by a modest *m. infraspinatus* fossa. The head is relatively broad and spherical, and comes to a slight point posteriorly. The bicipital groove is wide relative to the size of the humerus, shallow, and its lateral rim curls over slightly medially. The little that is visible of the deltoid crest appears fairly strongly developed, although not to the degree seen in KNM-ER 4420.

Distally, the humerus shows a number of adaptations to a terrestrial habitus. As seems to be typical of colobines, the articular surface is narrow relative to the total biepicondylar width. The medial trochlear flange is long and sharp, particularly in comparison to modern colobines. The *zona conoidea* is more prominent than in most cercopithecines, but not as large as in the cf. *Rhinocolobus* humerus KNM-ER 1542o. The capitulum is more cylindrical than that of *Colobus, Procolobus,* and *Rhinocolobus,* but more spherical than that of KNM-ER 4420, or *Papio*. It is also fairly long. The supraradial fossa is deeper and taller than the supraulnar on AL2-64 as is the normal condition in the Colobinae (Szalay and Delson, 1979). On AL222-14, the supraradial is deeper but similar in height to the supraulnar. The medial epicondyle is long, and retroflexed, at approximately 45º, though not as far as *T. darti* or *Papio*. The olecranon fossa is proximodistally short, and broad. In overall morphology, the humerus appears similar to that of KNM-ER 4420, but less extreme in its adaptations towards terrestriality. Whether this difference is because KNM-ER 4420 is larger or because it was more adapted to terrestrial locomotion is unclear.

AL2-65 is the proximal end of the left ulna preserving the olecranon, trochlear and radial fossae, and 1.5 cm of the shaft distal to the radial articulation. The olecranon process is tall, modestly retroflexed, and tilts medially. The trochlear notch is deep, and the medial end of its superior border is only slightly more proximal than the lateral end. This feature is different than most terrestrial papionins where the medial end is significantly more proximal than the lateral. The radial articulation is singular. The radial notch is deep and cuts considerably into the area of the trochlear articular surface. Thus, when it is articulated with the head of the radius AL2-66 in the pronated position it matches the oblong radial head tightly. The shaft distal to the radial notch is mediolaterally thin, but deep anteroposteriorly. The area of the interosseus border is damaged, but part is preserved just distal to the radial notch, which is strongly marked. The distal end of the right ulna, AL2-37, is also present, preserving the head and styloid process. As is typical for the family, the styloid has a large articulation for the pisiform and triquetrum, which is separated from the head by a well-marked sulcus.

AL2-66 and AL2-67 are the proximal and distal ends of the left radius respectively. AL2-66 preserves the head, neck, tuberosity and 2 cm of the shaft. In proximal view, the head is broad and oval in outline, being considerably broader in the transverse dimension than its width in the anteroposterior direction. The neck is short, robust and square. The shaft is damaged at the oblique line, but it does not appear to have a well-marked interosseus border. Not enough of the shaft is preserved to discern its degree of curvature.

Hindlimb

Parts of both os coxae are preserved. Of the left side there is only a small fragment, AL2-71 with the acetabulum and a bit of the surrounding bone, with the head of the proximal femur AL2-72 still fixed in the acetabulum. AL2-80 is the right innominate, which preserves the acetabulum, and some of the right ilium, including the sacral articular facet. There are also many small fragments of this ilium present, but unattached. The ilium is narrow and tall, as is typical for the family. Both ischial tuberosities are preserved, which are large, but the attached callosities probably would not have been continuous in the midline, as would be expected for a colobine.

Large parts of both femora are preserved. Left proximal femur AL2-72, which is still in the acetabulum of AL2-71, preserves the head, neck, greater trochanter and part of the shaft. AL2-73 is a segment of the midshaft, and AL2-74 is the distal end of the left femur with approximately 1/3 of the shaft. Of the right femur, AL2-70/80 preserves the head, neck and small portion of the shaft with the lesser trochanter, and provides the antimere of the area obscured by the acetabulum on the left. AL2-81 is the middle ½ of the femoral shaft. AL2-28 is the distal articular surface and 1/3 of the shaft. Thus a fair amount of femoral morphology is preserved.

The head is spherical, with a large and round *fovea capitis*. The articular surface does not spread onto the posterior surface of the neck, implying less abduction of the hip. Relative to the size of the head, the neck is long compared to other colobines, and oriented at an angle of approximately 60º to the shaft. One of the most striking features of the proximal femur is the large and prominent greater trochanter. It is extremely tall and straight. It does not curve medially as in *Theropithecus* (Krentz, 1993). The gluteal fossa is deep, but doesn't extend below the level of the *m. quadratus femoris* insertion. The lesser trochanter is also long, and is oriented posteriorly.

Distal to the lesser trochanter, the shaft is robust, and thickens distally. In anterior view the shaft is straight without either a normal or reverse carrying angle. In lateral view, the midshaft is quite bowed, especially in comparison to other colobines. The patellar groove is fairly tall, but is also broad and deep. The lateral margin is stronger than the medial, and is elevated considerably to form a prominent ridge. The medial and lateral condyles are symmetrical, and deep in lateral view. Both patellae are preserved, AL2-75 and 76 are the left and right respectively. They are large sesamoids that articulate well with their respective grooves on the femora.

AL2-77 and 117 are the left and right proximal tibiae respectively. AL2-78 is the distal end of the left tibia. Proximally, the condyles are transversely narrow and deep in the anteroposterior plane. The tuberosity is large and prominent, and the shaft is narrow and deep in cross-section. Unfortunately, not enough is present to estimate overall length. The medial malleolus is broken. The astragalar facet is highly asymmetrical, indicating that the lateral border of the astragalus would have been much higher than the medial.

Of the fibulae, distal right and proximal left fragments are preserved, numbered AL2-38 and 39 respectively. They are typical of cercopithecids in morphology. The astragalar facet of the lateral malleolus would have been relatively vertically aligned.

Only two elements of the tarsus have been preserved, both catalogued as AL2-44. One is a left cuboid. In overall proportions, it is proximodistally longer than it is wide. Although it is slightly damaged distally, both proximal and distal facets for the ectocuneiform can be seen. This condition is typical of Asian colobines, and may be primitive for the subfamily (Strasser, 1988). Unfortunately a population is required to determine the significance of this feature, as it varies to some degree within species. The left navicular is also preserved. Additionally, a fragment of the proximal end of the left second metatarsal (AL2-122) and distal fragments of two metatarsals (AL2-41 and –42) are preserved.

Remarks

This material is tentatively placed in *Cercopithecoides* for several reasons. These include the broad interorbital pillar, which is unlike *Nasalis, Libypithecus,* and *Rhinocolobus.* The nasals are longer than those of *Rhinopithecus* and *Rhinocolobus*, and significantly shorter than those of *Nasalis.* The face is less projecting than that of *Paracolobus* and *Rhinocolobus*.

The symphysis is shallow, similar to *Cercopithecoides* and *Procolobus* but different from *Kuseracolobus, Paracolobus, Rhinocolobus* and *Colobus*. The corpus is shallow and broad, similar to *Cercopithecoides* and *P.(Procolobus)*, but distinct from *Kuseracolobus, Rhinocolobus, Paracolobus,* and to some extent *Colobus.* The corpus is deepest inferior to the $M_{1\text{-}2}$, much like *Cercopithecoides*. The gonial region is only very slightly expanded, similar to *Cercopithecoides* and *Paracolobus*, but distinct from *Kuseracolobus, Rhinocolobus, Paracolobus mutiwa* and most *Colobus*. The ramus is short and deep similar to *Cercopithecoides*, but unlike *Rhinocolobus* and *Paracolobus.* One feature of the mandible that is unlike other species of *Cercopithecoides* (except for the new species from Lothagam) is the absence of a median mental canal.

Finally, in the postcranium, there are many features all related to terrestrially. This is unlike most extant colobines or *Rhinocolobus,* but similar to *Cercopithecoides,* and to a lesser extent *Paracolobus.* The humerus has a long medial trochlear keel, and a retroflexed medial epicondyle. The ulnar olecranon is moderately retroflexed. On the femur, the greater trochanter is long and the lesser trochanter is posteriorly oriented.

It seems clear, for the reasons given in the diagnosis, that this taxon is specifically distinct from *C. kimeui* and *C. williamsi*. However, its status relative to the new species from Lothagam will need to be evaluated. Unfortunately that material has not yet been studied.

cf. *Cercopithecoides* sp. indet.

Afar specimens included: MAK-VP-1/35, ?BOU-VP-15/6

Description:

MAKA-VP-1/35 (plate 35) is a right mandibular corpus fragment with $M_{2\text{-}3}$, and the alveoli for M_1 and part of P_4. BOU-VP-15/6 (plate 35) is an edentulous corpus fragment, with the roots for P_4-M_3, which is nearly identical in its morphology to MAK-VP-1/35. Its colobine status is further indicated by the expanded gonial area, a feature unknown in cercopithecines. It is here tentatively assigned to the same taxon. The Maka mandible is close in dental size to cf. *Rhinocolobus* from Hadar, and *Rhinocolobus* from the Omo, and considerably smaller than *P. mutiwa*. Unlike *Rhinocolobus*, the corpus is shallow and thick. Of the cf. *Rhinocolobus* mandibles from Hadar, AL435-1 preserves the most corpus depth. It still lacks the inferior margin, and therefore would have been deeper, but even in its preserved area it is greater in depth than the Maka mandible (MAK-VP-1/35 vs. AL435-1: M2/3: 24.1 vs. 27.6; M1/2: 23.5 vs. 25.8), and the Maka mandible is substantially shallower than complete mandibles from the Omo. The corpus of MAK-VP-1/35 is also relatively broad, with a wide extramolar sulcus. Among the known large African colobines, the Maka mandible is most similar to *Cercopithecoides williamsi* in its corpus breadth and depth. Depth increases only slightly posteriorly. Although the gonial area is mostly absent, what is preserved indicates that it may well have been slightly expanded. The corpus lacks any indication of the large *prominentia laterales* typical of *C. kimeui.*

Dentally, MAK-VP-1/35 is indistinguishable from the cf. *R. turkanaensis* material from Hadar. The two molars have low basal flare, a high amount of cuspal relief, and sharp well-developed cross-lophs. On the M_3 the distal lophid is broader than the mesial. Dental dimensions for this material are in table 4.14. This specimen is tentatively identified as representing the genus *Cercopithecoides*. It seems clear that it does not represent *C. kimeui,* or the Lothagam species, but cannot be allocated with any certainty to *C. williamsi*.

Table 4.14 Dental dimensions for cf. *Cercopithecoides* sp. indet.

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
MAK-VP-1/1	4	8.3	7.5	8.8	8.0	9.7		4.3		4.7	2.6	6.3
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
MAK-VP-1/1	2	8.3	7.7	8.6	8.0	13.5	4.5	4.8	4.5	5.1	3.4	6.7

Genus *Colobus* Illiger, 1811

(= or including *Colobus* Gray, 1821, lapsus. *Guereza* Gray, 1871. *Stachycolobus* Rochebrune, 1887. *Pterycolobus* Rochebrune, 1887. *Pterygocolobus* Trouessart, 1897, lapsus?)

Type species *C. polykomos* (Zimmerman, 1780)

Other included species: *C. vellerosus* Geoffroy, 1830; *C. guereza* Rüppell, 1835; *C. satanas* Waterhouse, 1838; *C. angolensis* Sclater, 1860.

Generic Diagnosis:

This diagnosis is modified from Napier (1985), Strasser and Delson (1987) and Groves (1989). A small to medium sized genus of African colobines, similar in size to *Procolobus (Piliocolobus), Presbytis, Trachypithecus, Semnopithecus, Mesopithecus* and *Libypithecus*, significantly smaller than the large fossil genera *Cercopithecoides, Paracolobus,* and *Rhinocolobus,* moderately smaller than *Kuseracolobus* and the Leadu colobine, but larger than *P. (Procolobus)* and *Microcolobus.* The best diagnostic features are all characteristics of the soft anatomy, such as a three chambered stomach, pelage color, contiguous ischial callosities, and large larynx. Obviously, these are not available for the material discussed here. Therefore, this diagnosis will focus on the craniodental anatomy.

The interorbital distance is broad, unlike *Nasalis, Libypithecus,* and *Rhinocolobus*. The nasals are short, which is distinct from *Nasalis*, but longer than those of *Rhinocolobus* and *Rhinopithecus*. The calvaria generally lacks a sagittal crest, or if present, only near inion. This is different from *Libypithecus, Paracolobus* and *Procolobus*. The choanae are low and wide, unlike those of *Procolobus (Piliocolobus)*. The pterygoid fossae are shallow and broad, and generally not perforated at their apex.

The mandibular symphysis lacks a median mental canal, which is different from that of *P. (Procolobus), Cercopithecoides*, and Turkana basin *Rhinocolobus*. The symphysis lacks the rugosity and mental ridges of *P. (Procolobus).* Also, the symphysis is generally less sloping than that of *Procolobus (Piliocolobus)*. The corpus is generally deep, deepens posteriorly, and lacks large *prominentia laterales*, separating it from

Cercopithecoides and *Procolobus.* The gonial area is usually modestly to greatly expanded, once again different from *Cercopithecoides* and *Procolobus*.

The distinctive features of the dentition include P^3 protocone reduction, which is different from most Asian taxa, *Libypithecus, Kuseracolobus,* the Leadu colobine, and *Rhinocolobus*. Also, the incisors have only a small lingual cingulum, and the lower M_3 typically lacks a tuberculum sextum.

Colobus sp. *C.* cf. *angolensis*

(= *Colobus sp. indet.* Szalay and Delson, 1979, in part. *Colobus cf. guereza* Kalb et al., 1982a; 1982b, in part)

Holotype: BMNH ZD.1860.7.23.1

Afar specimens included: See appendix 6

Range for fossils of *Colobus* or *Procolobus*: (~3.3) 1.88 – Recent

Afar Range: ~0.5 – ~0.25 Ma (2.5 - ~0.25)[3]

Distribution: Wad Medani; Andalee; Issee; Asbole; Bouri Fm., ?Hata Mbr.; Shungura Fm. J(or K), L Mbs.; Kibish; Koobi Fora KBS, Okote Mbs; Kanam East; Kapthurin; Olduvai Beds I,II(M+U), III and above; Taung (upper).

Specific Diagnosis:

This taxon was included in an initial description of the site of Andalee by Kalb et al. (1982), and identified as *Colobus* cf. *guereza.* This assemblage is better allocated to *C.* cf. *angolensis.* This is a small species of the genus *Colobus*, which lacks the most

---

[3] Extended range includes Genus et species indet. Small below.

distinctive feature of *C. guereza*. The females have canines that are significantly smaller than the males and are of a morphology typical of cercopithecid females. This is unlike the large and masculine type canines of females of *C. guereza*. In the mandibles of the males, the gonial region is possibly not as expanded as in males of *C. satanas* and *C. polykomos*.

Description:

The best specimen is a partial face of a male, KL191-23 (plate 36), with complete but damaged dentition except for the right I^2 and C^1. It preserves nearly the complete lower face, palate, and choanae, the left orbit and supraorbital rim, and a small bit of the frontal and left temporal line. Most of the neurocranium is missing as are the left zygomatic arch posterior to the orbit, and the upper and lateral portions of the right orbit and zygoma. There is also a large amount of more fragmentary material. KL191-96 is a badly crushed male lower face with the interorbital pillar, the lower part of the orbits, rostrum and bases of the zygomata, the right M^{1-3}, the left M^1, and very damaged right P^{3-4}. KL183-3 is a left maxillary fragment from a male with P^3 – M^1 and part of the canine root. KL188-1 consists of separate right and left maxillae and premaxillae of a female, with the complete dentition, other than the left C^1. KL191-98 is a right maxillary fragment of an adult female with the I^1 through M^3 preserved, but the premolars and first molar are damaged. KL191-62 is a right premaxillary fragment with I^1-C from a female. KL191-24 is the left side of a heavily crushed juvenile cranium with the left I^1, dp^3-M^1. KL191-99 is a left maxillary fragment with the P^4 through M^3. KL191-141 is a left maxillary fragment with P^4 – M^2. KL189-8 is a right maxillary fragment with M^{2-3}. These last four specimens are all of unknown sex. The facial description is largely based on that of KL191-23 as it is by far the most complete and least distorted of these specimens.

In cranial size this species is similar to females of other species of *Colobus*, being only larger than *Procolobus verus*. Dentally, it is similar in size to modern *Colobus* and *P. (Piliocolobus)*, but larger than *P. (Procolobus)*. Dental measurements for *Colobus* sp. are given in table 4.15. Other similar colobines in the African fossil record (generally assigned to *Colobus* sp. based on size) are known from Members K-L or the Shungura Formation, the KBS and Okote Members of the Koobi Fora Formation, the Kapthurin Formation of the Baringo Basin, Kanam East, and the “Upper” beds at Taung.

Rostrum

The infraorbital foramina are variable, being single or double, and are large, forming a triangular aperture between the orbit, zygomatic arch and rostrum. They are positioned relatively far medially, approximately 1/3 of the distance between dacryon and the lateral margin of the orbit, and are about 2-3 mm from the inferior orbital rim. They are approximately 0.5 cm medial to the zygomatico-temporal suture. They do not seem to be as large as those of most *P. (Piliocolobus)*.

The maxillary fossae are shallow, but present, being largely formed by the prominent root of the upper canines. This is similar to other members of the genus *Colobus*, but more pronounced than *C. guereza*. They are not as deeply excavated as those of *Procolobus* (Verheyen, 1962). Slight maxillary ridges are present. They are continuations from the canine root, but continue posteriorly to nearly the base of the orbits. Once again, they are not as well developed as those of males of *Procolobus*. On the dorsal surface of the muzzle, the nasals project slightly superior to the maxillary ridges.

In lateral view, the rostrum is a nearly straight slope from glabella to prosthion, although the slope is slightly steeper superiorly. Rhinion projects out of this line a small amount. Overall, the rostrum is short relative to overall cranial size, as is typical for the subfamily, but is still shorter than that of *Cercopithecoides williamsi, Paracolobus, Rhinocolobus,* and *Nasalis*. It is, however, longer than that of *Rhinopithecus*. The lower face projects further anterior to the zygomatic arch less than that of *Paracolobus* and *Rhinocolobus*, but more so than *P. (Procolobus)* and *Rhinopithecus*, partly due to the large incisors and modestly projecting premaxillae. The border of the piriform aperture is inclined at an angle of approximately 40º to the occlusal plane. The premaxillo-maxillary sutures begin about midway along the length of the nasals, and run inferiorly around the margin of the piriform aperture, then at approximately mid-height of the piriform aperture they continue laterally to the canine instead of following the aperture border.

In anterior view, the piriform aperture is rounded and oval in outline, except that it comes to a point at nasospinale, being “V” shaped inferiorly. It is widest at approximately mid-height, and is wide overall compared to those of many colobines. In piriform aperture width, it is more like *C. guereza* and *Procolobus* than other *Colobus* (Hull, 1979).

The maxillary dental arcade is well preserved in the male KL191-23, and KL188-1 for the female. The male arcade is parabolic in outline. The M^3’s are roughly the same distance apart as the C^1’s with the M^1 and M^2 being positioned slightly further apart. The incisors project anterior to the canines and are arranged in a broad arc, with the central

Table 4.15 Summary dental dimesnions for *Colobus* cf. *angolensis*. Sample means, Standard deviations, minumums and maximums are provided. For individual specimen measurments see table 4.24.

	Colobus sp. Andalee													
		Width Mesial Width (M's)				Other Measures Height (I's and C's) Flange Height (P3) Distal Width (M's)				Length			
	N	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max	Mean	S.Dev	Min	Max
I^1	5	4.3	0.4	3.7	4.7	8.6				4.7	0.5	4.2	5.2
I^2	4	4.1	0.2	3.8	4.3					3.8	0.5	3.2	4.4
C^1 (?)	3	4.3	0.7	3.5	4.7					5.4	0.8	4.7	6.3
C^1 (?)	1	7.2								9.2			
P^3	4	5.4	0.1	5.3	5.5					4.9	0.1	4.8	5.1
P^4	6	6.5	0.7	5.9	7.4					4.9	0.5	4.4	5.8
M^1	8	6.1	0.3	5.7	6.5	5.7	0.3	5.2	6.0	6.8	0.5	6.0	7.3
M^2	7	6.8	0.3	6.4	7.1	5.9	0.2	5.7	6.2	6.9	0.4	6.4	7.4
M^3	6	6.6	0.1	6.4	6.8	5.7	0.2	5.5	6.0	7.3	0.5	6.7	8.1
M^x	1	6.3				5.1				7.1			
dC^1	1	2.9				3.1				3.9			
dP^3	3	3.9	0.3	3.6	4.1	3.5	0.4	3.1	3.8	5.2	0.3	5.0	5.5
dP^4	2	5.0	0.1	4.9	5.1	4.8	0.2	4.7	5.0	6.3	0.2	6.1	6.4
I_1	1	4.0				6.6				4.1			
I_2	2	4.2	0.1	4.1	4.3	6.7				2.6			
C_1 (?)	1	3.9				7.5				6.0			
P_3 (?)	2	3.9	0.1	3.8	4.0	7.0	0.3	6.8	7.2	6.3	0.4	6.0	6.6
P_3 (?)	3	4.7	0.8	3.9	5.6	8.1	1.4	7.1	9.1	6.9	1.0	6.0	7.9
P_4	6	4.3	0.2	4.1	4.5					5.5	0.9	4.2	6.4
M_1	12	4.7	0.3	4.1	5.1	5.3	0.4	4.2	5.8	6.7	0.5	5.5	7.5
M_2	13	5.6	0.5	4.9	6.3	5.7	0.4	4.9	6.1	7.0	0.6	5.6	7.6
M_3	9	5.9	0.4	5.3	6.5	5.8	0.7	4.3	6.4	9.2	1.3	5.9	10.1
M_x	5	5.0	0.3	4.7	5.4	5.2	0.3	4.8	5.7	6.5	0.6	5.8	7.2
dC_1	1	3.9				4.0				4.5			
dP_3	2	2.9	0.2	2.8	3.0	3.2	0.1	3.1	3.2	5.5	0.0	5.4	5.5
dP_4	3	3.9	0.3	3.7	4.2	4.1	0.1	4.0	4.2	6.1	0.4	5.8	6.6

incisors extending further than the laterals. This may be related to the large size of the central incisors. This pattern is quite different from that seen in *Kuseracolobus, Paracolobus*, the Leadu colobine and *Cercopithecoides.* The female arcade is similar, but more parabolic, due to the smaller canines. The palate is relatively shallow, and even in depth from anterior to posterior.

Zygomatic arch

The zygomatic process of the maxilla is superior to the M^1/M^2 contact. Its inferior border undercuts the inferior orbital rim by a few millimeters, due to slight infraorbital depressions. In anterior view, the inferior border of the zygoma begins less than ½ cm superior to the alveolar margin. It then curves superiorly and laterally, and then runs directly laterally. The zygoma overall is shallow and wide which matches the shape of the face overall, and may be related to the large orbits relative to the size of the rostrum. The zygomaticomaxillary suture is positioned laterally, being further than ½ of the way from dacryon to the lateral orbital margin, and runs from superomedial to anterolateral. Distal to the orbit, the zygomatic arch is broken.

Orbital region

The orbital region is really only preserved on the left side of KL191-23. The orbit is oval in outline and considerably broader than high. As is typical of *Colobus*, but unlike *P. (Piliocolobus)*, the supraorbital torus is of moderate superoinferior thickness, thickening laterally, and lacks supraorbital fossae or notches (Verheyen, 1962). The torus is most inferior in the midline, then rises very slightly laterally, before curving inferiorly again to meet the maxilla.

The interorbital distance is broad, as is typical for the subfamily. Glabella is not prominent, with the frontal sloping smoothly from the supraorbital torus anterioinferiorly to meet the nasals. Thus, nasion is the most anterior point on the frontal bone. The frontonasal and frontomaxillary suture is well marked and prominent in lateral view. The lacrimomaxillary suture lies within the orbit, and the lacrimal fossa occupies part of the maxilla.

Calvaria and basicranium

Little of the neurocranium is preserved. A small part of the frontal remains posterior to the left orbit of KL191-23. The calvaria is separated from the supraorbital torus by a very slight ophryonic groove, which is only present away from the midline. The temporal lines are prominent and strongly marked, but are widely separated, and do not appear to curve sharply towards the midline as they do in *Procolobus* or *Paracolobus* (Napier, 1985; Strasser and Delson, 1987). They probably would not have formed a sagittal crest, at least not on the anterior part of the calvaria, as they do in *Procolobus* and *Paracolobus*.

On the basicranium, little can be seen. The choanae are relatively low and broad. The pterygoid plates are broken away, except for a small bit of what was the floor of the pterygoid fossa is preserved, but damaged. It appears that the pterygoid fossae were not perforated.

Mandible

There is a large collection of mandibles of this taxon present. The best of these is KL188-2, a nearly complete mandibular corpus of a female (plate 37). The dentition is nearly complete, only the right canine is damaged, which is broken at the cervix. Both rami are missing as is most of the margin on the right side, and the left distal to M_1. KL188-3 (plate 37) is a mandibular corpus of a subadult male preserved from the right P_4, around the symphysis, to the left M_2; the adult canines are just erupting, as are the mesiobuccal flanges of the P_3s. There are 11 additional mandibular fragments that preserved some corporal morphology, these are listed in appendix 6.

The symphysis is vertical and relatively deep. It lacks a median mental canal, which is typical of most colobines, but distinct from *Cercopithecoides*, *Rhinocolobus*, and *Paracolobus*. Lingually, both transverse tori are strongly developed. The *plenum alveolare* is steeply inclined, and reaches posteriorly to the middle of P_3, and the inferior torus to the distal end of P_4. The symphysis is similar to that of other species of *Colobus*, *Kuseracolobus, Rhinocolobus,* and *Paracolobus*, but distinct from *Procolobus, Cercopithecoides,* and the Leadu colobine.

While there is considerable variation in corpus depth, it is generally robust and deepens posteriorly, though there is often a bulge under P_4/M_1. The oblique line merges into the corpus at around M_1 and is separated from the alveolar process by a wide extramolar sulcus. Viewed laterally the ramus may sometimes obscure the posterior M_3.

In spite of the large number of specimens, the rami are not well preserved. They are vertical in orientation. The lateral surface is marked by a strong muscle scar for the masseter, and the gonial region is mildly expanded.

Dentition

While the upper incisors show many features that are typical of colobines, they are distinctive teeth. They possess lingual cingula, and the upper lateral incisor is caniniform. The upper central incisor is, however, more spatulate than is generally the case in colobines, and is significantly larger than the lateral incisor (see table 4.15). In this respect, this specimen more closely resembles *Procolobus badius* than the other species of *Colobus*. The lower incisors have enamel on their lingual surfaces. The lower lateral incisors have distinct distal cuspules, or "lateral prongs". The canines are sexually dimorphic teeth, with the upper canines of the males having a mesial groove that extends onto the root. This morphology is typical for cercopithecids, but unlike those of *C. guereza*, where the female canines are similar to those of males.

The P^3 protocone is nearly absent as in other *Colobus* and *Procolobus*, but unlike Asian colobines and some African fossils. It is fairly triangular in occlusal view as a result. As is typical for the family, the P^4 is a bicuspid tooth, but has a talon which is better developed than that of the P^3.

The molars are clearly colobine, with widely spaced cusps, and low basal flare. The cusps are connected by well-developed transverse loph(id)s, and show a high amount of relief relative to crown height. The M^3 is the largest of the upper molars, but the M^2 is the widest. This is in part because the M^3 has a longer distal fovea than the other upper molars. The lower molars have very tall cusps and low lingual notches. They increase in size from mesial to distal. The M_3 has a large hypoconulid, although it is absent on KL183-10, and generally lacks a tuberculum sextum. The distal lophid of the M_3 is wider in some specimens, but not all. The mean is actually close to both lophs being equal in width.

Postcrania

There is a sizeable collection of postcranial material from Andalee. Some of this is easily referable to *T. o. leakeyi* because of its large size. As discussed above under *Cercopithecus*, while that taxon is distinctly smaller than *Colobus* cf. *angolensis*, it is close enough in size to the colobine to make identification of many elements difficult on this basis, especially when a typical amount of sexual dimorphism in both species is taken into account. However, there are two clearly distinctive morphologies present allowing some postcranial elements to be distinguished with confidence. At this time these include only distal humeri and proximal femora. This is because these are the only elements that are relatively complete and show two clearly distinct morphologies. These elements are described below. Based on these, there is clearly a smaller, more semi-terrestrial taxon, and a larger more arboreal one. This latter group has been allocated to *Colobus*.

Humerus

There are four distal humeral fragments that almost certainly represent this species, KL183-18, KL188-42, KL188-43, and KL191-77. These are all significantly larger than the two distal humeri assigned to *Cercopithecus* from Andalee (KL191-83 and KL191-469) and are morphologically distinct from them. They are in the size range for modern *Colobus*. The medial epicondyle is long and oriented more medially than the *Cercopithecus* humeri. The most obvious difference is the significantly shorter medial trochlear flange of the *Colobus* humeri.

Femur

There are three proximal femora assignable to this taxon. These are KL183-21, KL189-10, and KL191-85. They are all significantly larger than the specimen assigned to *Cercopithecus* (KL188-45) and show contrasting morphology. The head is marked by a fovea capitis that is more circular in outline, a feature more common in *Colobus* (Krentz, 1993). The greater trochanter projects proximally only slightly beyond the height of the head in KL189-10. It is shorter than the head in KL191-85, although it may be slightly damaged. The greater trochanter is broken in KL183-21. The lesser trochanter is oriented posteriorly in all three specimens, and is less prominent than that of KL188-45.

Remarks

This colobine material is allocated to the extant genus *Colobus* based on several features. While the calvaria is not preserved, the temporal lines are widely spaced on the frontal KL191-23 and do not appear as though they would have formed a sagittal crest, at least anteriorly. The supraorbital rim is thin, and not perforated by supraorbital foramina or notches. The choanae are broad and low. The mandibular symphysis is not pierced by a median mental foramen, and the corpus of most specimens deepens posteriorly. The corpus of most specimens also generally lacks well developed *prominentia laterales*.

The Andalee material is tentatively allocated to the extant species *C. angolensis*, primarily because the females have small canines, and lack the large masculine form canines of *C. guereza*. Additionally, the incisors of Afar *C. sp.* are mesiodistally longer and more heteromorphic than those of *C. guereza*. Therefore this identification has been tentatively made as *C.* cf. *angolensis*.

Genus et species indet. Small, cf. *Colobus*

Afar specimens included: BOU-VP-12/192

Description:

This specimen is an isolated upper second incisor from the 2.5 Ma Hatayae Member of the Bouri Formation. Fortunately, the I^2 of colobines is morphologically distinct from that of cercopithecines. The crown is caniniform and triangular in outline when viewed labially, so that the crown narrows considerably towards the apex. The lingual surface is marked by a basal cingulum. This specimen is slightly smaller than its homologue in the Leadu colobine, and within the lower part of *Kuseracolobus* variation. It also is within the upper part of the range for modern *Colobus*. Thus, it cannot be assigned here to any genus with confidence, but it is clearly from a colobine. This is important because this specimen is only the second colobine specimen from the Hatayae Member (the other being BOU-VP-15/6 described above), and it is almost certainly from a different species given its smaller size.

Genus et species indet. Medium, size cf. A: Eck 1977

Afar specimens included: BOD-VP-3/2, KL44-4b,c, WEE-VP-5/7

Description:

There are four isolated colobine teeth that are similar in size to both *Kuseracolobus aramisi* and the Leadu colobine. As these two species are only distinguished in the mandible and postcranium, it is impossible to be certain whether these teeth represent either of the above species or some other as yet unknown taxon. Given the stratigraphic position of KL44-4b,c and WEE-VP-5/7, however, and the association of these specimens with other cercopithecids more like those at Hadar, it does seem more probable that they are conspecific with Leadu. KL44-4b and c are isolated right lower molars. These may be an M_1 and an M_2 respectively as KL44-4b is slightly smaller than KL44-4c. WEE-VP-5/7 is also a right lower M_1 or M_2. BOD-VP-3/2 on the other hand, is intermediate in age between the Leadu colobine and Aramis. Its status is therefore more questionable. This specimen is a moderately worn left upper M1. Measurements for these specimens are given in table 4.16.

Table 4.16 Dental dimensions for Colobinae indet. size A.

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
BOD-VP-3/2	12	8.4	7.5	7.9	6.8	8.9					2.7	3.64
LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
WEE-VP-5/7	10	6.3	6.1	6.5	6.3	8.1					1.6	3.7
KL44-4b	8	6.4	6.1	6.7	6.6	9.3					2.4	3.97
KL44-4c		7.4	7.3	7.7	7.4	10.1					3.4	6.74

Genus et species indet. Large, cf. size B: Eck 1977

(= or including Colobinae gen. et sp. nov. 1. Szalay and Delson, 1979, in part, cf. *Rhinocolobus*, Delson, 1984;1994)

Afar specimens included: AL100-356, AL109-14, AL403-44, BUN-VP-2/28, BUN-VP-2/39, KL1-1

Description:

There are five isolated molar teeth of large colobines in the sample. These are all within the size range of *Rhinocolobus turkanaensis* (dental dimensions given in table 4.17) and derive from similar stratigraphic levels, with the two from Bunketo, and AL403-44 being from below the Sidi Hakoma tuff, AL109-14 from the Sidi Hakoma Member above the tuff. AL100-356 is from Ahmado, which may be roughly equivalent in age to the Sidi Hakoma Mbr. (Kalb, 1993). Thus, they all date to approximately 3.4 Ma. Given the presence of two colobines of similar dental size in the Afar region: cf. *Rhinocolobus turkanaensis* from Hadar and cf. *Cercopithecoides* sp. indet. from Maka, and the fact that these two taxa are virtually indistinguishable dentally, it is best to leave these specimens unidentified to genus. All of these molars are normal for colobines with low notches, high cuspal relief, and sharp cross-loph(id)s. AL100-356 is the only upper molar in this group, an M^3, and shows a distal loph that is considerably narrower than the mesial. The crown is virtually unworn, and there is no root. The cusps are quite tall, and the buccal notch fairly short. There are two lower molars, AL403-44 and BUN-VP-2/38, that could be either M^1's or M^2's. Two of these teeth are M_3's, AL109-14 has a distal lophid that is even with the mesial lophid, whereas BUN-VP-2/39 has a distal lophid that is narrower than the mesial.

Postcrania

There are also colobine postcrania, which are equal in size to what would be expected for a colobine with dentition of the size of the teeth in this category. KL1-1 is a nearly complete right humerus from a large colobine. It is from Wilti Dora, and probably stratigraphically equivalent to the approximately 2.5 Ma Matabaietu Formation. It may represent the same species as KL57-1, with which it is stratigraphically equivalent, or perhaps *Rhinocolobus*. It is fairly arboreal in its morphology relative to AL2-64, AL222-14, and AL577-1. The greater tuberosity is below the head in height, and is well marked by a *m. infraspinatus* fossa. The head is large and spherical. The shaft is straight relative to other cercopithecids, and is similar to KNM-BC 3 in this regard. Distally, the medial epicondyle is long and extends medially. The medial flange is not well developed, but the *zona conoidea* is prominent. The supraradial notch is higher than the supraulnar. It is comparable in its proximal morphology with BUN-VP 2/8. Distally it is also compatible with BUN-VP 2/9, and AL300-1, though it is not quite as broad overall. The whole humerus is quite similar to KNM-BC 3, although it is a little smaller.

Table 4.17 Dental dimensions for Colobinae indet. size B.

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL100-356	0	9.8	8.5	7.6	5.6	10.5	4.7	3.1	5.3	4.3	3.3	6.6
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL109-14	0	9.2	8.9	9.2	8.9	15.7	6.1	4.9	5.5	5.8	3.0	7.5
BUN-VP-2/39	3	8.6	8.1	8.2	7.6	14.0					3.1	7.3
LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL403-44	2	7.9	6.7	8.5	7.6	10.2	4.7	4.9	4.8	4.3	3.1	6.3
BUN-VP-2/38	5	8.3	7.8	8.4	8.0	10.7					3.0	6.9

Remarks

Papionins other than *Theropithecus* are most common at the earliest levels of the sequence in the Aramis Member of the Sagantole Formation, making up just under half of the cercopithecids present. They do not, however, reach the abundance of papionins at

Kanapoi or even Laetoli. From approximately 3.4 Ma on they are rare, being only fairly well represented in the Kada Hadar Member of the Hadar Formation, where they represent just over 20 percent of the cercopithecids recovered. This is largely due to a single locality, AL363, where at least three individuals of *Pp.* cf. *jonesi* were recovered. Given the relatively small sample from this member, and the low overall abundance of this taxon in the Hadar Formation and similar levels, this relatively high abundance is probably the result of sampling error. Furthermore, there is no stratigraphic level within which occurs more than a single non-*Theropithecus* papionin. In the 4.4 to 4.2 Myr range there is *Pliopapio alemui*; from about 3.4 to 2.9 Ma is *Parapapio cf. jonesi*; at ca. 2.5 Ma is *Papio sp.* A; and in the Middle Pleistocene is cf. *Papio hamadryas* ssp.

The genus *Theropithecus* is one of the most common and abundant mammalian genera during the Pliocene and Pleistocene. It is the most abundant taxon in the Afar depression from the Middle Pliocene through the earlier part of the Middle Pleistocene (3.4 to 0.64 Ma, see Figure 6.5). It appears that the genus is represented by a single evolving lineage throughout this period, divided into three roughly time successive subspecies. In this sample, these subspecies are generally separated by large gaps in the record so that they appear quite distinct: *T. oswaldi darti* from below the Sidi Hakoma Tuff and from the Hadar Formation; *T. o. oswaldi* from Matabaietu and equivalent sites and the upper part of the Kada Hadar Member; and *T. o. leakeyi* from Bodo and Andalee. However, when these samples are considered in the context of the larger African record the intervening gaps are smaller and filled by intermediate forms. The total African record is still quite sparse between approximately 1.4 and 1 Ma.

The Afar sample is important for understanding the evolution of this lineage. In spite of *T. oswaldi* being the most common and well known primate lineage in the African Neogene, the Afar Depression is the only basin with relatively complete cranial material from all three subspecies, including the only such sample of *T. o. leakeyi* known. Furthermore, the *T. o. darti* sample includes the only well preserved crania for this subspecies outside of Makapan.

The cranial material of *T. o. leakeyi* increases the confidence in the conspecific status of *T. o. darti* in this group. Several of the features used to separate *T. o. darti* from *T. oswaldi* by Eck (1993) are also found in the geologically youngest and morphologically most derived samples. These include a concavo-convexo-concave dorsal rostrum and elevated nasals. This draws into question their importance in separating these taxa. Furthermore, given that most of the morphological difference among subspecies can be explained by anagenetic trends, which in some ways mirrors geographic clinal variation in modern species such as *P. hamadryas ssp.* it seems appropriate to unite them in a single species.

Additionally, most of the material in this sample assigned to *T. o. oswaldi* is from the ca. 2.5 Ma time horizon of the Matabaietu Formation. This is some of the oldest material of this subspecies known, and therefore can shed light on the transition between *T. o. darti* and *T. o. oswaldi*. Both the size and morphology of this sample clearly place it within the latter subspecies, implying that *T. o. oswaldi* of this earliest population was very similar to that of later populations from Kanjera, Koobi Fora, Swartkrans, and Peninj.

Kalb et al. (1982b) mentioned the presence of *Dinopithecus cf. ingens* from the Matabaietu Formation, now dated to about 2.52 Ma. This material, a female upper dentition and some associated cranial fragments (KL40-1) is from a large individual. This specimen is here referred to *Theropithecus oswaldi oswaldi*. This diagnosis is based on the size of the canine, which is relatively small in comparison to the molar teeth, and the morphology of the molars. The molar morphology of this specimen is compatible with both primitive *Theropithecus* and high-crowned individuals of *Papio*. A second specimen, WIL-VP-2/15 is a sub-adult maxilla that also has molars of similar morphology, though these are higher crowned than those of KL40-1. I have decided to refer both of these tentatively to *T. o. oswaldi* as they are equivocal in morphology, and given the lack specimens that can be unambiguously assigned to *P. (Dinopithecus)* it seems more probable that they represent variation within *T. o. oswaldi*. If material that could be confidently assigned to *P. (Dinopithecus)* were recovered, then these specimens would need to be reexamined in light of that material.

The colobine sample from the Afar basin is very large and diverse. This diversity is spread through time, however, with only a single species present during many time periods. There are also times when as many as three species are present (see Figure 6.1). The relative abundance of colobines in the sample also varies considerably, from a maximum of over 50% in the Aramis Member of the Sagantole Formation, to a minimum in the Kada Hadar Member of the Hadar Formation, where they are absent (see Figure 6.5). The bulk of colobine specimens is concentrated during two separate time periods: the Early Pliocene, and the later middle Pleistocene. During the interval between these two periods, colobines generally represent approximately 10 percent or less of specimens identifiable to subfamily. One curious feature of this sample is that the periods of maximum colobine species diversity do not coincide with the periods of maximum abundance of the subfamily. Both periods of maximum abundance occur when only a single species is present.

The extant African colobines are only a small fraction of the diversity of the subfamily that was present in the Pliocene and Pleistocene. The Afar material adds to the known diversity of this radiation, with at least two species of colobine not known from other sites. These are *Kuseracolobus aramisi* and cf. *Cercopithecoides* sp. nov.

Table 4.18 Dental dimensions for *Cercopithecus* sp. W = Width, L = Length, H = Height, WS = Wear State, IC = Intercusp, AW = Mesial Width, AWN = Mesial Notch Width, PW = Distal Width, PWN = Distal Notch Width, ICA = Mesial Intercusp, ICP = Distal Intercusp, ICB = Buccal Intercusp, ICL = Lingual Intercusp, NH = Notch Height, FL = Flange Length. See Table 3.3 for explanations of measurements taken.

	UI1			**UI2**			**UC**		
	W	L	H	W	L	H	W	L	H
Females									
KL191-87	4.5	4.6	5.1	4.0	3.2	5.0	4.3	5.2	7.1
Sex Unknown									
KL191-71	4.4	5.0	5.7						
KL191-93	4.6	5.5	8.0						

	UP3					**UP4**				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
KL191-87	4	4.8	3.4		3.4	3	5.9	5.0	3.7	5.3
Males										
KL183-9	3	3.9	3.7			2	4.7	3.9		
Sex Unknown										
KL188-9						6	5.0	4.4		
KL191-67						6	4.9	4.5		3.2
KL191-174							5.4	4.1		

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL191-87	12	5.9	5.2	5.5	5.4	5.9					2.4	3.2
KL191-163	10	5.6	4.7	5.2		6.3						
Males												
KL183-9	15	5.8		5.2		5.7						
Sex Unknown												
KL188-9	15	5.8		5.5		6.3						
KL191-27	2	6.1	5.4	5.4	4.8	6.4					2.7	3.5
KL191-67	11	5.8		5.4		6.1						
KL191-101	4	5.1	4.4	4.2	3.8	5.5					2.2	2.7
KL191-174						5.8						

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL191-87	7	6.6	6.1	6.1	5.8	6.6					3.0	4.3
KL191-163	8	6.0	5.4	5.7	5.1	7.0						
Sex Unknown												
KL188-9	8	6.8	5.6	6.1	5.3	6.7					2.8	3.6
KL189-4	11	6.6	6.5			6.5					1.4	3.0
KL191-67	9	6.7		5.9		6.9						
KL191-97	5	7.1	5.8	6.7	6.1	7.4					3.3	3.5
KL191-174	10	6.9	6.0	5.9	5.5	6.9					2.9	3.4

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL191-87	2	5.4	4.3	4.2	4.2	5.3					2.7	4.0
Sex Unknown												
KL188-9	2	5.4	4.5	4.5	3.7	5.9					2.4	2.8
KL189-4	7	6.6	6.3	5.4	4.1	7.2					2.0	3.5

Table 4.18 (Continued)

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-62				5.9		6.7						

	LI1			**LI2**			**LC**		
	W	L	H	W	L	H	W	L	H
Females									
KL188-5				3.6	2.7	4.8			
KL188-15	4.0	3.0	3.9	4.0	2.9	4.2	4.5	3.2	
KL189-3	4.0	3.3	4.9	4.1	3.0	5.3	5.5	3.6	7.0
KL191-86	4.3	3.2	4.6	4.0	3.3	4.2			
Males									
KL191-58							7.7	5.0	10.0
KL191-106	3.9	3.4	7.8	4.0	3.7	6.7	5.3	5.7	
Sex Unknown									
KL188-21	3.8	3.2	4.8	4.0	3.2	4.7			

	LP3				**LP4**					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
KL188-4	3.4	5.2	7.0	3.7	3		4.8		2.2	2.9
KL188-5	2.9	4.4	6.0	3.1	3	5.4	6.1		1.9	2.6
KL191-105	3.0	5.1	6.9	3.8	2	4.9	5.5	1.3	2.2	3.1
Males										
KL188-7					3	3.7	4.6	1.7	1.9	2.6
KL191-58	4.0	7.3	11.0		1	4.2	5.0	1.8	1.7	3.1
KL191-104	3.0	4.7	9.3	3.5	4	3.6	5.2		1.6	3.0
KL191-106	3.4	5.3	9.5		2	4.4	5.0	1.5	2.1	2.9
Sex Unknown										
KL183-4					8	3.6	4.2			
KL187-2					0	3.5	4.4	2.0	1.9	3.1
KL188-33					4	3.6	4.6		1.8	3.0
KL191-108					2	3.7	5.1		1.8	3.0

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-4	14	4.9		4.8		5.5					2.2	2.7
KL188-5	14	4.5		4.9		5.7						
KL191-105	8	4.9	4.4	4.9	4.7	6.0					2.1	3.3
Males												
KL188-7	9	5.0	4.5	5.2	5.1	6.0					2.1	2.8
KL191-58	8	5.2	4.8	5.4	5.4	6.9					2.0	3.4
KL191-104	12	4.6				5.9						
KL191-106	9	4.9	4.6			5.9					2.4	3.3
Sex Unknown												
KL183-4	16	4.3		4.4		4.8						
KL183-5	9	4.6	4.3	4.6	4.0	6.1					1.3	2.7
KL187-2	7	4.9	4.7	5.0	4.8	6.0					1.7	2.8
KL188-11	16	4.7		5.2		5.7						

Table 4.18 (Continued)

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL183-6	8	5.1	4.8	4.9	4.5	5.9					2.2	3.2
KL191-105	5	6.0	4.9	5.6	4.5	6.1					2.6	3.8
Males												
KL188-7	5	6.2	5.7	5.7	5.1	6.2					2.2	3.7
KL191-58	7	6.4	5.7	6.1	5.7	7.2					2.3	3.6
KL191-104	5	5.9	5.5	6.0	5.0	6.3					2.0	3.9
KL191-106	4	6.5	6.1	6.2	5.8	6.6					2.5	4.3
Sex Unknown												
KL183-4	10	5.1		4.9		5.7					1.9	
KL183-5	5	5.6	4.8	5.4	4.9	6.5						
KL183-8	2	4.7	4.4	4.8	4.5	6.2					2.5	4.2
KL187-2	5	5.9	5.7	5.6	4.8	6.7					2.1	3.2
KL188-11						6.9						
KL191-100	16	6.2		6.1		7.2						
KL191-108	5			6.0		6.7					2.3	3.8
KL191-162	4	6.6	5.8			6.9					2.7	4.3
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL183-6	2	5.3	4.7	4.0	3.5	6.0					1.7	3.3
KL191-105	3	5.6	4.5	4.3	3.9	6.1					2.6	4.1
Males												
KL191-58	3	6.0	5.2	5.1	4.5	6.6					2.6	3.5
KL191-104	0	5.5	5.1	4.8	4.4	6.2	2.3	1.8	3.1	2.9	1.7	3.6
KL191-106	1	6.8	5.5	5.6		6.1					1.8	4.0
Sex Unknown												
KL183-4	6	5.1	4.6	4.2	3.8	5.9						
KL183-5	3	5.1	4.5	4.5	4.1	6.5					2.0	3.7
KL183-8	0	5.1	4.6	4.6	4.2	6.5					2.6	4.0
KL187-2	0	5.5	4.8	4.6	3.8	6.4	2.4	1.6	2.4	3.7	2.1	3.2
KL188-11	8	5.7	5.6	4.7	4.5	6.9					2.2	3.1
KL188-19	1	5.5	4.9	4.5	4.1	6.7					2.1	3.9
KL188-28	4	5.0		4.0	3.6	6.2					1.9	3.5
KL191-100	12			5.8		8.5						
KL191-162						6.9						
LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL188-30	3	5.0		3.9							2.1	3.6
UdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-27		3.8		3.9		5.3					1.6	2.5
KL191-101	9	4.3		3.8		5.3						
UdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-27	7	5.2	4.4	4.8	4.1	5.7					1.8	2.7
KL191-101	10	4.4		4.2		5.1						

Table 4.19 Dental Dimensions for *Pliopapio alemui*. Abbreviations as in Table 4.18.

	UI1			UI2			UC		
	W	L	H	W	L	H	W	L	H
Females									
ARA-VP 1/816	5.0	5.8	6.5						
ARA-VP 1/1007						4.1	(5.0)	5.8	9.3
ARA-VP 1/1723							5.1	5.6	10.1
Males									
ARA-VP 6/933		8.2	11.3			10.1		11.1	32.1
Sex Unknown									
ARA-VP 1/820	5.3	6.0	9.8						
ARA-VP 1/890	4.6	5.9	9.7						
ARA-VP 1/1539				6.0	3.9	8.5			
ARA-VP 1/1542				6.0	4.2	8.3			
ARA-VP 1/2075	5.5	6.6	10.3						
ARA-VP 6/1277				5.2	3.8	9.6			
ARA-VP 6/1292	5.4	6.1	10.2						

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
ARA-VP 1/1007	1	6.5	4.9		4.5	1	5.9	5.0	3.7	5.3
ARA-VP 1/1723	3	5.6	4.7		5.7	3	6.5	4.9		5.4
Males										
ARA-VP 6/933			5.8		6.4			5.3		7.0

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/1007	9	7.8	6.7	7.2	6.0	7.8			3.5		3.1	4.5
ARA-VP 1/1723	10	7.4	6.6	6.9	6.1	8.1					3.1	4.1
Males												
ARA-VP 6/933						8.6					4.2	5.2

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/1723	6	9.0	7.8	7.9	6.8	9.2			4.2		3.3	5.8
Males												
ARA-VP 6/933						10.2					4.5	6.2

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/1723	1	8.0	7.0	6.1	5.3	8.1	3.9	2.7	3.7	3.3	2.6	5.8
ARA-VP 1/2354	4	9.1	7.4	7.4	6.3	9.4					3.6	6.1
Males												
ARA-VP-6/933						9.5					4.2	8.0
Sex Unknown												
ARA-VP-1/852	3	8.0	7.3	6.4	5.7	8.7					2.9	5.7

Table 4.19 (Continued)

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/19	4	9.3	8.0	8.3	7.1	9.8					3.3	6.0
ARA-VP 1/20	7	8.2		7.9		8.3						
ARA-VP 1/23	5	9.0	7.4	8.3	7.1	9.6					3.3	5.6
ARA-VP 1/132	13	9.4	8.5	8.4	7.7	10.0					3.4	4.8
ARA-VP 1/330	9					9.4						
ARA-VP 1/333	8	8.9	8.0	8.4	7.0	9.0					4.1	5.2
ARA-VP 1/339	7	7.0	6.3	6.6	6.0	8.3					3.2	4.4
ARA-VP 1/359	0	8.8	6.5	7.8	5.7	8.9	4.1	2.2	3.2	3.2	3.7	5.6
ARA-VP 1/403	0	7.1	6.4	6.9	5.6	8.6	3.4	3.1	4.4	3.5	3.4	4.9
ARA-VP 1/499	3	8.5	7.3	7.1	5.6	9.0					3.1	5.9
ARA-VP 1/884	0	9.6	7.5	9.0	6.1	9.4	3.7	3.5	4.2	3.9	4.9	7.3
ARA-VP 1/936	10	7.9	7.6	7.4	6.8	8.4					3.5	4.4
ARA-VP 1/944	6	8.5	7.6	8.0	6.5	9.4					3.2	5.6
ARA-VP 1/1347	5	8.9	7.5	7.7	6.4	9.4					3.5	5.1
ARA-VP 1/2045	1	7.7	6.6	6.4	5.4	8.8					3.3	4.8
ARA-VP 1/2078	1	7.5	6.2	6.6	5.6	8.1					3.0	4.9
ARA-VP 1/2079	9	9.5	8.6	7.3		9.3					3.4	5.3
ARA-VP 1/2354	8	9.6	8.5	8.0	7.1	9.9					3.8	5.7
ARA-VP 6/9	9	9.9	8.6	8.0	6.7	10.9					3.5	5.8
ARA-VP 6/57	6					8.5						
ARA-VP 6/63	4	9.1	7.9			(9.45+)					3.3	5.8
ARA-VP 6/577	5					9.0						
ARA-VP 6/628	5	8.8	6.8	8.0	6.0	8.6					3.3	4.8
ARA-VP 6/629	9	8.9	8.3	8.4	7.9	9.4					3.1	5.0
ARA-VP 6/632	6			7.8	6.9	7.9					2.7	4.7
ARA-VP 6/1289	10	7.3	6.5	7.1	6.2	8.6					3.5	4.5
ARA-VP 6/1296	11	7.8	6.4	7.2	6.6	8.5					3.0	
ARA-VP 6/1562	1	7.7	6.1	7.1	6.0	8.0					3.4	4.7
KUS-VP 2/85	6	9.6	7.9	8.6	7.1	9.6					3.3	5.4
KUS-VP 2/139	3	8.2	7.1	6.9	6.1	8.6					2.9	5.1
SAG-VP 7/155	0	8.4	7.3	8.1	6.3	9.7					3.6	5.8

	LI1			**LI2**			**LC**		
	W	L	H	W	L	H	W	L	H
Females									
ARA-VP 1/563	5.1	3.3	4.6	5.0	3.5	5.2	6.0	4.3	9.1
ARA-VP 1/1006				3.8		4.7	5.7	3.4	6.9
Males									
ARA-VP 1/73				4.5	3.3	11.1	9.3	5.4	17.4
ARA-VP 1/744	4.3	3.3	8.2	5.3	3.4	9.8	(6.5)	(4.8)	(14.5)
ARA-VP 6/933		5.8	11.2		5.5	10.4			24.9
Sex Unknown									
ARA-VP 1/191	5.2	5.4	9.5						
ARA-VP 1/1262	3.5								
ARA-VP 1/2168				5.5	4.4	10.7			
ARA-VP 6/597		4.7	4.4						

Table 4.19 (Continued)

	LP3				LP4							
	W	L	FL	H	WS	W	L	IC	NH	H		
Females												
ARA-VP 1/133					2		4.8					
ARA-VP 1/563	3.8	7.4		4.3	4	5.4	6.1		2.4	3.6		
ARA-VP 1/1006	3.6	5.5	7.2	3.3	3	4.9	5.5		1.9	3.1		
Males												
ARA-VP 1/73	3.7	9.2	15.6	7.0	3	4.6	5.9					
ARA-VP 6/933						6.5				7.9		
Sex Unknown												
ARA-VP 1/893					2	5.6	6.8		3.2	4.5		
ARA-VP 1/1408					5	5.1	6.4		2.5	3.7		
ARA-VP 1/2080					3	5.7	7.2	3.2	3.4	5.1		
ARA-VP 1/2431					2	6.7	7.2	4.0	2.0	4.9		
ARA-VP 6/623					1	5.4	6.5	3.5	2.3	4.8		
ARA-VP 6/625					1	5.1	6.6	3.2	2.4	4.6		
ARA-VP 6/627					5	5.4	6.6		2.0	3.8		
LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/133	10	5.6	5.4	5.7	5.7	7.3					2.4	4.2
ARA-VP 1/563	10			6.6		7.8						
ARA-VP 1/953	16	6.3		6.6		7.7					2.5	
ARA-VP 1/1006	8	5.9	5.7	5.9	5.7	7.2					2.7	3.9
Males												
ARA-VP 1/73	12	6.5	5.8	6.5	6.2	7.8					2.5	4.4
ARA-VP 6/933						8.2						
Sex Unknown												
ARA-VP 1/548	1	5.3		5.7		7.3		3.1		3.1	2.3	4.3
ARA-VP 1/740	2	5.9	5.4	6.2	5.8	8.6	2.9	3.5	3.9	4.0	2.9	4.9
ARA-VP 1/743	0			6.4	5.4	8.6					2.9	
LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/133	8	6.5	6.3	6.7	6.3	8.7				3.6	2.6	4.6
ARA-VP 1/563	7	7.9		7.7		9.8						
ARA-VP 1/953	12	7.9	7.5	7.8	7.1	9.6					3.2	4.5
ARA-VP 1/1006	5	6.9	6.7	7.1	6.7	9.2					2.9	4.1
Males												
ARA-VP 1/73	6	7.5	7.2	7.6	7.0	9.0					2.6	5.0
ARA-VP 6/933						10.4						
Sex Unknown												
ARA-VP 6/8	5	6.4	6.0	6.8	6.5	8.8				4.0	3.2	5.0

Table 4.19 (Continued)

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 1/133	4	6.8	6.4	6.4	6.0	9.7				4.4	2.4	5.3
ARA-VP 1/953	7	7.9	7.0	7.1	6.3	12.4					3.5	4.9
ARA-VP 1/1006	1	7.4	6.6	6.4	5.6	10.5			4.7	4.3		
Males												
ARA-VP 1/73	1	7.5	7.0	6.9	6.3	11.8		4.1		4.1	2.9	5.4
ARA-VP 1/744	0	6.7	6.1	6.1	5.6	10.8	3.1	3.1	4.1	4.2	2.8	5.5
ARA-VP 6/933						12.9						
Sex Unknown												
ARA-VP 1/8	3	7.4	6.9	6.1	5.8	10.7					3.0	5.6
ARA-VP 1/9	6	7.8	7.0	7.0	6.7	12.1					2.8	4.5
ARA-VP 1/12	5	7.5	7.4	6.5	6.3	10.8					3.1	
ARA-VP 1/24	8			7.3	7.1	(11.9)					3.2	
ARA-VP 1/45	8			6.9	6.8	11.8						
ARA-VP 1/185	5	8.4	7.8	8.0	7.3	13.0					3.3	5.1
ARA-VP 1/190	4	7.8	7.3	7.0	6.6	11.1					3.1	5.3
ARA-VP 1/289	4	8.1	7.7	7.8	6.8	12.0					3.7	5.3
ARA-VP 1/390	10			7.3	6.8						2.8	
ARA-VP 1/492	5	8.7	7.6	7.7	6.6	13.2					2.9	
ARA-VP 1/1377	6	8.1	7.6	7.6	7.0	12.2					3.8	6.2
ARA-VP 1/1569	2			7.2	7.0	11.7						
ARA-VP 1/1571	2	7.5	7.2	6.5	5.8	11.3					3.2	5.3
ARA-VP 1/1573	1	8.0	7.6	6.7	6.4	12.5					3.2	5.2
ARA-VP 1/1574	2	7.1	6.4	7.0	6.8	11.6					3.2	5.4
ARA-VP 1/1615	1	8.3	7.5	7.3	6.5	11.9					3.5	5.9
ARA-VP 1/1948	3	6.9	6.4	6.2	5.8	10.9					3.2	4.9
ARA-VP 1/2085	2		6.2	6.8	5.5	11.7					3.3	5.4
ARA-VP 6/8	2	6.5	6.3	6.8	5.9	10.6	3.3	3.6	4.0	3.8	3.0	4.9
ARA-VP 6/586	3			6.4	5.7	11.1						
ARA-VP 6/600	5	8.1	7.2	6.9	6.4						2.6	5.2
ARA-VP 6/659	1	8.6	7.4	6.4	6.3	11.8					2.7	5.0
ARA-VP 6/799	3	7.0	6.6	6.0	5.7	9.8					2.8	4.6
KUS-VP 2/98	7	7.7	7.6	6.7	6.3	(11.2)					3.1	4.9
SAG-VP 7/103	4	7.4		(6.5)		11.7					2.9	
SAG-VP 7/106	4			7.4	6.4						2.8	

Table 4.19 (Continued)

LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/135	1	7.3	6.5	6.7	6.2	9.7					2.8	4.9
ARA-VP 1/362	9	8.6	7.5			10.5					2.6	4.7
ARA-VP 1/404	1	7.8	7.3	7.8	7.2	9.9					3.0	5.5
ARA-VP 1/491	4	8.4	7.5	8.0	7.5	10.3					2.6	5.0
ARA-VP 1/496	7	6.6	6.1	6.6	6.4	8.1					2.3	3.5
ARA-VP 1/545	4	7.2	7.1	6.5	6.4	9.6					2.6	4.3
ARA-VP 1/948	4	7.8	7.8	7.5	7.3	9.5					3.0	5.3
ARA-VP 1/1097	4	6.8	6.1	7.3	7.1	9.1					3.6	4.9
ARA-VP 1/1266	6	5.9	5.5	6.5	6.2	8.0					2.4	3.7
ARA-VP 1/1553	10	6.1	6.2	6.4	6.3	8.3					3.2	4.4
ARA-VP 1/1554	0	7.3	7.2	6.7	6.1	9.5					2.8	5.5
ARA-VP 1/1555	3	7.0	6.2	6.6	6.1	9.5		3.7	4.6	4.3	2.8	5.3
ARA-VP 1/1556	6			7.3	7.1	9.2					2.9	4.2
ARA-VP 1/1558	0	5.9	5.3	6.2	5.6	8.1					3.3	4.9
ARA-VP 1/1559	5	5.9	5.7	5.9	5.7	8.1					2.4	3.5
ARA-VP 1/1560	1	7.5	6.9	6.6	6.4	9.7					3.1	5.4
ARA-VP 1/1917	15	6.2	6.2	6.4	6.2	7.2					2.5	3.1
ARA-VP 1/1951	4			7.1	6.8	8.8					3.1	4.9
ARA-VP 1/2059	8					8.9					3.0	4.7
ARA-VP 1/2086	3	7.4	6.9	7.0	6.3	9.6					3.1	5.1
ARA-VP 1/2090	3	6.8	5.9	7.0	6.4	8.7					3.2	4.7
ARA-VP 1/2494	5	6.4	5.9	6.4	6.0	8.1						5.0
ARA-VP 6/61	1	6.1	5.3	6.5	5.3	8.5					3.0	4.5
ARA-VP 6/62	4	6.5	5.2	6.8	5.5	9.2					2.6	4.2
ARA-VP 6/576	6	8.9	8.2			(9.51)						5.4
ARA-VP 6/602	9	7.7	7.0	7.5	6.7	9.6					3.1	4.6
ARA-VP 6/1281	10	7.2	6.9	7.6	7.0	9.5					3.2	4.3
ARA-VP 6/1284	4										3.4	5.5
ARA-VP 14/19	3	6.3	5.8	6.0	5.3	8.5					3.1	4.6
KUS-VP 2/142	3	8.3	7.8	7.3	7.2	10.2					3.3	5.7

UdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/885		6.1		5.8		6.7						
ARA-VP 1/1983		6.7		6.3		7.2						
ARA-VP 1/2470		6.4		5.4		7.3						
ARA-VP 6/643		6.6		5.8		7.2						

LdC	W	L	H
ARA-VP 1/740	4.6	3.0	5.3

LdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/740		4.0		4.4	4.1	6.8					1.4	2.2

LdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/548		4.5				6.5						
ARA-VP 1/740		4.9	4.6	5.3	4.9	7.4					2.3	2.6
ARA-VP 1/743				5.2	4.9	7.5					2.0	2.8
ARA-VP 1/1662		5.0		5.0	4.5	7.2					2.4	3.4
ARA-VP 6/647		4.5	4.1	4.9	2.5	6.9					1.6	3.3

Table 4.20 Dental dimensions for *Parapapio* cf. *jonesi*.

	UI1			UI2			UC		
	W	L	H	W	L	H	W	L	H
Females									
AL363-15	5.9	7.7	10.0	6.7	4.9		5.4	7.4	12.8
Males									
AL363-1							7.6	9.9	

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
AL363-15		7.2	5.8		5.2	3	9.5	5.8	4.2	5.8
Males										
AL363-1	8	6.9	5.5			8	7.0	5.4		3.4

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	10	10.2	8.9	9.8	7.8	8.2					4.6	5.4
Males												
AL363-1	16	8.2		8.3		8.0						

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	4	11.9	8.7	10.5	7.5	10.6	5.1	5.1	4.5	4.8	5.3	6.2
Males												
AL363-1	16					10.6						

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	1	10.6	8.2	8.9	6.3	10.2	4.8	3.8	5.0	4.9	4.7	6.1
Males												
AL363-1	16	10.4		9.2		11.5					4.1	6.1

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL100-381	0	7.4		7.2	6.1			3.4		3.2	4.0	

	LI1			LI2			LC		
	W	L	H	W	L	H	W	L	H
Females									
AL363-15	4.7	5.5	8.8	3.9	4.7	7.5	6.5	3.8	10.5
Males									
AL363-1							10.5	6.2	17.6

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
AL363-15	5.1	5.6	8.4	5.5	4	6.0	6.3		3.0	4.8
Males										
AL363-1	4.8	9.0	12.6	5.8	8	6.5	6.4		3.2	4.1
Males										
MAK-VP 1/112					3	6.4	7.3		3.1	5.4

Table 4.20 (Continued)

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	14	7.6		7.4		7.9					3.1	4.6
Males												
AL363-1	16					7.6						
Sex Unknown												
MAK-VP 1/112	11	7.2		7.7		10.0					3.0	4.9
LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	5	9.2	7.7	9.2	7.6	10.0	5.4	5.3	4.6	4.6	4.3	5.6
Males												
AL363-1	16	9.2		8.9		10.4					3.5	5.0
Sex Unknown												
AL217-8	6			9.8	8.5	11.2					3.6	
AL363-12	6					9.7						
AL465-1	6			7.8	7.6	11.1				5.1	3.3	5.8
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL363-15	1	9.7	7.8	8.4	6.6	13.6	5.3	3.9	5.5	5.1	4.0	5.7
Males												
AL363-1	16	9.5		8.4		14.1					3.1	4.3
Sex Unknown												
AL217-8	1	9.6	8.3	9.2	7.7	14.1	4.8	4.4	4.8	5.1	4.0	6.7
AL363-12	3					11.6						
AL465-1	0	8.2	7.5	7.6	7.4	13.9	4.7	4.7	5.1	4.4	3.8	6.1
MAK-VP 1/49		(9.4)		7.9		14.3					3.1	
LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL100-355	10	6.6	6.2	6.5	6.1	9.3					2.7	4.0

Table 4.21 Dental dimensions for *Theropithecus oswaldi darti*.

	UI2			UC		
	W	L	H	W	L	H
Females						
AL185-5	6.2	5.3	11.0	6.4	7.0	
Males						
AL205-1				10.1	10.1	
AL310-19						32.0
MAK-VP-1/100				9.2	12.1	
Sex Unknown						
AL186-16	6.6	6.3	11.5			

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
AL185-5						3	8.0	7.3	4.6	7.7
AL321-12	8	7.0	6.8		5.5	7	7.7	6.0		6.8
Males										
AL205-1	8	8.3	7.0		8.3	6	8.9	7.9		7.8
AL208-10						7	8.2	7.3		7.2
AL310-19	1	8.0	7.6	4.6	8.6	3	8.8	8.1	5.2	9.2
MAK-VP-1/100	2	8.0	7.4		7.7	1	9.3	7.6	4.3	8.0
Sex Unknown										
AL52-1						5		6.5		
AL186-16						0	8.5	8.0	4.9	8.1
AL200-17						4	8.6	7.3		7.5
AL249-24	5	7.7	6.2		7.5					

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL185-5	11	8.8	8.2	8.0	7.0	10.8					5.8	7.0
AL321-12	15	9.1		8.6		10.7					5.6	6.2
Males												
AL205-1		9.6				10.6						
AL208-10	16	10.0		9.9		11.7						
MAK-VP-1/100	10	10.1	8.7	9.3	8.2	10.8					4.6	4.9
Sex Unknown												
AL52-1	16	9.1		8.8		10.5					5.2	5.5
AL186-16	2	10.0	8.7	9.7	6.8	12.2	4.5	3.4	5.2	4.6	5.0	7.0
AL200-22	12	12.1	10.9	11.5	9.8	12.7					4.0	7.0
AL231-9	12					12.0						
AL269-1	0	8.2	7.5	8.1	7.2	11.5	3.6	3.6	5.4	6.1	4.6	6.4
AL300-6	9	9.6	8.2	9.4	8.0	10.5					5.3	6.0
MAK-VP-1/66	15	9.9	8.9	9.6	8.9	11.9					4.1	4.7

Table 4.21 (Continued)

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL185-5	4	11.4	10.1	10.0	8.1	13.1		5.0		5.2	7.2	7.5
AL321-12	12	10.7	9.6	9.9	8.0	12.3					6.5	8.2
Males												
AL205-1						12.5						
AL208-10	14	11.7		10.5		13.0					6.7	8.1
MAK-VP-1/100	8	11.7	9.9	10.9	8.8	13.4					5.4	7.4
Sex Unknown												
AL116-23	1	11.5	9.5	11.5	9.0	14.1	5.0	3.7	5.6	5.2	6.0	8.4
AL225-5	3			10.3	8.4	13.2		5.1	6.4	5.9	6.1	9.4
AL231-9						14.8						
MAK-VP-1/66	11	12.9	11.8	11.7	10.1	15.2					5.0	8.3
UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL321-12	9	10.9	9.5	9.1	7.9	13.4					7.0	7.3
Males												
AL208-10	9	12.1		11.0	9.6	14.1					5.7	8.2
MAK-VP-1/100	1	11.4	8.4	10.5	7.5	12.7	5.1	3.8	5.5	5.1	5.1	8.3
Sex Unknown												
AL100-362	0	10.2	9.4	7.8	6.9	12.2	6.1	5.0	6.0	5.5	4.1	8.6
AL200-12	0	12.6	10.9	10.9	8.2	13.7	5.7	3.7	5.7	5.3	7.0	9.2
AL231-9	3			10.5	9.4	15.2						
MAK-VP-1/66	3	13.3	11.6	11.3	9.6	15.5					5.9	10.2
UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL100-361	15	8.3	8.2	8.0	7.1	10.4					3.9	5.6
AL128	7	12.3	10.5	12.6	9.4	13.7					6.0	8.7
AL200-23	8	13.7	11.2	13.4	9.9	14.9					6.5	9.3
AL366-1	3	12.9		12.3		13.7						
AL391-2	11			9.8	8.7	12.8					5.0	
AL391-3	4	12.9	10.8	11.3	9.7	15.5					6.0	10.0
AL400-11	0	11.4	9.4	10.2	9.0	14.0					4.6	7.7
BUN-VP-2/32	1	11.6	9.4	10.7	8.3	11.9					5.5	7.6
BUN-VP-2/33	0	11.8	9.3	9.9	7.6	12.6					4.5	
BUN-VP-2/36	0	11.3	9.3	10.1	8.1	12.4					5.7	6.9
BUN-VP-2/37	0	9.9	7.8	8.8	7.0	11.5					4.2	7.2
MAK-VP-1/56	16	(12.5)		11.7		12.8						
MAT-VP-7/4	3	10.9	9.2	10.3	8.5	12.9					4.7	7.9

Table 4.21 (Continued)

	LI1			LI2			LC		
	W	L	H	W	L	H	W	L	H
Females									
AL126-30							7.0	3.8	5.8
AL129-8							6.5	4.3	7.1
AL269-3							6.6	3.8	
Males									
AL142-19				6.5			11.8	7.5	27.5
AL163-11							11.3	6.8	
AL208-10							10.2	7.0	
AL329-1	6.5	6.4	10.7	6.2	5.3	10.7	13.0	7.5	
Sex Unknown									
AL284-2				4.3	5.5	11.6			

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
AL126-30	4.7	7.2	9.8	6.0	6	6.2	7.7			
AL129-8	5.2	8.0	8.5	6.3	7	6.5	7.6		3.1	
AL173-26	5.7				8	6.9	7.3			
AL185-5	5.4	7.3	12.3	7.4	3	6.7	8.3	3.2		3.5
AL196-3					6	6.7	7.3			
AL269-3					8	5.6	7.1			
AL270-1					8		7.6			
AL426-1					0	6.8	7.1	3.6	2.6	5.5
Males										
AL58-23					3	7.5	9.0		4.0	6.7
AL142-19	6.9	11.4	19.1	9.6	7	7.2	8.3		4.0	5.9
AL153-14	6.4	9.3	17.4	8.0	5	7.9	8.2		3.6	5.1
AL163-11	6.6	13.5	16.7	7.7	8	8.8	9.3		2.6	
AL205-1	6.8	12.4	13.9	8.9	5	7.8	8.7			3.6
AL208-10	6.0	11.5	17.0	7.1	8	7.3	8.2		3.7	4.5
AL329-1	6.3	10.8	20.0	8.2	2	8.2	9.5	4.5	3.4	7.3
AL486-2	6.3				8					
Sex Unknown										
AL178-12a					4	6.6	7.8		2.3	4.6
AL200-24					4		7.5			
AL217-1					8		6.9			
AL225-9					6	7.4	7.9		2.6	4.8
AL269-3					0	7.1	9.3	3.3	6.7	3.5
AL310-15					8	6.7	8.5			
AL390-10					2	7.4	8.5	4.4	3.7	5.3

Table 4.21 (Continued)

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL126-30	16	8.3		8.5		9.5					3.1	3.3
AL129-8	15	8.0		7.8		8.7					3.5	
AL153-18	7	8.1	7.3	7.8	7.3	10.8					2.4	4.8
AL173-26	16	7.7				9.5						
AL185-5	11					10.5						
AL186-17	16					9.0						
AL196-3	16					10.3						
AL269-3	16					9.8						
AL270-1	16					8.6					3.5	
AL345-1	11	7.7		7.0		10.4					3.4	5.3
AL426-1	5	7.6	7.3	7.7	6.9	9.9					3.4	4.8
Males												
AL58-23	9	8.1	7.8	8.3	8.2	11.1					3.9	6.3
AL142-19	14	8.0		8.2		10.2					3.3	4.7
AL148-107	7	8.4	8.0	8.0	7.7	11.2					3.0	5.8
AL153-14	14	8.7		8.8		10.4					3.5	5.3
AL163-11	16	9.8				10.3						
AL187-17	16	9.0	8.6	9.1	9.1	10.4					2.9	4.5
AL205-1	16					10.0						
AL208-10	16	8.4		8.4		10.3						
AL329-1	6	8.3	8.1	8.1	7.9	11.2					3.8	6.0
AL415-1a	10	8.1	7.9	8.2	8.0	11.5					3.4	5.1
AL486-2	16	8.2		9.4		9.5						
Sex Unknown												
AL55-43	3	8.4	7.3	8.4	7.5	11.6	4.2	4.8	4.5	5.3	3.7	5.7
AL56-17	11	9.0		8.5	8.0	11.2					3.3	5.1
AL137-2	15	7.8				9.7					3.0	4.0
AL158-91	4	8.9	7.9	8.4	7.5	11.4	4.7	4.5	5.0	4.3	3.6	6.4
AL178-12a	12	7.7	7.6	7.6	7.8	11.1					2.6	4.3
AL200-24	11			8.8	7.4	11.9					3.0	
AL217-1	16					8.7						
AL217-7	16	9.7		9.9		10.5						
AL225-9	16	9.4	9.2	9.8	9.6	10.6					3.0	5.6
AL252-6	7	8.3	8.0	8.2	8.1	11.2					4.1	5.9
AL269-3	6	8.1	7.5	7.7	7.2	10.8					3.7	5.9
AL284-2	1	8.7	8.1	8.5	8.3	12.8	5.0	5.0	6.1	6.0	4.0	6.3
AL288-45	16	7.3		7.3		8.5						
AL310-15	16	8.3				10.1					2.3	5.4
AL390-10	7	8.8		9.2	8.8	11.0					3.3	
BUN-VP-2/31	0	7.9	6.8	8.0	6.5							
MAK-VP-1/43						9.2						

Table 4.21 (Continued)

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL126-30	14	10.4		10.2		11.3					3.5	5.2
AL129-8	10	9.2	8.9	8.8	8.7	11.3					3.1	5.3
AL173-26	16	10.2		9.4	9.3	11.9					2.8	
AL185-5	4	10.2	9.3	9.2	8.6	13.4				6.0	3.9	7.4
AL186-17	16	8.7				11.2						
AL196-3	13	10		9.4		13.0					3.5	5.4
AL200-21	6	11.2	9.7	10.6	9.0	13.5					4.0	7.8
AL204-4	13	10		10.4		13.3						
AL269-3	16					12.8						
AL270-1	16			10.5		11.2					3.5	
AL426-1	0	10.1	9.0	9.5	8.3	11.7	4.6	4.2	4.7	5.0	3.1	6.5
Males												
AL58-23	6	10.4	10.1	10.3	9.4	13.6					4.8	8.8
AL142-19	7	10.3		10.0		13.1						
AL148-107	0	10.2	9.5	9.4	8.3	13.2	6.3	4.7	5.9	5.7	3.5	8.1
AL153-14	10	10.3	10.0	9.9	9.5	13.0					4.1	6.6
AL163-11	16	12.2				13.4					3.5	5.0
AL187-17	11	11.2	10.7	10.5	10.0	14.2					2.8	6.6
AL200-20	2	9.6	8.9	9.3	8.8	13.5						
AL208-10	15	10.1		10.5		12.4					4.6	
AL329-1	2	11.2	10.0	9.7	8.6	14.3	5	5.7	5.4	5.4	4.2	8.9
AL415-1a	2	10.6	9.4	9.7	8.8	13.7					4.6	7.4
AL486-2	16	11.3		10.8		12.1						
Sex Unknown												
AL174-10				12.6		16.3						
AL178-12a	8	10.3	8.9	8.5	8.2	13.4					3.2	5.8
AL133-54	5	10.0	9.1	8.4	8.2	13.2					3.4	6.4
AL161-23	10	9.1	9.0	8.4	8.3	11.5					3.5	4.8
AL188-19	16					11.8						
AL269-3	0	10.9	9.8	9.9	8.8	14.0	5.4	4.9	5.5	6.0	4.4	7.1
AL310-15	13					13.0					3.4	
AL487-2	16	10.7				12.5						
AL148-120	12					13.7						
AL200-14	4	9.9	9.6	9.4	8.7	13.6					2.0	7.7
AL200-24	9					13.7					2.8	
AL252-6	0	10.3	9.2	10.0	8.6	13.9	5.8	4.7	7.5	6.5	3.3	6.9
AL144-1	15	10.8	10.5	10.9	10.2	13.0					3.6	4.3
AL217-1						11.1						
AL217-7	12	11.6	11.1	11.0	10.1	12.8					3.3	5.6
AL225-9	12	11.1	11.0	10.9	10.7	13.8					4.2	6.1
AL236-28	10	11.0	10.1	9.8	9.6	13.4					3.0	5.8
AL390-10	4	11.3	9.7	10.2	9.7	13.4					4.2	8.7
MAK-VP-1/43	10	9.0	9.3	8.8	8.8	12.2					3.6	4.9
MAK-VP-1/109	11	10.3	10.0	10.2	10.2	12.2					4.2	6.1

Table 4.21 (Continued)

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL126-30	10	11.0		10.0		17.0					3.6	
AL129-8	4	9.0	8.2	8.1	7.1	15.1					3.1	6.0
AL173-26	9	10.5	10.5	9.2	8.1	16.2					3.2	6.2
AL186-17	16	10.2		9.3		15.5					3.4	3.7
AL196-3	6			10.0	8.2	16.0						
AL200-21	0	12.5	10.8	10.4	8.8		3.7	3.9	5.5	6.6	3.8	8.9
AL269-3	16	12.0		10.7		17.0						
AL270-1	16	10.8		10.1		15.8					4.3	
Males												
AL58-23	2	12.1	11.4	10.7	9.6	18.1	6.4	5.4	6.4	6.9	4.8	9.5
AL153-14	4	11.6	10.8	10.8	10.1	18.2				7.1	4.7	8.1
AL163-11	14	13.0		10.0		20.4					4.5	5.9
AL208-10	14	11.5		11.1		15.7						
AL329-1	0	12.3	10.6	10.3	9.7	18.5	5.5	5.4	5.7	6.0	5.1	9.6
AL486-2	15	11.8		10.3		18.5						
Sex Unknown												
AL100-291	8	11.6		9.6	9.8	15.4					4.6	7.2
AL100-349	8	8.4	8.2	8.1	7.9	14.4					3.4	5.8
AL100-388	4	10.6	9.1	9.0	8.0	15.4		4.8		6.3	4.5	7.8
AL126-78	6	11.7	10.4	10.6	9.3	18.3					5.0	7.3
AL144-1	8	10.8	10.2	9.1	9.0	16.6					3.8	5.6
AL148-120	5	11.4	10.6	9.9	9.1	17.4						
AL161-23	7	9.6	9.0	8.4	7.9	15.2					4.0	6.1
AL174-10	8	13.2	11.8			20.4						
AL178-12a	2	10.2	8.4	8.7	7.7	16.4	4.8	4.6	6.2	7.1	3.8	6.5
AL188-19	12	10.8		9.1		17.0						
AL199-14	7	11.5		10.3		16.1						
AL200-24	2	11.2	9.7	9.0	8.4	18.3	6.6	5.3	7.4	7.9	4.1	8.0
AL208-6	15			10.7		18.0					5.0	
AL217-1	16					14.7						
AL223-28	8	12.1	10.9	11.1	10.2	17.9					4.4	8.3
AL225-9	6	12.5	11.1	9.9	9.5	18.7					5.2	9.5
AL236-28	7	11.8	10.3	10.6	9.4	17.4					4.3	7.1
AL258-2	6	11.3	10.8	10.4	9.5	16.2					4.5	7.1
AL289-5	0	11.1	9.6	10.5	9.1	17.8						
AL304-1	5	11.6	9.9	10.1	8.7	17.9					4.7	7.8
AL310-15	7	11.1	10.5	10.0	9.1	18.6					4.0	5.5
AL317-2	8	10.5	9.9	10.1	9.2	17.1					3.6	5.9
AL403-43	6	12.2	10.5	10.9	9.6	17.8					4.2	6.9
MAK-VP-1/109	5	11.0	9.5	10.0	8.9	16.1					4.1	7.0
MAK-VP-1/130	5	10.6		9.1	8.2	15.8					3.3	6.6
MAK-VP-1/17	14	11.3	10.9	10.0	9.7						4.1	6.2
MAK-VP-1/43	0	9.5										
MAT-VP-7/2	0	10.0	9.2	8.8	7.9	15.0					3.6	6.5
WEE-VP-5/6	15	11.7		10.1		(14.5)						

Table 4.21 (Continued)

LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL100-345	9				12.5						3.1	4.8
AL100-350	0	9.5	7.7	9.1	8.6	12.2	4.4	4.1	5.4	6.1	3.9	6.6
AL100-351	16	10.0		9.0		10.9						
AL100-353	12	10.2		9.7	8.7	12.1					3.9	
AL100-357	3	8.1	7.6	7.5	7.4	11.1					3.2	5.9
AL100-358	2	9.3	8.6	8.7	8.6	11.8					3.6	6.4
AL100-359	4	10.0	9.1	9.5	9.1	13.5					3.5	9.4
AL100-360	1	9.7	8.7	8.7	7.9	12.1					3.4	6.7
AL100-363	0	8.8	8.0	8.8	8.4	12.9					3.6	6.7
AL100-386	12	8.9	8.8	8.5	9.2	11.1					3.8	5.1
AL199-8	9	11.0				13.8						
AL400-8	2	8.1	7.7	8.3	7.8	11.2					2.9	6.2
AL401-8	8	11.5	10.4	10.4	9.4	13.9					3.7	7.1
BUN-VP-2/30	0	11.4	9.8	10.2	9.5	13.8					3.4	7.1
MAT-VP-7/3	9	10.2	9.6	9.8	9.0	12.3					3.8	5.9

	Udl1			**UdC**		
	W	L	H	W	L	H
AL132-26	3.2	3.8	6.3	4.2	5.7	6.9

UdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL132-26	6	6.5	5.6	6.6	5.6	8.7					3.2	4.5
AL186-16	14			7.5		7.5						

UdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL132-26	3	7.9	6.3	7.8	6.3	10.0	3.3	3.3	4.4	4.6	3.3	5.0
AL156-28		7.9		6.4		9.7						
AL186-16	10	9.0		8.2		10.8					3.5	4.7
AL269-1	8	7.0	6.4	6.8	5.9	9.0					3.6	4.2

	Ldl1			**Ldl2**			**LdC**		
	W	L	H	W	L	H	W	L	H
AL284-2							5.5	3.2	4.5
AL316-9				2.97	4.52	6.03	4.58	5.01	7.2
AL327-2	3.3	4.0	5.6	2.6	4.4	5.4	5.8	3.6	5.5

LdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL284-2	12	4.6		5.2		8.1					2.0	3.5
AL269-3	16			4.9								
AL316-9	3	4.7	4.0	4.3	3.5	8.3	1.6	2.0	4.2	3.9	2.2	2.9
AL327-2	0	4.8		6.0	5.3	8.6	2.1	2.7	2.8	3.5	2.4	3.7
AL415-1a	16	4.4		5.0		7.5						

LdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL55-43	15	6.4	6.1	6.9	6.7	9.1					2.4	3.3
AL269-3	16	5.9		6.0		8.7						
AL284-2	10	6.7	6.2	6.6	6.3	9.7					2.7	3.5
AL316-9	0	5.7	5.1				2.7	2.9	3.8	4.5	2.0	4.0
AL415-1a	16	6.4		6.6		8.5						

Table 4.22 Dental dimensions for *Theropithecus oswaldi oswaldi*.

	UI2			UC		
	W	L	H	W	L	H
Females						
KL38-1				7.5	9.7	
KL40-1				7.4	10.0	
KL235-1	6.1	6.2		7.0	8.7	9.4
Males						
AL416-2					17.7	31.1
KL39-1				9.2	10.6	
KL74-2c				14.9	11.2	

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
KL38-1	2	9.5	7.0	4.0	6.9	1	9.2	8.5	5.0	7.8
KL40-1	3	9.4	8.0			2	10.1	8.2		
KL235-1	6	8.7	7.7		6.7	5	10.2	7.7		7.3
Males										
AL416-2	6	10.1	7.8			4	10.0	7.5		7.4
KL39-1						8	8.9	8.7		
Sex Unknown										
KL18-1	8	8.0	6.4			8	8.8	7.1		

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL38-1	14	10.9	10.4	10.9	10.1	13.1					3.9	5.6
KL40-1	7	11.9	10.6	11.3	9.7	13.1					5.4	7.3
KL235-1	16	11.5		10.9		11.5					4.9	6.4
Males												
AL416-2	16	11.0	10.7			14.2						
WIL-VP 2/15	8	12.1	10.6	11.6	9.9	14.1					5.5	8.5
KL39-1	16					10.0						
Sex Unknown												
KL18-1	16	10.1		9.3		10.5						

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL38-1	9	13.0	11.5	12.0	9.5	15.0					5.8	7.2
KL40-1	4	13.5	11.4	12.5	10.6	14.7					5.9	14.8
KL235-1	9	12.8	12.2	12.4	10.9	14.5					6.3	9.4
Males												
AL416-2	12	14.9	12.4	13.3		16.8					4.8	7.9
KL39-1	16	13.3		13.1		14.4					4.5	8.5
KL74-2c	16					13.0						
KL157-1	8	12.6	11.6	11.8	11.1	15.6					5.2	7.0
Sex Unknown												
WIL-VP 2/15	4	14.0	12.1	12.9	10.2	16.1					6.3	12.0

Table 4.22 (Continued)

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL40-1	0	13.9	11.3	12.1	10.1	14.9					6.4	10.1
KL235-1	4			11.4	9.9	14.1					6.2	
Males												
AL416-2	5	15.2	11.9	14.2	11.2	16.8					5.4	10.7
KL39-1	15	12.9		12.2		16.0					5.8	7.1
KL74-2c	16					13.9						
KL157-1	6	12.4	11.1	10.9	10.0	16.5					4.6	8.2
Sex Unknown												
AL666-5	12	13.9	12.6	12.4	11.0	17.7					6.0	8.8
WIL-VP 2/15	0	13.2	10.4	11.4	9.0	15.7	6.0	5.4	5.8	5.4		

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL653-3	16	14.4	13.4			15.5						
WIL-VP 2/14	8	14.0	12.9	13.0	11.9	17.8					6.5	9.9
KL11-4	3	11.8	10.5	11.9	10.9	13.3					5.2	8.1
KL13-3	16	13.0		12.7		13.2						
KL19-1	5			13.1	11.6						6.6	
KL29-1		12.1		11.4		15.4						
KL45-1	16	9.5		8.9		11.0						

	LI1			**LI2**			**LC**		
	W	L	H	W	L	H	W	L	H
Females									
AL596-1	7.0	5.1	7.2	5.6	5.6	7.4	8.6	6.2	10.6
KL46-1							6.7	4.7	
Males									
MAT-VP 4/14	5.8	5.2							

	LP3				**LP4**					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
AL596-1	6.1	8.9			6	7.3	9.4			5.5
KL46-1	5.5	7.0	9.2		5	7.1	7.4		2.5	
Males										
MAT-VP 4/14	5.1	8.3	14.9		3	7.1	9.6		3.9	6.4
KL74-2a	8.5	12.5	19.4		8	8.8	9.0			
Sex Unknown										
AL532-1b					2	8.4	10.0	4.8	4.3	6.3
AL607-1					5	7.9	10.3		2.2	6.2
KL22-1					8	8.2	10.3			

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL532-1b	11	9.5		9.4	8.8	11.9					4.7	
AL596-1	16					12.8						
AL606-1	6	10.0		10.1		12.4						
AL607-1	16	11.0		11.8		12.3					3.5	
KL46-1	16	8.7	8.5	9.6	9.0	10.3					3.4	5.8
Males												
MAT-VP 4/14	8	9.2	8.2	10.3	9.5	12.2					4.0	5.9
KL74-2a	16	10.7				13.0						
Sex Unknown												
GAM-VP 1/8	1	9.6	8.5									
KL22-1	16					12.5						
KL44-3a	14	9.4	8.8	10.0	8.8	11.8					2.5	4.9

Table 4.22 (Continued)

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
AL596-1	12			9.9	9.6	14.1					3.6	6.4
KL46-1	12	10.6	10.5	10.6	10.3	13.2					3.2	7.9
Males												
MAT-VP 4/14	3	10.9	9.5	10.7	9.5	14.8					4.7	7.9
KL74-2a	16					15.3						
Sex Unknown												
AL532-1b	3	12.2	11.0	10.4	9.8	14.9	6.1	5.3	5.9	5.3	4.8	8.6
AL535-5	7	8.9	8.4	9.5	8.8	13.6					2.7	6.2
AL537-4		13.0		13.4		17.1						
AL606-1	0			11.6		15.3						
AL607-1	12	14.4	12.0	12.8	10.8	17.4					3.6	8.5
MAT-VP 5/30a	9	10.1	9.4	9.5	9.3	13.9					2.8	6.0
KL16-5	14	13.7		12.8		16.5						
KL22-1	16	13.2		11.8		16.4						
KL44-3a	10	11.4	11.0	11.0	10.4	13.6					2.7	7.8
KL65-1	9	11.6	10.5	11.0	10.3	14.9					3.9	7.7

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL46-1	7	11.3	10.3	10.2	10.1	16.8					3.5	7.2
Males												
MAT-VP 4/14	0			11.8	10.1							
KL74-2a	16	15.1		13.0		21.8						
Sex Unknown												
AL532-1a	0	13.4	11.3				7.0					9.7
AL537-4		14.6				22.3						
AL607-1	4	15.2	11.5	12.3	9.5	21.9	4.3	3.9	5.1	8.3	5.4	10.3
MAT-VP 2/12		(13.3)		(12.7)								
MAT-VP 5/21	16	10.1		8.6		18.6						
MAT-VP 5/30a	0	11.4	9.2									
MAT-VP 5/30b	0					18.8						
MAT-VP 6/15	10	(12.0)		11.8	11.0	(19.9)						
WIL-VP 3/1	11	12.2	11.4	11.5	11.3	19.2					4.8	7.6
KL16-5	16	14.4		12.7		21.0						
KL22-1	16	14.4										
KL44-3a	6	12.3	11.0	10.6	9.2	18.9					3.2	9.6
KL65-1	4	12.1		11.0	10.1	20.0						
KL74-2b	16	14.1		11.4							4.9	

LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
AL558-1	0	12.6	11.3	10.8	9.6	16.4	7.1	4.1	6.9	6.9	5.1	10.6
MAT-VP 6/16	16	12.4		11.8		14.1						
KL44-1	9	10.5		10.5	9.7	14.1						
KL44-4a		8.4	8.0	9.1	8.5	11.9					4.0	6.1

LdC	W	L	H
MAT-VP 4/14	8.07	4.53	13.9

AL537-5	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
LdP3	16					9.8						
LdP4	6					11.3						

Table 4.23 Dental Dimensions for *Kuseracolobus aramisi*.

	UI1			UI2			UC		
	W	L	H	W	L	H	W	L	H
Females									
ARA-VP 6/1686	4.9		4.0	4.3	4.7	5.7	5.1	6.4	6.8
KUS-VP 2/70				4.6	4.3	5.8	4.8	6.9	9.1
Males									
ARA-VP 1/6							7.5	10.2	
ARA-VP 1/87							7.1	10.6	21.7
Sex Unknown									
ARA-VP 1/490				5.0	5.4	7.6			
ARA-VP 1/795	5.1		4.8	5.1	4.8	6.1			
ARA-VP 1/872				4.8	5.4	7.5			
ARA-VP 1/1537	5.2	5.9	7.9						
ARA-VP 1/1661				4.6	4.8	7.7			
ARA-VP 1/1891				4.7	5.1	8.1			
ARA-VP 1/1950				4.5		7.4			
ARA-VP 1/2065				5.1	5.5	7.6			
ARA-VP 14/18				6.1	6.3	7.4			
ARA-VP 6/25	4.9	5.5	9.0						
ARA-VP 6/88	5.8	6.0	8.6						
ARA-VP 6/595	5.2	6.1	8.3						
ARA-VP 6/800				4.6	5.4	8.3			
SAG-VP 7/1				5.5	5.8	8.5			
SAG-VP 7/57				5.2	5.1	8.5			

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
ARA-VP 6/1686	4	6.1	5.5		5.3	4	7.1	5.7		5.2
KUS-VP 2/70	3	6.6	4.9		4.7			5.1		4.3
Males										
ARA-VP 1/6	5	5.9	5.7		5.4	5	6.5	5.8		5.9
Sex Unknown										
ARA-VP 1/197	2	6.0	5.9		5.7	3	6.4	5.5		5.7
ARA-VP 1/389	3	6.1	5.2		4.7	3	6.2	5.2		4.4
ARA-VP 1/1593	1	6.2	6.2	3.8	6.6					
ARA-VP 1/2060	1	6.6	5.2	4.3	5.8					
ARA-VP 1/2095	1	7.1	6.7	3.5	6.5					
KUS-VP 2/146	2	7.4	6.1		7.1					

Table 4.23 (Continued)

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 6/1686	11	7.2	6.9	7.3	6.7	7.9					2.9	4.2
KUS-VP 2/70	8	7.4	6.3	6.7	6.1	7.9					2.2	4.6
Males												
ARA-VP 1/6	9	7.3		6.7		8.2					2.1	4.3
ARA-VP 1/87	5	7.3	6.8	7.0	6.2	7.6					2.7	5.0
Sex Unknown												
ARA-VP 1/177	0	6.8	6.1	7.0	6.1	7.3	3.9	3.0	3.7	3.4	2.9	4.9
ARA-VP 1/178	1	6.9	6.3	6.6	6.4	7.6					2.8	4.5
ARA-VP 1/197	9	6.4		6.7		7.8					2.7	4.8
ARA-VP 1/900	14	7.2	7.0	7.1	6.8	7.7					2.8	4.2
ARA-VP 1/2175	0	6.8	6.4	6.4	5.6	8.1					2.6	4.2
ARA-VP 1/2451	7	7.9	7.6	7.4	6.9	9.0					3.0	5.5
UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 6/1686	7	8.2	7.0	7.6	6.9	8.8					2.4	4.9
KUS-VP 2/70	4	7.6	7.0	7.2	6.4	8.6				3.4	2.6	4.6
Males												
ARA-VP 1/6	8	7.7		7.2		8.9					2.9	4.0
ARA-VP 1/87	2	7.9	7.3	7.3	6.6	8.7		4.3	4.2	3.7	2.3	4.7
Sex Unknown												
ARA-VP 1/197	6		7.2	7.0		8.5					2.6	4.8
ARA-VP 1/900	9	7.7	7.0	7.1	6.6	8.2					3.0	4.7
ARA-VP 1/2451	4	8.7	7.8	7.9	7.0	9.0					3.1	5.4
UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 6/1686	4	8.4	7.3	6.7	6.0	9.1					2.3	5.2
Males												
ARA-VP 1/6	3	8.0	7.2	6.8	6.5	8.9					2.4	5.1
ARA-VP 1/87	0	7.8	7.6	6.9	6.1	9.2	4.8	3.8	4.1	4.3	2.3	6.4
Sex Unknown												
ARA-VP 1/197						8.7						
ARA-VP 1/793	5					8.6						4.9
ARA-VP 1/2451	2	8.7	8.2		7.1	9.5						

Table 4.23 (Continued)

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/18	1	7.8	6.9	7.1	9.6	8.5	4.2	3.7	4.2	4.2	3.1	5.8
ARA-VP 1/21	2	8.1	7.3	7.3	6.1	8.7					2.9	5.7
ARA-VP 1/22	3	8.6	7.5	7.2	6.6	9.3					2.8	5.7
ARA-VP 1/49	4	7.7	7.0	7.4	6.6	7.9					2.9	4.9
ARA-VP 1/50	4	8.0	7.0	7.3	6.3	8.0					3.4	5.5
ARA-VP 1/134	1	8.4	7.7	7.7	7.0	9.7	5.3	4.7	4.9	4.7	3.1	5.5
ARA-VP 1/179	5		7.4	7.2	6.4	8.7					2.9	5.5
ARA-VP 1/186	7	8.8	7.9	7.6	6.8	9.9			4.3		3.1	5.7
ARA-VP 1/205	4	7.8	7.2	7.5	6.7	8.0					3.0	4.7
ARA-VP 1/379	10	8.7	7.8	8.1	7.1	8.3					2.4	4.5
ARA-VP 1/497	7	9.1	7.8	8.2	7.1	9.2					2.8	5.1
ARA-VP 1/551	0	8.6	7.6	7.3	6.4	8.6	5.0	2.6	3.9	3.9	3.0	6.0
ARA-VP 1/694	4	7.9	6.9	7.5	6.4	8.2					3.2	5.2
ARA-VP 1/742	1	8.1	7.1	7.5	10.4	8.3	4.5	4.3	3.6	3.4	2.8	5.6
ARA-VP 1/788	0	7.9	7.3	6.7	11.0	8.3	4.3	4.3	3.8	3.3	2.6	4.5
ARA-VP 1/794	0	9.0	7.7	7.7	6.6	8.9	4.8	4.5	4.5	3.8	2.7	5.3
ARA-VP 1/850	5	8.2	7.4	7.6	7.0	8.3					2.9	4.9
ARA-VP 1/889	1	7.7	7.0	6.7	6.0	8.3	4.6	4.2	3.6	4.0	2.9	4.9
ARA-VP 1/892	2		6.8		6.9	8.5					3.0	
ARA-VP 1/943	9	9.1	8.5	7.5	6.8	9.5					3.2	6.1
ARA-VP 1/1238	1			7.5	7.1						2.9	
ARA-VP 1/1255	1	8.7	7.0	7.9	6.6	9.1					2.6	5.4
ARA-VP 1/1256	2	7.7	6.7	7.2	6.4	8.4					2.6	4.0
ARA-VP 1/1258	4	7.9	7.0			9.8					2.7	5.9
ARA-VP 1/1562	9		7.3	6.7	6.5	8.2					2.5	4.6
ARA-VP 1/1563	1	7.5	6.7	7.5	6.5	8.2					3.1	5.5
ARA-VP 1/1566	2	8.4	6.5	7.9	6.5	8.7					2.6	5.0
ARA-VP 1/1867	11	8.7	7.8	8.0	7.1	8.7					2.8	4.7
ARA-VP 1/1888	1	8.1	7.0		6.3	8.4					2.6	5.1
ARA-VP 1/1918	10					8.5					2.9	
ARA-VP 1/1919	4	8.1	7.0	7.3	6.2	8.4					3.0	4.8
ARA-VP 1/1986	7	9.4	7.8	8.6	7.6	9.4					3.2	5.6
ARA-VP 1/2068	3	8.2	7.5	7.0	6.5	8.8					2.4	5.0
ARA-VP 1/2072	12	9.1	8.1			10.0					2.7	5.4
ARA-VP 6/579	6	7.5	6.5	7.3	6.1	7.9					3.0	4.8
ARA-VP 6/630	6	7.5	6.3	7.3	6.1	8.5					2.9	
ARA-VP 6/637	7	8.9	8.0		7.6	8.7					2.7	4.9
KUS-VP 2/93	0	8.8	7.4	7.8	6.6	9.0					2.7	4.7
KUS-VP 2/94	3	8.7	7.4	7.4		9.1					2.5	5.1
KUS-VP 2/96	4	8.0	7.1	7.6	7.1	8.6					3.0	5.2
SAG-VP 7/107	3	8.0	6.8	7.3	6.2	8.2					3.2	5.4

Table 4.23 (Continued)

	LI1			LI2			LC		
	W	L	H	W	L	H	W	L	H
Females									
ARA-VP 6/706							5.7	3.7	
ARA-VP 6/796				4.3					
Males									
ARA-VP 1/5					3.0		7.8	5.6	
ARA-VP 1/87							8.4	5.3	16.6
ARA-VP 1/290	4.2	3.5	7.5	4.6	3.5	6.7			
ARA-VP 1/306							8.8	5.7	
Sex Unknown									
ARA-VP 1/196				4.6	3.7	5.1			
ARA-VP 1/1540				4.6	3.1	7.3			
ARA-VP 1/1924	4.6	(3.82)	(6.54)						
ARA-VP 6/97				3.8	3.6	6.7			
ARA-VP 6/1285				5.5	3.8	7.8			
ARA-VP 14/23				5.0	4.4	5.9			
KUS-VP 2/116				4.7	3.8	8.5			

	LP3				LP4					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
ARA-VP 6/654	5.1	5.6	8.2	5.4	4	5.1	6.8		2.1	3.5
ARA-VP 6/796	4.5	6.3		4.9	6	5.2	6.0		2.6	3.4
Males										
ARA-VP 1/5	4.5	7.0	11.0	5.4			6.6		1.6	3.6
ARA-VP 1/87	4.6	7.4	11.1	6.5	2	5.3	6.8	2.6	2.4	3.9
ARA-VP 1/290					1	5.2	6.7	2.3	2.3	4.0
ARA-VP 1/306	4.8	7.3	12.8	6.4						
ARA-VP 1/383	5.0		11.7	4.3	4	5.0	6.1		2.0	4.1
ARA-VP 1/1808					3	5.4	7.5		2.0	4.9
Sex Unknown										
ARA-VP 1/169					3	5.0	6.7		1.6	3.6
ARA-VP 1/180					0	4.8	6.0	2.3	1.8	4.4
ARA-VP 1/336					3	5.3	6.7		2.0	4.6
ARA-VP 1/566					1		6.8	2.4		
ARA-VP 1/894					3	5.1	6.6		1.6	3.6
ARA-VP 1/1546					6	5.7	7.3		1.9	4.1
ARA-VP 1/1721					5	5.0	6.0		1.4	3.6
ARA-VP 1/2473					6	5.2	6.7		1.7	3.2
ARA-VP 6/626					2	4.7	7.3		1.8	5.6

Table 4.23 (Continued)

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
ARA-VP 6/796	13	5.9		5.5		7.2						
Males												
ARA-VP 1/5	9					8.4					2.2	3.5
ARA-VP 1/87	4	6.2	5.9	6.2	6.0	7.7					2.5	5.3
ARA-VP 1/290	3	5.8	5.5	5.6		7.9					1.8	4.2
ARA-VP 1/306	6	6.6	6.0	6.9	6.4	8.7					2.6	4.7
ARA-VP 1/383	13	5.9	5.7	6.3	6.1	7.7					2.3	3.6
KUS-VP 2/2	9	6.4	6.2	6.8	6.9	8.4					2.6	4.5
Sex Unknown												
ARA-VP 1/198	9	5.9	5.6	5.9	5.6	8.1					1.5	4.1
ARA-VP 1/564	13			6.4	6.0	7.5					2.2	
ARA-VP 1/566	5	5.8	5.2	6.1	5.8	8.0					2.5	4.4
ARA-VP 1/785	16	6.1		6.3		8.2					2.5	
ARA-VP 1/1774	15					6.9						
KUS-VP 2/5	6	6.3	5.9	6.7	6.3	8.3					1.9	4.2
LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
ARA-VP 1/87	2	7.3	7.1	7.3	6.9	8.9					1.8	4.9
ARA-VP 1/306	5	7.5	7.2	8.0	7.8	9.9					2.3	5.8
Sex Unknown												
ARA-VP 1/7	8	6.5	6.3	6.4	6.3	8.0					1.9	4.7
ARA-VP 1/70						9.4						
ARA-VP 1/198				7.1		8.2						
ARA-VP 1/564	10	7.6	7.1	7.5	7.1	8.4					2.5	4.5
ARA-VP 1/566	2	7.1	6.5	6.8	6.5	8.7	3.2	4.0	3.6	3.6	2.6	4.6
ARA-VP 1/785	14					8.9					2.5	
ARA-VP 1/1774	11					8.0					1.5	4.2
KUS-VP 2/5	3	7.4	7.0	7.7	7.2	9.4					2.1	5.0

Table 4.23 (Continued)

LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Males												
ARA-VP 1/87	1	7.4	7.5	7.1	6.9	12.4	4.9	5.1	4.9	4.4	1.9	5.2
ARA-VP 1/306	3	7.6	7.2	7.6	7.4	11.9	4.7	5.1		4.6	2.0	5.2
Sex Unknown												
ARA-VP 1/7	7	6.7	6.7	6.5	6.4	10.7					2.1	5.2
ARA-VP 1/10	0	6.9	6.8	6.9	6.6	12.0	4.6	4.7	4.1	3.6	2.1	5.8
ARA-VP 1/11	3			7.0	6.9						2.4	5.6
ARA-VP 1/70						11.3						
ARA-VP 1/116						13.1						
ARA-VP 1/130	3	7.6	7.1	6.9	6.7	11.5		4.6		3.9	2.6	5.6
ARA-VP 1/170	8	7.2	6.9	6.9	6.5	11.2					2.6	5.1
ARA-VP 1/198	5	7.4	7.1	7.3	7.0	11.2					1.7	5.8
ARA-VP 1/238	10	7.3	6.8	6.8	6.8	11.3				4.2	2.4	4.4
ARA-VP 1/308	7	(7.1)		7.2	7.1	12.9					2.2	5.6
ARA-VP 1/329	4	7.4	7.2	7.2	7.1	12.1					2.0	5.4
ARA-VP 1/331						12.8					2.8	5.7
ARA-VP 1/337				7.2	7.2							
ARA-VP 1/351	1	6.3	6.1	6.3	6.3	10.5	3.8	3.8	4.2	4.2	2.6	4.6
ARA-VP 1/550	6	7.2	7.2	7.2	7.1	12.0					2.4	5.5
ARA-VP 1/559	6	6.9	6.9	6.8	6.9	11.5					2.4	4.9
ARA-VP 1/564	7	7.6	7.0	7.5	7.4	11.3					2.1	4.5
ARA-VP 1/785	13	7.4		7.1		(12.5)					1.6	
ARA-VP 1/1570	11										2.1	4.8
ARA-VP 1/1572	6	6.8	6.8	7.0	6.9	11.2					2.0	
ARA-VP 1/1715	7		7.1	7.2	7.0	11.8						
ARA-VP 1/1774	6			7.2		11.2					1.8	5.0
ARA-VP 1/1869	6	6.9	6.9	7.2	7.2	11.7					2.0	5.6
ARA-VP 1/2091	6			7.5	7.4						2.3	
ARA-VP 1/2159	9	6.5	6.5	6.3	6.1	10.8					1.8	3.7
ARA-VP 6/87	1	7.9	7.6	7.7	7.6	13.5					2.6	6.3
ARA-VP 6/570	9	7.5	7.3	7.3	7.1	11.9						6.3
ARA-VP 6/583	3	7.5	7.3	7.4	7.3						2.4	5.2
ARA-VP 6/584	3			7.1	7.1						2.1	5.2
ARA-VP 6/585	4					13.2						
ARA-VP 6/1294	7	7.6	7.3	7.2	7.1	12.1					2.3	5.5
KUS-VP 2/20	5	7.4	7.4	7.2	7.1	12.3					2.1	5.5

Table 4.23 (Continued)

LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/14	0	6.8	6.5	6.7	6.3	8.8	4.4	4.1	4.5	4.5	2.4	5.1
ARA-VP 1/15	3	6.7	6.3	6.8	6.5	8.6		4.2	4.2	4.2	2.0	4.5
ARA-VP 1/46	6					9.3					2.5	5.5
ARA-VP 1/286	8					8.8					2.6	5.6
ARA-VP 1/324	9										2.2	5.0
ARA-VP 1/338	10	6.4	6.1	6.6	6.4	8.1					2.0	4.1
ARA-VP 1/549	0	7.9	7.3	7.7	7.3	9.1					2.0	5.2
ARA-VP 1/790						8.9						
ARA-VP 1/879	0	5.8	5.5	6.0	5.7	8.0	3.8	3.1	3.7	2.9	2.1	4.4
ARA-VP 1/887	1	6.4	6.0	6.5	6.0	8.4	3.0	3.8	4.5	4.4	1.9	5.8
ARA-VP 1/939	0			7.7	7.6						2.7	5.8
ARA-VP 1/950	0	7.5	7.2	7.6	7.5						2.2	6.1
ARA-VP 1/1267	1	6.3	5.8	6.5	6.1	8.6	3.9	3.9	4.1	4.2	2.1	5.4
ARA-VP 1/1549	1	6.4	6.0	6.3	6.1	8.2	3.6	4.2	3.7	3.8	2.4	5.0
ARA-VP 1/1550	13			6.7	6.4						2.3	
ARA-VP 1/1551	6	5.9	5.4	6.1	5.8	7.7					2.1	4.8
ARA-VP 1/1557	0	6.6	6.1	6.7	6.4	8.9	3.9	3.7	4.3	3.3	2.6	5.7
ARA-VP 1/1601	7	8.2	7.5	7.6	7.2	8.7					2.7	4.5
ARA-VP 1/1720	7	6.4	6.0	6.7	6.3	(8.72)					2.4	4.8
ARA-VP 1/1807	5	8.1	7.4	8.2	7.7	9.7					2.0	5.7
ARA-VP 1/1809	8	7.1	6.5	7.0	6.6	8.8					2.3	4.8
ARA-VP 1/2046	8	7.3	6.8	7.3	7.1	8.8					2.5	5.0
ARA-VP 1/2064	5	6.8	6.6	7.2	7.1	8.4					2.2	5.6
ARA-VP 1/2069	10			6.6	6.4	8.6					2.2	
ARA-VP 1/2073	10	6.6	6.2	6.3	6.4	8.4					1.7	4.5
ARA-VP 1/2074	14	6.8	6.5	7.1	7.0	8.6					2.0	3.9
ARA-VP 1/2087	7	6.4	5.8	6.2	6.1	8.0					2.4	4.7
ARA-VP 6/56	10	7.6	7.2	7.9	7.4	8.9					2.1	5.7
ARA-VP 6/60	1		7.3	7.5	7.4	9.1					1.9	5.0
ARA-VP 6/286	7	7.0		7.4		8.9					2.3	4.6
ARA-VP 6/578	1	7.0	6.4	6.8	6.8	8.7					2.4	5.8
ARA-VP 6/605	2			7.7	7.5	9.5					2.2	
ARA-VP 6/606	4	7.5	7.4								2.4	6.2
ARA-VP 6/608	8	6.0	5.8	6.4	6.2						2.1	
ARA-VP 6/641	0	6.7	6.3	6.6	6.0	8.6					1.9	4.9
ARA-VP 6/798	10	7.4	6.8	7.3	7.1	9.0					2.1	5.8
ARA-VP 6/1295	8	6.3	5.6	6.5	6.2	8.3					2.1	4.3
ARA-VP 6/1619	1	5.7	5.5	6.1	6.2	8.2					2.2	4.5
ARA-VP 6/1620	1	7.4	7.1	7.6	7.4	(9.05)					2.3	5.3
KUS-VP 2/89	11	8.1	8.1	8.5	7.7	10.0						
KUS-VP 2/97	7	8.1	7.6	7.9	7.9	9.7					2.4	6.1
SAG-VP 7/101	12			6.3	6.1						1.8	

Table 4.23 (Continued)

UdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/177	9	5.7		(5.5)		6.5					1.8	2.7
ARA-VP 1/178	6	5.7	4.4	5.7	4.6	6.5						
ARA-VP 1/2070	0	5.7	4.9	5.7	5.0	7.0					2.3	3.5
ARA-VP 1/2175	4	5.7	5.2	5.5	4.9	6.9					1.9	3.5

LdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
ARA-VP 1/16	1	4.7	4.5	5.0	4.7	7.0					1.8	4.1
ARA-VP 1/48	0	4.3	3.8	4.4	4.1	6.3					1.6	3.4
ARA-VP 1/1241	8	4.6	4.3	4.7	4.4	6.7					1.3	3.2
ARA-VP 1/1271	0	4.5	4.2	5.0	4.5	6.9					2.2	4.3

Table 4.24 Dental dimensions for *Colobus* cf. *angolensis*.

	UI1			UI2			UC		
	W	L	H	W	L	H	W	L	H
Females									
KL188-1	4.5	4.8		4.3	4.4		4.6	4.7	
KL191-62	4.3	5.2		3.8	3.5		3.5	5.1	
KL191-98	4.7			4.2	3.2		4.7	6.3	
Males									
KL191-23	4.5	5.1		4.2	3.8		7.2	9.2	
Sex Unknown									
KL191-24	3.7	4.4	8.6						
KL191-116		4.2							

	UP3					UP4				
	WS	W	L	IC	H	WS	W	L	IC	H
Females										
KL188-1	8	5.4	4.8			8	5.9	4.4		
Males										
KL191-23	7	5.5	5.1			6	6.0	4.6		
KL191-96			4.9			8		4.8		
Sex Unknown										
KL183-3		5.3			4.5	3	7.2	5.3		5.3
KL183-16							7.4	5.8		5.2
KL191-141						4	5.9	4.5	2.2	4.0

UM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-1	16	6.2		5.8		6.4						
Males												
KL191-23	15					6.5						
KL191-96	16	6.2		5.9		6.5						
Sex Unknown												
KL183-3	3	6.5	5.7			7.3					1.8	4.5
KL191-24	0	6.3	5.2	6.0	5.1	7.1					3.1	4.9
KL191-56	0	5.7	5.1	5.2	4.7	7.3					2.1	4.0
KL191-59c		5.9	5.4	6.0	5.2	7.0					2.9	4.6
KL191-141	8	5.9	5.4	5.4	5.0	6.0					2.3	

UM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-1	9	6.7	6.2	6.2	5.8	6.7					2.4	3.8
KL191-98	12	7.1				7.1					2.9	3.8
Males												
KL191-23	8					7.2						
KL191-96	12	6.4	6.1			6.6					2.2	4.1
Sex Unknown												
KL189-8	8	6.8	6.6	5.8	5.6	7.4					2.8	4.7
KL191-99	16	6.7		6.2		6.7					2.3	3.2
KL191-141				5.7	5.2	6.4						

Table 4.24 (Continued)

UM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-1	2	6.6	6.1	5.9	5.2	7.6					3.4	4.5
KL191-98	6	6.8	6.4								2.8	4.2
Males												
KL191-23	4	6.7		6.0		8.1					2.6	4.5
KL191-96	7	6.5	6.2	5.7	5.5	7.4					2.1	4.7
Sex Unknown												
KL189-8	4	6.4	5.9	5.5	4.8	7.0		3.0			2.5	
KL191-99	5	6.6	6.1	5.7	5.3	6.7					2.5	4.2

UMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-33	4	6.3	5.9	5.1	5.0	7.1					2.1	4.4

	LI1			**LI2**			**LC**		
	W	L	H	W	L	H	W	L	H
Females									
KL188-2				4.1			3.9	6.0	7.5
Males									
KL188-3	4.0	4.1	6.6	4.3	2.6	6.7			

	LP3				**LP4**					
	W	L	FL	H	WS	W	L	IC	NH	H
Females										
KL188-2	3.8	6.0	6.8		6	4.3	5.3		1.9	2.8
KL190-3	4.0	6.6	7.2	3.2	4	4.5	4.7		2.0	3.0
Males										
KL188-3	3.9	6.0			0	4.3	6.1	2.1	1.9	4.1
KL188-8					4	4.2	4.2		2.9	
KL190-6	5.6	7.9	7.1		8	4.4	6.4		1.9	3.0
KL191-102	4.6	6.7	9.1		4	4.1	6.1		2.4	3.3

LM1	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-2	15	5.1		5.3		6.5						
KL190-3	15	4.9		5.6		6.8					2.0	2.8
Males												
KL188-3	5	4.9	4.9	5.5	5.4	7.1					1.7	4.2
KL188-8	16	4.4		5.1		6.7						
KL190-6	16			5.4		6.9						
Sex Unknown												
KL183-10	12	4.1		4.2		5.5						
KL188-16	4			5.8	5.9	7.2						
KL188-6	1	4.6	4.3	5.2		6.7					1.6	3.9
KL189-9	10	4.4				6.8						3.2
KL190-1	1	5.1	4.8	5.7	5.3	7.3					1.7	4.0
KL190-2	3	5.1	5.0	5.5	5.3	7.5	2.9	3.0	3.6	3.8	2.3	4.7
KL191-68	10	4.8		5.0		6.1					1.8	2.0

Table 4.24 (Continued)

LM2	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-2	10	5.8	5.8	5.9	5.7	6.7					2.3	3.8
KL190-3	9	5.7	5.6	6.1	5.9	6.8					2.1	4.0
Males												
KL188-3	1	6.1	5.5	6.1	5.8	7.6					1.7	4.6
KL188-8	12	5.4		5.6		7.1					2.2	3.4
KL190-6	14	6.3				7.5					2.3	3.5
KL191-102	8			6.0	6.0							
Sex Unknown												
KL183-10	8	5.0		5.1	4.5	5.6					1.9	
KL183-11	6	5.1	4.7	4.9	4.6	6.0					2.2	3.9
KL188-18	7	5.8	5.6	6.0	5.8	7.4					1.6	4.4
KL189-9	5	5.5	5.0	5.7	5.3	7.1						2.0
KL191-28						7.3						
KL191-59a	0	4.9	4.8	5.4	5.3	7.4	2.6	2.9	3.5	3.2	1.8	4.4
KL191-64	7					7.6						
LM3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Females												
KL188-2	4	5.7	5.4	5.8	5.5	9.2					2.7	5.0
KL190-3	5	6.0	5.7	6.0	5.7	9.1					1.9	4.2
Males												
KL191-60	0	6.5	6.1	6.3	6.0	10.0					1.8	4.8
Sex Unknown												
KL183-10	5	5.3	4.6	4.3	4.3	5.9					1.7	2.9
KL188-18	4					9.7						
KL191-161						9.4						
KL191-28	7	5.7	5.5	5.6	5.5	9.7					2.2	4.7
KL191-64	2	6.4		6.4	6.0	10.1					2.3	
KL191-66	1			6.2	5.5	9.9					2.3	
LMX	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL183-15	14	4.9		5.3		5.8					1.8	
KL188-24	8	5.39	5.4	5.0	5.0	6.4					2.4	3.7
KL188-27	10	4.73		4.8		6.0						
KL191-91	0	4.88	4.5	5.4	5.1	7.0					1.6	4.5
KL191-153	1	4.89	4.8	5.7	5.5	7.2					2.2	4.5

Table 4.24 (Continued)

UdC	W	L	H
KL191-116	2.9	3.1	3.9

UdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-24	8	4.1	3.6	3.8	3.6	5.3					2.3	3.4
KL191-56	8	3.6		3.1		5.0						
KL191-59c		4.0	3.3	3.8	3.1	5.5					2.4	2.9

UdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL191-24	5	4.9	4.3	5.0	4.5	6.4					1.9	3.5
KL191-59c		5.1	4.5	4.7	4.5	6.1					2.2	3.6

LdC	W	L	H
KL188-6	3.9	4.0	4.5

LdP3	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL188-6	9	3.0	2.7	3.2	3.2	5.5					1.7	2.2
KL191-110	0	2.8	2.1	3.1	2.8	5.4	1.3	1.1	2.7	2.5	1.8	3.0

LdP4	WS	AW	AWN	PW	PWN	L	ICA	ICP	ICB	ICL	NH	H
Sex Unknown												
KL188-6	8	3.7	3.4	4.1	3.8	5.9					1.4	3.2
KL190-1	9	3.9	3.8	4.2	4.0	6.6					1.2	2.9
KL191-110	0	4.2	3.7	4.0	3.6	5.8	2.3	2.1	2.6	2.6	1.8	2.7

Chapter 5

Systematic Paleontology of the Turkana Cercopithecidae

The Pliocene and Pleistocene strata from the Turkana basin are the most thoroughly studied, and well-dated in Africa (e.g. Brown and Feibel, 1991; Brown, 1994; 1995). While sediments in the basin span nearly the entire Pliocene and Pleistocene, those from the three main paleontological collecting regions are most complete for the period between approximately 3.4 and 1.5 Ma. The stratigraphy of the Turkana Basin formations included here is briefly summarized in Chapter 2.

The paleontological collections from the Turkana basin are some of the largest in Africa, with thousands of cercopithecid specimens. Many of these have been published (Patterson, 1968; Leakey and Leakey, 1973b; 1976; Leakey, 1976; 1982; 1987; 1993; Eck, 1976; 1977; 1987a; 1987b; Eck and Jablonski, 1987; Harris et al., 1988; Leakey et al., 1995; in press). In total, the sample includes at least 14 species of cercopithecids, which is similar to the Afar basin. Of these, however, only 3 are likely to be shared between the two basins. Furthermore, while the total number of species present is the same as the Afar, the number present at any single time period is generally higher in the Turkana basin. By far the most abundant taxon is *Theropithecus*, which represents the vast majority of the cercopithecid assemblage for the time span from 3.4 to about 1 Ma.

The purpose of this section is largely to provide a basis for comparison with the cercopithecid record from the Afar region. Additionally, most of the material from the Turkana basin has been published, at least partially. As a result, this section will not describe the different cercopithecid taxa present in the detail that was done for the Afar depression. Instead, reference will be made to relevant publications wherever possible, and description will be kept to a minimum. They will generally focus on those taxa and anatomical regions not present in the Afar region, or on areas where shared taxa differ in morphology. Additionally, diagnoses and synonymies for taxa found in the Afar depression will not be repeated here, instead the reader is referred to that section.

Family Cercopithecidae Gray, 1821

Subfamily Cercopithecinae Gray, 1821

Tribe Cercopithecini Gray, 1821

Genus *Cercopithecus* Linnaeus, 1758

Type species: *Cercopithecus diana* Linnaeus, 1758

Other included species (following Napier, 1981): *C. dryas* Schwartz, 1932; *C. solango* Thys van den Audenaerde, 1977; *C. neglectus* Schlegel, 1876; *C. hamlyni* Pocock, 1907; *C. lhoesti* Sclater, 1899; *C. preussi* Matschie, 1898; *C. mitis* Wolf, 1822; *C. nictitans* Linnaeus 1766; *C. petaurista* Schreber 1774; *C. erythrogaster* Gray, 1866; *C. ascanius* Audebert, 1799; *C. cephus* Linnaeus, 1758; *C. erythrotis* Waterhouse, 1838; *C. campbelli* Waterhouse, 1838; *C. mona* Schreber, 1774; *C. pogonias* Bennett, 1833; *C. denti* Thomas, 1907; *C. wolfi* Meyer, 1891; *C. aethiops* Linnaeus, 1758.

Generic diagnosis: See Afar section.

Cercopithecus sp. indet.

(= or including Cercopithecus sp. (B) Leakey, 1976)

Turkana specimens included: specimens listed in Eck, 1987b; plus specimens given in Leakey, 1976; 1988, except for those included under Cercopithecini gen. et sp. indet. below.

Range: ~3.3 Ma - Recent

Turkana range 3.3 – 1.55 Ma

Distribution: Asbole; Andalee Mbr., Wehaietu Fm.; Members B, C, G, J, Shungura Fm.; Usno Fm.; KBS Mbr., Koobi Fora Fm.; Kanam East; Taung, Upper.

Description:

Eck and Howell (1972) and Eck (1987b) have described the fossils assignable to *Cercopithecus* from the Omo Shungura and Usno Formations. Leakey (1976; 1988) has briefly described the material from Koobi Fora. It is quite likely that these samples represent more than a single species as they span a period of almost 2 Myr and vary considerably in both size and morphology. However, they are described here together because they cannot be definitively diagnosed from one another in any consistent manner and are all clearly distinct from Cercopithecini gen. et sp. indet, described below.

As discussed by Eck (1987b), there is a large range in size among *Cercopithecus* specimens from the Shungura Formation with some individuals close in size to *C. nictitans*, and others similar to *C. aethiops*. There appears to be no clear temporal pattern, with both Members B and G containing specimens similar in size to both of these taxa. All of the cercopithecin specimens from Koobi Fora, other than ER 396, are from the KBS Member and are similar in size to *C. aethiops*. P994-8 from Member J is roughly contemporaneous with the KBS, and is also similar in size to *C. aethiops*. Sexual dimorphism cannot be invoked to explain all of the variability in the Shungura sample, as the mandible L621-4 is clearly that of a male, yet is in the smaller *C. nictitans* size group. While the dental size range preserved is large, it is not entirely inconsistent with a single species, especially given the temporal range. Two specimens (W8-2v and W8-9o) from the Usno Formation are quite small, but are larger than would be expected for upper molars of Cercopithecini gen. et sp. indet. (ER 396). The Usno teeth are intermediate in size between smaller species of *Cercopithecus*, and *Miopithecus*, whereas ER 396 is almost within the *Miopithecus* range. It is possible that these two specimens represent the same species as ER 396, but they are as likely to be conspecific with the *C. nictitans*-sized group from the Shungura Fm. Thus they are tentatively allocated to this group.

Fossils of *Cercopithecus* are rare at both the Omo and Koobi Fora. In the Shungura Formation, *Cercopithecus* is present in Members B, C, G, and J, and represented by only one to four specimens in each. This is a very small proportion of the over 6,000 cercopithecid specimens from the Shungura Formation. Bobe (1997) has shown that at the Omo there is a taphonomic bias towards larger taxa. It therefore seems probable that *Cercopithecus* was present in the region (or at least in the Omo river watershed) for most of this interval, but its recovery from any particular member may be unlikely due simply to sampling error. Given the morphological similarity of cercopithecin cranial and dental elements and the limited material available, it is difficult to assign any of this material to particular taxa, or to estimate the number of species present.

Cercopithecini gen. et sp. indet.

(= or including *Cercopithecus sp.* A Leakey, 1976)

Range: ca. 3 Ma

Turkana Specimens included: KNM-ER 396

Description:

This taxon is represented by a single specimen from low in the Koobi Fora sequence. It was described by Leakey (1976;1988) and is a mandible of a very small cercopithecin. It clearly lacks a hypoconulid on the M_3, and the molars are relatively long and narrow. They are, however, not as elongate as those of *Erythrocebus*. Similar to other cercopithecins, but distinctly unlike *Allenopithecus*, their crowns lack basal flare. It is similar in size to the largest individuals of modern *Miopithecus*. Thus, on morphological grounds this specimen is clearly from a cercopithecin other than *Allenopithecus*. Moreover, it seems to lack the elongate molars of *Erythrocebus*. While this does not rule out the possibility that ER 396 is a very diminutive patas monkey, it does appear unlikely. This specimen lacks any morphology that would allow it to be either excluded from or included in either *Cercopithecus* or *Miopithecus*. If size were used to make this decision, then it would be included in the latter genus. However, this is unsatisfactory as a character for diagnosis, and therefore it seems appropriate to leave this specimen as indeterminate for both genus and species, but definitely specifically distinct from the later Koobi Fora and Omo material.

Tribe Papionini Burnett, 1828

Genus *Parapapio* Jones, 1937

Type species: *Parapapio broomi* Jones, 1937

Other included species: *Pp. antiquus* Haughton, 1925; *Pp. jonesi* Broom, 1940; *Pp. whitei* Broom, 1940; *Pp. ado* Hopwood, 1936; *Pp. sp. nov.* Leakey et al.,in press.

Generic Diagnosis: See Afar section.

Parapapio ado (Hopwood, 1936)

(= or including *Cercocebus ado* Hopwood, 1936. *Papio (Simopithecus) serengetensis* Dietrich, 1942, in part. *Parapapio jonesi* Broom, 1940: Patterson, 1968. Papionini gen. et sp. indet. (B), Leakey and Leakey, 1976. *Parapapio ado*: Leakey and Delson, 1987.)

Holotype: BM(NH) M14940

Turkana specimens included: KNM-KP 286

Range: 4.17 – 3.49 Ma

Turkana range: 4.17 – 4.07 Ma

Distribution: ?Tulu Bor Mbr., Koobi Fora Fm.; Kanapoi; Upper Unit of the Laetolil Beds.

Specific Diagnosis:

This diagnosis follows the description of Leakey and Delson (1987) for the material from Laetoli. A medium sized papionin, similar to smaller *Parapapio* from South Africa in size. The mandibular symphysis is sloping in lateral view. The incisive area projects anteriorly so that the incisors are positioned relatively far rostrally to the canine, and are more proclined in orientation. Its profile is sigmoidal in outline, being convex down from its posterior limit anteriorly to approximately the level of the median mental canal, where it then becomes more concave down as the incisive portion of the alveolar process projects anteriorly. The symphysis is relatively long and shallow overall. Related to this, the inferior transverse torus typically projects further posteriorly than the superior. The mental ridges are typically present, and often rugose in the males. The corpus lacks fossae. It is roughly even in depth from anterior to posterior. The teeth are similar to those of most papionins in morphology, with the molars showing a relatively large amount of flare.

Description:

The only published specimen from Kanapoi, KP 286, is a reconstructed male mandible collected in 1966. It was described by Patterson (1968) and assigned to *Parapapio jonesi*, largely on the basis of molar size. Leakey and Delson (1987) included this specimen in *Pp. ado*, the same species as is found at Laetoli. A larger number of specimens from more recent work at Kanapoi have been collected. They were included in the faunal list of Leakey et al. (1995) and allocated to *Pp.* cf. *ado*. The Kanapoi sample is the only material from the Turkana basin that can be allocated to *Pp. ado* with any confidence. All of the other material is either non-diagnostic or possibly from a separate taxon, and therefore best left as small papionins of indeterminate affinity.

KNM-KP 286 is composed of several elements, including a symphysis with the roots of the canines and incisors. Another small fragment preserves the left P_4-M_1 in a small bit of the corpus, another has the left M_3 and anterior portion of the ramus. Part of the right corpus and anterior ramus with the M_{2-3} is also preserved (Patterson, 1968).

This mandible displays all of the diagnostic features of *Pp. ado*. The symphysis is sloping and long. The incisor region projects anteriorly beyond the canines, and the incisive alveoli are “pinched” between the canines. The mental ridges are well developed and rugose. The corpus is not well preserved, but it does not appear that there would have been fossae, although it is possible that they were present.

Remarks:

Pp. ado cannot be allocated to the genus *Parapapio* with complete confidence as there is no facial material available to confirm this status. Following Leakey and Delson (1987) it is tentatively placed in *Parapapio* due to its typical papionin dentition, and lack of mandibular corpus fossae, and general lack of features that would rule out its being placed in *Parapapio.* Furthermore, its symphyseal morphology is distinct from that of *Papio* and *Pliopapio*. Until more diagnostic material is available, it tentatively left in the genus *Parapapio*.

Genus *Lophocebus* Palmer, 1903

(= or including *Cercocebus* Geoffroy, 1812: Leakey, 1976; Leakey and Leakey, 1976, in part. *Semnocebus* Gray, 1870, *nec* Lesson, 1840. *Leptocebus* Troussart, 1904. Papionini sp. B Eck, 1976, 1977, in part.)

Type species: *Lophocebus albigena* (Gray, 1850)

Other included species: *L. aterrimus* (Oudemans, 1890); *L.* sp. nov.

Generic Diagnosis:

A genus of medium-sized papionins with infraorbital fossae that are very deeply excavated, and undercut the orbital rim, similar to *Cercocebus* and to some extent *Gorgopithecus*, but otherwise distinct among cercopithecids. The rostrum is short relative to neurocranial length in comparison to most other papionins, including *Cercocebus* (see figure 4.5). It is also relatively narrow in comparison to the breadth of the neurocranium (Groves, 1978), with only *Pliopapio* having a narrower rostrum (see figure 4.4). The mandibular corpus bears a distinct anterior fossa, which is different from *Parapapio*, *Cercocebus*, *P. (Dinopithecus)*, and *T. oswaldi*.

The molar crowns have more basal flare than those of all other cercopithecids except for *Cercocebus* and *Allenopithecus* (see figures 4.7-4.8). As is typical of papionins, but different from *Cercocebus*, the upper molars are longer than they are broad (Groves, 1978). Furthermore, the P^4 is relatively narrow in comparison to the breadth of the M^1, as is typical of most papionins, but distinct from *Mandrillus* and *Cercocebus* (Fleagle and McGraw, 1999). In the extant species, the upper central incisor is large in comparison to the molar teeth (Groves, 1978). Only *Miopithecus* and several species of *Cercopithecus* match it in this respect. The postcranium is also distinguished by its adaptations to more arboreal behaviors than that of most other African papionins.

Lophocebus sp. nov.

(= or including *Cercocebus* sp. Leakey, 1976; Leakey and Leakey, 1976; Papionini sp. B Eck, 1976, 1977, in part).

Turkana specimens included: NME Omo K6 ’70 C146; plus specimens from Koobi Fora listed in Leakey and Leakey (1976).

Range: 1.88 to 1.39 Ma to Recent

Distribution: Shungura Fm., Member K., Koobi Fora Fm., KBS-Okote Mbs.; Olduvai, Upper Bed II.

Description:

The sample from Koobi Fora largely derives from sediments of the Okote Member at Ileret, and has been described by Leakey and Leakey (1976). The single specimen from the Shungura Formation, Omo K6 ’70 C146 is fragment of a right mandibular corpus that most likely represents the same taxon as at Koobi Fora, although this cannot be certain without maxillary specimens. It was briefly described by Eck (1976) as possibly *Parapapio* similar in dental size to *Pp. jonesi* or *Pp. broomi*. It preserves the P_4 through M_3 and much of the corpus, but does not preserve the inferior margin.

This taxon is larger in molar size than all extant *Lophocebus* and *Cercocebus*, and is similar in size to larger *Macaca* such as *M. sylvanus* and *M. thibetana,* but smaller than *P. hamadryas* other than *P. h. kindae*. Dental dimensions for the Koobi Fora material have been published by Leakey and Leakey (1976), those for Omo K6 ’70 C146 are given in table 5.1. In approximate rostral and mandibular size it is considerably larger than the extant mangabeys as well, once again being similar to large *Macaca* or the smallest *Papio*.

The diagnostic specimens of this species are all from Koobi Fora. The rostrum is only incompletely preserved, but it is was clearly short. Whether it is shorter than is expected for a papionin of this dental size is not clear, as none of the maxillae are complete enough to accurately estimate total length. The most striking feature of the maxilla is the very deep suborbital fossa. The fossa undercuts the inferior orbital rim, providing the most diagnostic feature of the taxon. Slight maxillary ridges mark the superior border of the maxillary fossa, at least in the males, a feature more typical of *Lophocebus*, but does occur variably in *Cercocebus*. The zygomata are all broken at the zygomaticomaxillary suture. The zygomatic process arises from the maxilla from above the mesial moiety of M^2.

The mandibular symphysis slopes at an angle of approximately 45 to 50º and is relatively deep. Mental ridges are clearly present, at least on the male specimens. It is also marked by a median mental foramen. None of the material preserves much of the inferior margin so it is difficult to estimate whether the corpus was deepest anteriorly or posteriorly. The lateral surface of the corpus has a well-marked corpus fossa that is deepest at below the M_1. This is a feature that is most common in *Lophocebus*, whereas *Cercocebus* either lacks a corpus fossa or it is not well defined or anteriorly placed. The plenum alveolare is deeply concave, and the superior transverse torus extends posteriorly to the distal end of the P_3. The inferior torus extended a small distance further posteriorly. The ramus is not well preserved, but there is a modest extramolar sulcus and retromolar gap.

As described by Leakey and Leakey (1976), the upper central incisor is a large tooth, with a crown that is broad, spatulate, and broadens towards the tip in labial view.

Relative to the size of the molars, the central incisor is smaller than in either modern genus of mangabey, similar to most papionins, but clearly larger than in *Theropithecus* (see figure 4.1). The P^4 is small relative to the size of the molars (see figure 4.6). In this respect it is similar to most African papionins, but distinct from *Allenopithecus*, *Cercocebus* and *Mandrillus* (Fleagle and McGraw, 1999). The molars show none of the derived features of the modern mangabey genera. They have a modest amount of basal flare, similar to that of *Papio*, *Macaca*, and most papionin genera (see figure 4.7-4.8). Possibly related to this, the molar crowns are narrower than those of *Lophocebus* or *Cercocebus*. Finally, the molars do not show the unique *Cercocebus* wear pattern, where all four cusps wear at a relatively even rate. Instead the buccal cusps of the lower molars and lingual cusps of the uppers wear more quickly.

Remarks

Lophocebus is known from Kanam East, and some material assigned to *Cercocebus* may also include *Lophocebus*, such as that from Makapansgat, Taung, Kromdraai, and the Hanging Remnant at Swartkrans. However, the Koobi Fora material is the only fossil assemblage that can be assigned to one of the modern mangabey genera with confidence. This is because all other material allocated to either *Lophocebus* or *Cercocebus* does not preserve the region of the suborbital fossa. All of the other features used to diagnose *Cercocebus* and *Lophocebus* from each other and from other genera are not unique and must be used in combination with the presence of very deep suborbital fossae. Therefore, while specimens from Makapansgat and Kanam East are significantly older than the Koobi Fora material, their diagnoses are far more tentative. Thus, the

Koobi Fora material is the earliest documentation of the modern morphology. While the lineages that led to *Cercocebus* and *Lophocebus* probably diverged from those of *Mandrillus* and *Papio* substantially earlier than this, they may not necessarily have displayed the modern morphology.

The Koobi Fora material shows a number of features that clearly indicate its status as a species of *Lophocebus*. These include the deep suborbital fossae, anteriorly placed and well-marked mandibular corpus fossa, the relatively small P^4, and the normal papionin wear pattern of the molars. Other features may show, depending on their polarity, that the fossil species is not as derived as extant *Lophocebus*. These features include the lack of strong molar basal flare and a relatively small central incisor. The above two traits, along with the relatively large size of the fossil species argue for specific distinction from *L. albigena* and *L. aterimus*.

Genus *Papio* Müller, 1773

Type species: *Papio hamadryas* Linnaeus, 1758

Other included species: *P. angusticeps* Broom, 1940; *P. izodi* Gear, 1926; *P. ingens* Broom, 1937; *P. quadratirostris* Iwamoto, 1982.

Generic Diagnosis: See Afar section.

Subgenus *(Dinopithecus)* Broom, 1937

(= or including *Papio* Müller, 1773: Maier, 1971; Eck, 1976, 1977, in part. *P. (Dinopithecus*): Delson, 1984.)

Type species: Papio (Dinopithecus) ingens Broom, 1937

Other included species: *P.(D.) quadratirostris* Iwamoto, 1982

Subgeneric diagnosis:

This diagnosis follows those of Freedman (1957), Szalay and Delson (1979), and Delson and Dean (1993). A subgenus of *Papio* large or very large in size, with *P. (D.) ingens* exceeded in size only by the largest *T. o. leakeyi*. There is some overlap in size of other populations with the largest members of extant *Papio*. As in other *Papio* there is distinct anteorbital drop, and flattening of the muzzle dorsum. It is distinct from *P. (Papio)* by having only very shallow or absent maxillary and mandibular facial fossae. Males often have distinct maxillary ridges that appear to be fairly variable in shape. The male neurocranium often develops a sagittal crest that may occur relatively far anterior.

Papio (Dinopithecus) quadratirostris Iwamoto, 1982

(= or including *Papio sp.* nov. Eck, 1976, 1977; *Papio (Chaeropithecus*) cf. *hamadryas* sspp., Szalay and Delson, 1979, in part. *Papio (Dinopithecus) quadratirostris*: Delson, 1984).

Holotype: NME "USNO" (see Delson and Dean, 1993)[1]

Turkana specimens included: NME Omo 42 ’72 1, Omo 47 ’70 2008, Omo 72 ’69 470, Omo 75N ’71 C2, Omo 75S ’70 1284, Omo 207 ’73 1762, Omo 243 ’73 4839, L147-25, L173-5, L185-6, L310-1

---

[1] no accession number available.

Range: 3.3 – 2.0 Ma (3.59-1.36 Ma) (Shungura range D – G13 = 2.52-2.0 Ma; also isolated teeth that may represent this taxon from Members A through L and the Usno Fm. See Papionini indet. sp. C below.)

Distribution: Usno Fm., Mbs. D, E, F, G, Shungura Fm, ?Leba

Specific Diagnosis:

A species of *Papio (Dinopithecus)* similar in cranial and dental size to the larger subspecies of *P. (P.) hamadryas*, such as *P. (P.) h. anubis* and *P. (P.) h. ursinus*, but significantly smaller than *P. (D.) ingens*. What is preserved of the cranium, particularly of the females, is generally more gracile than is the case in *P. (D.) ingens*. The maxilla of *P. (D.) quadratirostris* has larger maxillary ridges than are present on *P. (D.) ingens* (at least for the females), although they are still not nearly as well developed as those of extant *P. (P.) hamadryas*. The rostrum is more squared in parasagittal cross-section than is the case in *P. (D.) ingens*. However, it is not known if this distinction is accurate for the males because there are no well-preserved male maxillae of *P. (D.) ingens*.

Description:

Most of this material has not been formally published. As a result, this taxon will be described in more detail than are the others in this section. Eck (1976) described this taxon and Eck (1977) figured the rostrum L185-6 and the mandible Omo 75N ’71 2, and listed *Papio* sp. among the cercopithecid taxa present in the Omo sample. The holotype cranium has not been assigned a formal catalog number, but has been referred to as NME "USNO". The type is a well preserved partial cranium lacking most of the premaxillae and cranial base, but otherwise essentially intact with the left C-M^3 and right M^{2-3}. It has been thoroughly described and figured by several authors (Iwamoto, 1982; Eck and Jablonski, 1984; Delson and Dean, 1993). There is a fairly large sample tentatively assigned to this taxon from the Shungura Formation. Several specimens were figured by Delson and Dean (1993), including L185-6, the female cranium Omo 42 ’72 1, and the female mandible Omo 47 ’70 2008.

L185-6 is a male rostrum with the inferior limit of the orbits, base of the right zygomatic process, and the left M^{1-3} and right C root, P^3-M^3, as well as the alveoli for the incisors. Omo 42 ’72 1 is a reconstructed partial female cranium, preserving most of the rostrum, zygomatic arches, and the left P^3-M^3 and right P^4-M^3. Missing is much of the cranial base, foramen magnum, and most of the cranial vault. The dorsal surface of the rostrum, the interorbital pillar, and zygomatic arches are all somewhat damaged and distorted. Omo 207 ’73 1762 is a more fragmentary reconstructed female cranium. It preserves both maxillae, with left P^4-M^3 and right M^{1-3}, the interorbital region, parts of both zygomatic arches, the temporal bones, and a small bit of the occipital. Omo 243 ’73 4839 is a right maxillary fragment of a juvenile individual preserving the dC through dP^4 and M^1. It preserves a small amount of the palatal and zygomatic processes, as well as a bit of the lateral surface of the rostrum. L147-25 is a small piece of maxillary alveolar bone with the P^4-M^1 and Omo 75S ’70 1284 is a small piece of the left maxilla with M^3. Neither of these preserve any useful maxillary morphology.

P. (D.) quadratirostris is similar in overall cranial size to the largest specimens of modern *Papio hamadryas anubis* and *P. h. ursinus,* and to *Mandrillus,* but smaller than *P. (D.) ingens* from Swartkrans. Sexual dimorphism in cranial size appears to be similar to that seen in modern *Papio*. In molar size, it is similar to the largest modern specimens of *Papio hamadryas ssp.*, *T. brumpti* and *T. o. oswaldi*. Dental dimensions are given in Table 5.2.

Rostrum

Several of these specimens preserve the infraorbital foramina. All of the Shungura specimens preserve two infraorbital foramina where visible. L185-6 on the right, Omo 42 ’72 1 bilaterally, and Omo 207 ’73 1762 on the left. USNO preserves 4 foramina arranged in a diamond pattern. On all specimens they are positioned between 1.5 and 3 cm anterior and slightly inferior to the inferior orbital rim. This position is typical of larger papionins, except for *Theropithecus* where they tend to be placed more inferiorly due to the deeper face and maxillary fossae in *T. gelada* and *T. brumpti*.

All Shungura specimens preserve small, but distinct maxillary ridges. These are lower on the females than on L185-6. USNO on the other hand has rounded, less projecting, but larger maxillary ridges. In lateral view, they slope anteroinferiorly at an angle of approximately 15-20º to the occlusal plane. All of the specimens, other than the juvenile Omo 243 ’73 4839, preserve shallow maxillary fossae, particularly in the area behind the canine. These fossae do not extend posteriorly beyond the M^2. Neither of the females has suborbital fossae. L185-6 does not preserve the zygoma, but there is enough of the right zygomatic process to see that there was no fossa present. In all of these features, the Shungura material is similar to *P. (D.) ingens* from Swartkrans. On the Usno specimen the suborbital area lacks a fossa as well, but the zygomatic arches do jut more sharply laterally than they appear to in the other specimens.

Although the lack of deep maxillary fossae and ridges is similar to *Parapapio* the muzzle dorsum and rostral profile are clearly distinct from that genus. The dorsal surface is reasonably well preserved in USNO, L185-6, and Omo 42 ’72 1. The lateral walls are relatively vertical, and the dorsal surface is transversely flattened in all three. This produces a paracoronal cross-section that is fairly squared in shape, giving the taxon its specific name. In the two Shungura specimens, the nasals also project above the maxillae, producing the concavo-convexo-concave shape described by Eck (1993) for *T. darti*. In lateral view, the rostral profile shows a distinct anteorbital drop in L185-6, Omo 42 ’72 1, Omo 207 ’73 1762, and USNO. It is therefore concave from glabella to just in front of the orbits, where the profile flattens out and eventually near rhinion becomes convex up. Finally, in the area just above the incisor roots, the profile becomes concave again through prosthion. This profile is essentially the same as in *P. (Papio)*, *Mandrillus* and *T. brumpti*.

The sutures of the rostrum are reasonably well preserved in L185-6, Omo 42 '72 1 and partially in Omo 207 '73 1762 and USNO. The premaxillomaxillary suture follows a continuously arching course from the superior limit of the premaxilla to the alveolar process, so that in superior view it forms a nearly straight line. It deviates slightly laterally, however, just below the midpoint of the piriform aperture. It does not enter the piriform aperture at any point. The nasal process of the premaxilla does not extent more than about 1 cm posterior to rhinion in any specimen.

In all specimens, the rostrum is relatively long (see figure 4.5). Only the two females are shown in that plot as the USNO specimen lacks the premaxillae, and L185-6 lacks the neurocranium. When overall size is taken into account, it is in the shorter part of the range for *Papio hamadryas* females. Thus, the rostrum is long, but not as long as expected for a papionin of its size. The rostrum is similar in breadth to that of most other papionins.

The piriform aperture is nearly completely preserved in L185-6 and Omo 42 ’72 1, partially preserved in Omo 207 ’73 1762, and the superior 2/3 is present in USNO. In outline it is similar in shape to *P. hamadryas*. It is roughly oval in outline, but reaches its maximum breadth approximately 2/3 of the way between rhinion and nasospinale, just above the roots of the incisors. Its inferior limit is fairly rounded, and not as “V” shaped as in other taxa. In overall breadth it is similar to *P. hamadryas* and other large papionins.

The maxillary dental arcade is partially preserved in all of the Shungura rostral specimens, but only the left and distal half of the right cheek-tooth rows are preserved on USNO. The dental arcade is essentially “U” shaped in all specimens, but as is normal for most cercopithecines, that of the females is more parabolic. In all specimens the M^2 is the most laterally positioned tooth, and the cheek-tooth rows are slightly curved. This arch is stronger in USNO than in the Shungura specimens. In the males, the buccal surface of the canine projects laterally beyond the premolars, whereas in the females it is more in line with the premolars. The premaxillae extend considerably further anterior to the canine, unlike *Theropithecus* where the premaxillae tend to be shorter. Thus, the incisive alveoli form a projecting arch and the base of the “U” shaped arcade is more curved in *P. (D.) quadratirostris*, and not squared as in *Theropithecus*. The incisive area of the premaxillae is not preserved in USNO, but given the large distal sagittal crest near inion, it may have projected as well.

When viewed laterally, the dental arcade of the Shungura specimens is straight, and shows no evidence of a reverse curve of Spee. That of USNO is also straight, but could be argued to show a very slight reverse curve. The palate is well preserved in L185-6 and USNO, and partially preserved on the left side of Omo 42 ’72 1. In L185-6 and Omo 42 ’72 1 it is relatively broad and shallow, and generally of even depth from anterior to posterior. The alveolar processes form lateral walls that are fairly sloping, and not as steep as are those of *T. oswaldi* or some *T. brumpti*. In the holotype, the palate is somewhat deeper, and the alveolar processes taller, and the palate deepens slightly posteriorly.

Zygomatic arch

The zygomata are preserved, at least partially in both female specimens and USNO. The zygomatic process of the maxilla is partially preserved in L185-6. In all four of these specimens, the zygomatic process of the maxilla arises superior to the mesial to middle part of the M^3. This position is relatively far posterior, but is within the range of variation of most papionin taxa other than *Cercocebus* and *Lophocebus*. The anterior surface of the zygomata in Omo 42 ’73 1 angles posterolaterally, much as in *T. oswaldi* and *Pl. alemui* and is unmarked by suborbital fossae. Omo 207 ’73 1762 and L185-6 only preserve the base of the zygomatic process, but appear as though they would have been similar. Those of USNO are a somewhat different. The zygomatic process of the maxilla angles posteriorly, but then the zygomatic proper protrudes far more laterally than in Omo 42 ’72 1. While the anterior surface of the zygoma of USNO lack infraorbital fossae, the inferior border lies posterior to the zygoma at mid height, in other words, the anterior surface is convex out in the parasagittal plane. The inferior margin of the zygomatic arch in all of the specimens angles laterally on a straight course in all specimens, but more posteriorly in the Shungura material than USNO. The temporal surface is deeply excavated in all individuals in which it is preserved.

In superior view, the zygomatic arches of Omo 42 ’72 1 (and Omo 207 ’73 1762 depending on how they are reconstructed) are no more widely flaring than they are in most specimens of modern *Papio* or *Macaca*. They are more posteriorly angled than those of *P. (Papio)* are, perhaps due to the lack of suborbital fossae in the Shungura material. The bizygomatic breadth is greatest posteriorly, close to the base of the zygomatic process of the temporal. In the USNO specimen the zygomata jut laterally away from the maxilla, then curve at a near right angle posteriorly. As a result, the bizygomatic is greatest anteriorly, near to where the frontal process meets the zygomatic arch proper. In all specimens, the masseter scar terminates anteriorly near the zygomaticomaxillary suture. In the USNO specimen, the masseter scar is substantially larger then it is in the Shungura females. Unfortunately, this cannot be compared with L185-6.

Orbital region

Only the inferior portions of the orbits and interorbital pillar are preserved on L185-6. The orbits are reasonably well preserved on Omo 42 ’72 1, but damaged. Omo 207 ’73 1762 only preserves the frontal portion of the orbits, as well as a small bit of the interorbital pillar and frontal process of the right zygomatic bone. USNO preserves the entire left orbit and medial 2/3 of the right orbit. The supraorbital torus is similar in both of the Shungura females and USNO. It is prominent, and similar in superoinferior thickness to *Papio* and *Theropithecus*. The tori form individual arcs over each orbit, but not to the extent seen in *T. brumpti* or some *T. oswaldi* (e.g. KL157-1 described in the Afar section). Thus, it reaches its greatest height approximately over the midpoints of each orbit, and is slightly lower in the sagittal plane. The supraorbital notches are well marked in all specimens.

As is typical of most papionins, the interorbital region is narrow. Glabella is prominent, but not to the extent seen in *T. gelada*. The orbits of Omo 42 ’72 1 are taller than they are broad, and fairly oval in outline, being slightly wider superiorly. In USNO the orbit is slightly broader than high, but also broader superiorly. The lacrimomaxillary suture lies on the anterior rim of the lacrimal fossa in L185-6 and USNO, In Omo 207 ’73 1762 it is slightly rostral to the lacrimal fossa. This area is damaged in Omo 42 ’72 1. The lateral orbital margin is not well preserved in the Shungura material. In the Usno specimen, the frontal process of the zygomatic broadens inferiorly, producing the visor morphology described by Delson and Dean (1993).

Calvaria

Omo 207 ’73 1762 preserves the frontal near the orbits, and small portions of the temporal and occipital squamae, and the nuchal crest. Omo 42 ’72 1 preserves these areas, as well as a few isolated parietal fragments. The frontal of both specimens clearly shows a deep ophryonic groove. Posterior to this, the frontal would have risen so that bregma would lie superior to the supraorbital rim in Frankfurt orientation. It is unclear how strongly the temporal lines were developed, but both females clearly preserve sagittal crests near inion, which is a relatively rare feature among extant *P. hamadryas sspp*. females. The nuchal crest is tall and well developed in both specimens and forms a compound crest at inion where it meets the sagittal crest. The calvaria is well preserved in USNO. In this specimen the vault is fairly low and ovoid, being widest at the level of the external auditory meatus. In lateral view, a deep ophryonic groove is present, posterior to which, the frontal rises above the level of the supraorbital torus. The temporal lines are strongly developed, and meet at approximately bregma. Posterior to this is a low sagittal crest, that meets the nuchal crest at inion. Postorbital constriction is strong. This in combination with flaring zygomatic arches produces a large infratemporal fossa. In posterior view, the vault is broad and low, being widest at its base. This is similar to *Theropithecus*, but unlike most *Macaca* and *Papio.*

Basicranium

The basicranium is poorly preserved on Omo 42 ’72 1 and only the mastoid and glenoid regions are present on Omo 207 ’73 1762 and USNO. The mastoid processes are pyramidal in all specimens, and relatively tall, particularly on USNO. The postglenoid processes are fairly broad and flat in all specimens, and separated from the glenoid fossae by narrow sulci. The glenoid fossa is fairly sellar on the Shungura specimens, being convex down in the parasagittal plane and concave in the coronal. In the Usno specimen, they are flatter and longer in the anteroposterior direction (See Jablonski, 1993 for a more thorough discussion of glenoid fossa morphology).

Facial hafting

The relationship of the face and neurocranium of USNO has been thoroughly discussed by Eck and Jablonski (1987) and by Delson and Dean (1993). As these latter authors point out, the cranium is neither strongly klynorhynch as in *P. (Papio)* nor strongly airorhynch as in *T. gelada*, but may approximate the primitive condition for the subtribe, and is actually quite close to that of *Mandrillus* (Delson and Dean, 1993). In both of the Shungura females, this relationship is difficult to assess. This is because both specimens only poorly preserve the neurocranium, and in both there are few direct contacts between these two. However, they may be less klynorhynch than *P. hamadryas*, given the more prominent frontal, deeper ophryonic groove, and possibly higher bregma. Neither USNO nor these specimens shows the increase in midfacial height of *Theropithecus*.

Mandible

The mandible is represented by several specimens from the Shungura Formation. Omo 75N ’71 C2 is a nearly complete, large corpus with left C-M_3 and right I_2 fragment, and P_3-M_3 of a male individual. L310-1 is a left corpus fragment with part of the symphysis and damaged P_3-M_2. The buccal surface of the corpus is heavily damaged under the P_3 and in the area of the incisive alveoli, but the inferior margin is present for the entire length of the specimen. Omo 72 ’69 470 is a symphysis and nearly complete left corpus with M_3, but the alveoli for the right C through left M_2 are present, as are the roots for all of these other than the incisors. Omo 47 ’70 2008 is a nearly complete mandible of a female lacking only the left ramus and right coronoid, condyle and distal margin of the right ramus. The dentition is complete except for the lateral incisors and the left canine. L173-5 is a right corpus fragment of unknown sex preserving only the M_3 and the area under it to the inferior margin. Omo P707 ’70 2494 is a right corpus fragment of a subadult individual, with P_4-M_1, the roots of M_2 and the M_3 crown preserved in its crypt.

The symphysis is relatively deep and steeply sloping in profile, although there is some variability seen, with Omo 72 ’69 470 sloping more than the others. The symphysis is pierced by a median mental foramen, or two in Omo 72 ’69 470 and Omo 47 ’70 2008. The mental ridges are clearly present, but never strongly developed or rugose. They are weakest in the female. Both transverse tori are well developed. The superior extends posteriorly to the level of the distal P_3, and the inferior back to P_4 or mesial M_1.

The lateral surface of the corpus is only marked by very shallow fossae, even in the male specimens. In profile view, the corpus is deepest inferior to M_1, and is therefore generally anteriorly divergent, or approximately even in depth from anterior to posterior. The oblique line is poorly defined, and extends anteriorly to the distal part of M_3 and an extramolar sulcus is typically absent. There is a slight retromolar gap in most specimens. The ramus is only partially preserved. The best specimen is Omo 47 ’70 2008. The anterior margin is angled inferiorly. The lateral surface is not marked by strong masseteric muscle scar. There was probably a shallow triangular fossa.

Dentition

In addition to the specimens described above, L9-99 preserves an associated partial dentition, in a series of small fragments of alveolar bone. It includes the left and right dc through M^1, and the tips of the left and right I^1, and right I^2. The left lower dc is also preserved.

The lower central incisors of Omo 47 ’70 2008 are well preserved and not very worn. They lack lingual enamel as is expected for the subfamily, and are relatively tall and narrow. In labial view, their crowns are not strongly flaring, but relatively straight sided. They are also fairly large teeth, although they may not be quite as broad as those of *P. hamadryas*. They show none of the reduction seen in *Theropithecus*. The lower lateral incisor is only known by the broken crown preserved in Omo 75N ’71 C2. Little of the morphology can be seen, other than it was a relatively large tooth, and lacked lingual enamel. The alveoli of the mandible Omo 72 ’69 470 have large incisive alveoli with those of the central incisors being substantially larger than those of the laterals. Only the tips of the upper incisors are known from L9-99. They appear to be from fairly large spatulate teeth. The I^2 has a more asymmetrical crown than the I^1. The upper incisive alveoli of L185-6, Omo 42 ’72 1, and Omo 207 ’73 1762 are large, and presumably would have supported large incisors. The canines are typical of cercopithecids, being highly sexually dimorphic, and otherwise unremarkable in their morphology.

The upper premolars are typical bicuspid teeth. The P^4 is noticeably larger than the P^3. Its crown is also more quadrate with a larger distal fovea, although distal cuspules are absent. The P^4 is a large tooth, particularly relative to the size of the molars. In this feature it approaches the proportion seen in *Mandrillus*, *Cercocebus, Allenopithecus* and some *Macaca* (see figure 4.6). In this feature, USNO differs from the Shungura specimens. The upper premolars of USNO are relatively small, particularly the P^3.

The P_3 is highly sexually dimorphic as is typical of the family. While the P_3 mesiobuccal flange of the males is significantly longer than that of the females, it is short in comparison to other male papionins. In fact, the length of the mesiobuccal flange is similar to that seen in *T. oswaldi* and *Paradolichopithecus arvernensis*. This is intriguing, as the canines of the males do not appear reduced. The P_3 is otherwise typical with a high and prominent protoconid, and small talonid. The P_4 is more molariform, as is normal. It is not unusually large relative to the lower molars.

The molars are similar to those of most papionins. They do not show the highly derived morphology of *Theropithecus*. The cusps are low and rounded, and the crowns are moderately flaring, similar to those of *P. hamadryas*. They are less flaring than those of *Allenopithecus*, *Mandrillus, Lophocebus,* and *Cercocebus*. The buccal cusps of the lower molars often appear somewhat columnar as do those of *Theropithecus,* but they are never has high, and the buccal clefts are not flattened. The upper molars of USNO are quite worn, but the M^3's show a wear pattern that is similar to some primitive *Theropithecus*, such as that from Hadar. The lingual cleft of the left M^3 may also be somewhat flattened. However, some individuals of *Papio,* when worn to this level have the same appearance. Thus the molars of USNO could be argued to show some affinity to those of *Theropithecus*, but the derived features of this genus are not fully present.

The upper dC is similar to those of other cercopithecids, with a crown that is triangular in labial view, and labiolingually compressed. The lower dc also has a prominent central cusp, but develops a small distal cuspule as well. The dP^3 crown was relatively long and narrow, and the mesial fovea was long and triangular, possessing a well-developed cuspule on the mesial fovea anterior to the protocone. The mesial lophid was very narrow, the crown was flaring, the cusps lower, and the enamel thin. The dp^4 is less worn. It is more similar to the adult molars in proportion, but is still relatively narrower and more flaring, with lower cusps.

Remarks:

There has been a considerable amount of debate about the generic status of the holotype cranium. Iwamoto (1982) originally described the specimen as *Papio quadratirostris*. Eck and Jablonski (1984; 1987) reassigned it to *Theropithecus* as an early member of the *T. brumpti* lineage. Delson and Dean (1993) have reviewed this debate. It is included with the Shungura material for the reasons given by these authors.

Most of the sample derives from Shungura Formation Members D through lower G, dated from 2.52 to 2.0 Ma. The Shungura sample is therefore between 0.9 and 1.4 myr younger than the holotype cranium, which is from the Usno Formation and dates to approximately 3.4 Ma. However, this only covers the relatively complete material. There are approximately 160 additional isolated teeth of a large, non-*Theropithecus* papionin spanning a range from Members A through L, as well as from the Usno Formation (see Papionini gen. et sp. indet. C below). Many of these most likely represent *P. (D.) quadratirostris*. However, given the homogeneity of papionin teeth, those from members outside the D through lower G range may represent other taxa such as modern *P. (Papio)* in the uppermost levels or large *Parapapio* (e.g. *Pp. whitei*) in the lowermost levels, and therefore have not been included here.

There are several differences between USNO and the main Shungura sample. Among these are: the size of the premolars, the prominence of the nasals above the dorsal surface of the maxillae, the shape of the anterior surface of the zygomatic process, the thickness of the zygomatic arch, and possibly the molar morphology. Whether these differences are the result of evolution within a single lineage over the approximately 1 myr between the two samples, or whether they indicate the presence of two species is unclear. If Eck and Jablonski (1984; 1987) are correct (or if USNO is specifically distinct, but not early *T. brumpti*) then the Shungura sample would require a new name.

There are also fossils of large papionins from the Koobi Fora Formation, described below under Papionini gen. et sp. indet. C. All of these are from the upper Burgi and Okote Members and are therefore younger than the Omo material. The mandibles from Koobi Fora are essentially similar to those from the Shungura Formation. The maxillae, however, are different as they possess distinct facial fossae. Dentally, the Koobi Fora material is indistinguishable from the Shungura sample. Thus the question is whether the fossae indicate a more derived lineage such as a species of *P. (Papio)* or merely individual and/or temporal variation. Given that the female ER 144 has a deeper fossa than the male L185-6, sexual dimorphism is unlikely to explain this maxillary difference. Before assigning this otherwise similar material to a separate species, it seems prudent to await more complete facial and postcranial material.

Papionini gen. et sp. indet. Size A

Turkana specimens included: KNM-WT 16752; ER 3027; ER 3122; 34 isolated teeth from the Usno and Shungura Formations.

Description:

Papionins other than *Theropithecus* are quite rare in the Turkana basin, and small papionins comparatively rare among those. WT 16752 is well-preserved mandibular corpus of a small male papionin from the Lower Lomekwi Member of the Nachukui Formation. It is similar in dental size to *Pliopapio alemui* and to *Parapapio ado* from Kanapoi, but slightly smaller than *Pp. ado* from Laetoli. This mandible was classified as cf. *Pp. ado* by Harris et al. (1988), but it lacks several of the diagnostic features of this species, and is currently impossible to allocate to genus with any reliability. It preserves the right I_1-M_2, except that the crown of the canine is damaged, and the left P_4-M_3. The left corpus is relatively complete except for the alveolar area near the incisors and canine. The right corpus is more complete anteriorly, but lacks the inferior margin posterior to the P_3.

Harris et al. (1988) have already described this specimen. Therefore, this description will focus only on those features that make this specimen likely to represent a taxon other than *Pp. ado*. The symphysis is fairly short and rounded in profile, with an essentially continuous convex down shape. The incisive area is damaged, but appears to be relatively vertically oriented, and definitely not anteriorly projecting as it is in *Pp. ado*. The incisors are positioned in a typical papionin fashion, being arranged along with the canines in a simple transverse arc. This is quite different from *Pp. ado* where the roots of the incisors are positioned more anteriorly relative to the canine. Mental ridges are present but faint, and weakly developed. The corpus has shallow fossae inferior to the M_1. In lateral view, it is roughly even in depth from P_3-M_3, but its inferior margin is slightly convex down so that it is deepest under the M_1. The dentition is similar to that of other non-*Theropithecus* papionins, except that the molars are less flaring than those of

Cercocebus, *Mandrillus*, *Lophocebus*, and the *Pp. ado* from Kanapoi. Overall, this specimen is most similar to *Pliopapio alemui*, but differs in some details, such as the presence of shallow corpus fossae. Thus, without more complete material, it is best not to assign this specimen as to genus.

From Koobi Fora, there are two fossils of papionins of similar size. These are KNM-ER 3122 and 3027, both of which are from the Tulu Bor Member. They are both small fragments of mandibular corpus with $M_{2\text{-}3}$ and M_1 respectively. They are generally similar in molar size and morphology to KNM-WT 16752, *Pp. ado*, *Pliopapio alemui,* as well as the *Lophocebus* specimens from the KBS and Okote Members. They do not preserve enough morphology to diagnose beyond that they represent a small papionin. There is also a large sample of isolated teeth in this size category from the Usno Formation and the Shungura Formation Members B, C, E, J, L. Some of these, especially those from Members J-L may represent the same species of *Lophocebus* as Omo K6 ’70 C146 and the Ileret material, whereas those from other parts of the section may represent *Parapapio* or other taxa.

Papionini gen. et sp. indet. Size B

(= or including Papionini (B) Eck, 1976: Eck, 1976; 1977, in part; Leakey, 1976, in part)

Turkana specimens included: KNM-ER 145, ER 174, ER 1551, ER 3849; ER 3850; ER 3878; ER 4414; ER 6064; ER 6073; 54 isolated teeth from the Shungura and Usno Formations.

Description:

The material from Koobi Fora derives from the upper Burgi, KBS, and Okote Members, and consists of several maxillae and mandibles. In addition there is an isolated M_3 from the Lokochot Member. The Omo sample is from Members A3 through L2 in the Shungura Formation and the Usno Formation. It consists entirely of isolated teeth. The sample of dental material in this size range from the Omo may be a combination of small individuals of papionin C and large individuals of papionin A. Specimens from the upper Burgi Member at Koobi Fora, however, confirm the presence of an intermediate sized taxon. A mandible from the Upper Burgi Member (ER 6064), which is clearly that of a female, is substantially smaller than the female mandible ER 141, ruling out sexual dimorphism as the cause of the size difference between papionin B and C.

The maxilla of the Koobi Fora taxon is not completely preserved, but it clearly possesses a well-developed maxillary fossa, which makes it unlikely that this taxon is *Parapapio*. The mandible on the other hand, lacks any development of corpus fossae, a feature that is different from the mandible of *Papio* sp. A in the Afar depression. It has a relatively steeply sloping symphysis, and weakly developed mental ridges. The ramus is relatively tall and vertically oriented. The corpus is relatively even in depth. Thus the mandible makes it unlikely that this material represents a species of *P. (Papio)*. Of course it is possible that two taxa have been sampled, but there is no direct evidence for this.

Papionini gen. et sp. indet. Size C

(= or including *Papio sp.* Leakey and Leakey, 1976; *Parapapio whitei* Broom, 1940: Harris et al., 1988, in part)

Turkana specimens included: 164 isolated teeth from the Shungura and Usno Formations, see Harris et al. (1988) for Nachukui material, and Leakey and Leakey (1976) for the Koobi Fora specimens.

Description:

Two specimens from West Turkana, several from Koobi Fora, and a large collection of isolated teeth from the Shungura and Usno Formations are included here. The West Turkana specimens were described by Harris et al. (1988) as *Parapapio whitei*. WT 16751 is a left mandible fragment with the distal M_1, and $M_{2\text{-}3}$ it is from the lower part of the Lomekwi Member, and therefore dates to between 3.24 and 3.4 Ma. It preserves the corpus to its inferior margin. The molars are similar in size, or slightly smaller than those of *P. (D.) quadratirostris*. The corpus is shallower than that of *P. (D.) quadratirostris,* although this may be partly due to distortion near the inferior margin. The lateral surface of the corpus shows no hint of a fossa. Thus, this specimen is possibly a small female of *P. (D.) quadratirostris,* but given its temporal and geographic distance from the Shungura material, and the morphological homogeneity of papionin molars, it is not possible to be certain of this. As a result, this specimen is left as an indeterminate large papionin. The other West Turkana specimen, WT 16869, is an isolated left M_3 from the upper part of the Lomekwi Member and dates to between 2.52 and 2.6 Ma.

The Koobi Fora material has been described by Leakey and Leakey (1976) as *Papio* sp. nov. The majority of this material derives from the upper Burgi Member, with a single specimen from the Okote Member. This material is similar in size to *P. (D.) quadratirostris* from the Shungura Formation, but differs morphologically in that it clearly possesses a maxillary fossa that is more deeply excavated and extensive. It is otherwise similar in the preserved details. The mandible is very similar to the Shungura material and seems to lack a lateral corpus fossa. It is entirely possible that this material is the same species present in the Omo, but without more complete facial material it is impossible to be certain (see *P. (D.) quadratirostris* remarks above for further discussion).

The sample of isolated teeth from the Omo spans the sequence from Members A3 through L1 of the Shungura Formation and the Usno Formation. This represents a time span of over 2 Myr. Much of this material is probably *P. (D.) quadratirostris*, particularly the sample from Members D through G, where the more complete material *P. (D.) quadratirostris* was recovered. Whether this sample represents a single lineage throughout this span is impossible to determine given the morphological similarity of papionin molars. The range of variability in this sample is similar to that shown by extant species of large papionins, but this is probably due to the fact that this sample was originally distinguished based on size.

Genus *Theropithecus* Geoffroy, 1843

Type species *Theropithecus gelada* Rüppell, 1835

Other included species: *T. oswaldi* Andrews, 1916, *T. brumpti* Arambourg, 1947

Generic Diagnosis: See Afar section.

Theropithecus (Theropithecus) Geoffroy, 1843

Type species *Theropithecus gelada* Rüppell, 1835

Other included species: *T. oswaldi* Andrews, 1916

Subgeneric diagnosis: See Afar description

Theropithecus oswaldi (Andrews, 1916)

Holotype: BMNH-M11539 (syntype) from Kanjera, Kenya

Turkana specimens included: see subspecific descriptions below.

Range: 3.4+ – 0.25 Ma.

Turkana Range: 3.4+ - 1.0 Ma.

Distribution: see subspecific descriptions below, plus ?Mirzapur, India; ?Cueva Victoria, Spain.

Specific diagnosis: See Afar description.

Theropithecus oswaldi darti (Broom and Jensen, 1946)

Holotype: UWMA MP1(M201, 1326/1)

Turkana specimens included: KNM-ER ER 1562, ER 3025, ER 3030, ER 3038, NME Omo 18 ’68 373.

Range: 3.4 – 2.7 Ma

Distribution: Hadar Fm. Sidi Hakoma - Kada Hadar Lower; Ahmado, Leadu; Maka; Bunketo; Matabaietu; Wee-ee; ?Shungura Fm., C-6; ?Koobi Fora Fm. Lokochot, Tulu Bor Mbs.; ?Kanam East; Makapansgat.

Subspecific diagnosis: See Afar section.

Description:

The general morphology of *T. o. darti* has been discussed in the Afar section, and will not be repeated here, except as is necessary for some of the individual specimens discussed below. This taxon is only tentatively identified in the Turkana basin. It is known by a single mandible from the Shungura Formation, Omo 18 ’68 373, which was described by Eck (1987a). There are also three specimens from the Koobi Fora Formation tentatively assigned to this taxon as well. One of these was identified by Leakey (Delson et al., 1993) as *T. oswaldi*, without specifying which subspecies, but presumably it was *T. o. darti*, given her discussion (Leakey, 1993) and the small size of this specimen. The others were identified as *T. brumpti cf. baringensis*. Specimens assigned to *T. o. darti* are discussed individually below.

Maxillae

ER 1566 is a left maxilla with worn and damaged P^4-M^3, and the cervix and root of the canine. It is from an older male individual, and was assigned to *T. brumpti* by Delson et al. (1993). This specimen, however, shows several features that are more compatible with *T. o. darti*. Given that this represents an adult male, the maxillary ridges and fossae are weakly developed, and there would not likely have been suborbital fossae. In all of these features, this specimen is very similar to the male cranium AL205-1a from Hadar and the females from Makapansgat (UWMA MP 217, 222 and BPI 3073). They are more strongly developed than those of AL134-5a or AL321-12. The zygomatic process of the maxilla is positioned above the M2/M3 contact. This is relatively far anterior in comparison to BC 3 and adult male of *T. brumpti* (where it tends to be above the M_3). In conjunction with this, the rostrum would have been comparatively short, and the dorsal surface slopes more steeply relative to the occlusal plane than it does in BC 3 or *T. brumpti*.

ER 3025 is a series of cranial fragments of a male individual, and was briefly discussed by Leakey (1993). The surface is heavily cracked, filled with matrix, and partially crushed. The maxilla lacks fossae or ridges, so that the muzzle dorsum is sellar. The nasomaxillary suture is straight and does not flare laterally at its distal end. The zygomatic arch curves smoothly posteriorly and is “inflated” in appearance as in *T. oswaldi*. This specimen could be primitive *T. brumpti* or *?T. baringensis*, but is more consistent with *T. o. darti*.

Mandibles

Eck (1987) identified Omo 18 ’68 373 as a member of the *T. oswaldi* lineage, possibly *T. darti* based on the absence of a corpus fossa. He had concerns about the large dental size of the specimen in comparison to later *T. oswaldi* from the Shungura Formation. When the size of this specimen is examined relative to the larger African record for *T. oswaldi* it is clearly in line with that expected for *T. o. darti*, although it is at the largest end of the variation (see figure 4.10).

ER 1562 is a small mandible of a male individual from the Tulu Bor Member. It is broken into right and left fragments, and the surface is highly cracked and distorted.

The corpus completely lacks fossae, and shallows slightly posteriorly, and what is preserved of the ramus is relatively vertical. These features identify this specimen as a part of the *T. oswaldi* lineage, if it is indeed *Theropithecus*. The dentition is ambiguous in its morphology between *Theropithecus* and other papionins, with the buccal cleft not being as flattened and the buccal cusps not as columnar as those of well developed molars of the genus. On the other hand, the lingual notches are flattened and the cusps show a large amount of relief. Also the lingual basins are quite deep and the buccal margin forms a clear mesiodistally oriented lophid. The most troubling feature is the very small size of the dentition. It has the smallest known M_3 of any fossil *Theropithecus*, although it is only slightly below the range from Ahmado and Hadar. The small size is even more striking given that it is a male. In fact, in its dental size it is similar to *Parapapio* from Hadar. Delson (1984) assigned this specimen to that genus, referring it to the Hadar taxon. It is here retained as *Theropithecus*, because of the dental features described above, other than the features of the buccal cusps.

ER 3030 is a symphyseal fragment of male mandible from below the Lokochot Member. It is identified by Leakey (1993) as *T. brumpti* cf. *baringensis* and catalogued by Delson et al. (1993) as *T. brumpti*. The alveoli for the canines and incisors are preserved, as are the damaged left and right P_3’s. They clearly identify this specimen as an adult male. The symphysis is long and sloping, and is not deep or squared as KNM-BC 3 or *T. brumpti*. Mental ridges are clearly present but not strongly marked or rugose. Distinct, but shallow corpus fossae are present. The alveolar area for the incisors is small compared with that of BC3 and *T. brumpti*. Lastly, the mesiobuccal honing flanges of the P_3s are short in comparison to those of BC 3 and *T. brumpti*. In overall morphology it is most similar to the male AL205-1c and females AL183-6 and 196-3a from Hadar. It is, however, quite distinct from KNM-BC 3, and from other mandibles of *T. brumpti* from Koobi Fora such as ER 2015. As none of the molars are preserved, it is possible that this specimen does not represent *Theropithecus*, but given the short P_3 flange and small incisive area this is unlikely.

ER 3038 is a nearly complete, but broken and distorted mandibular corpus, figured in Leakey (1993). It preserves the roots of right I_{1-2}, most of the right P_3, and the left and right P_4-$M_{3.}$ It is most damaged in the area near the symphysis and both corpora are somewhat mediolaterally crushed. The symphysis appears to be more “squared” in profile, and less sloping than most *T. darti* from Hadar, and UWMA M633 from Makapansgat, but is similar to BPI M3073 in this regard. The symphysis has, however, a more sloping, curved, and rounded profile than KNM-BC 3 and most of the *T. brumpti* material from Koobi Fora or Omo. The lateral surfaces of both corpora have fossae, but these are relatively shallow, being substantially shallower than both BC 3 and BC 1647a. This may be due to the crushing of the corpus, but this seems unlikely, given its similarity of depth bilaterally. In lateral view, the corpus deepens slightly posteriorly (approximately 31 mm under the P_4 and 33 mm under the M_3). This is a morphology that occurs with some frequency among *T. o. darti* mandibles from Hadar, but rarely, if at all, in specimens of *T. brumpti* or *?T. baringensis*.

The dentition of ER 3038 is ambiguous in its morphology. The molars show some of the derived features of *Theropithecus*, but they are not strongly developed. In this respect they are similar to some specimens from Hadar (e.g. AL135-4a and AL129-8), but given its Early Pliocene age this might be expected of any population. The molars are small, being similar in size to that of BC 3 and BC 1647. They are in the lower middle of the *T. darti* range, and just slightly smaller than all known *T. brumpti*. In summary, this specimen is an early representative of *Theropithecus*, and its morphology is most similar to that of *T. o. darti*, but the possibility of it representing *?T. baringensis* cannot be ruled out.

Theropithecus oswaldi oswaldi (Andrews, 1916)

Lectotype: BM(NH) M11539 (syntype) from Kanjera, Kenya

Turkana specimens included: see Delson et al., 1993.

Range: 2.52 – 1.39 Ma

Turkana range: 2.4 – 1.39 Ma

Distribution: Ain Jourdel, Ahl al Oughlam, Hadar Fm., Upper Kada Hadar Mbr.; ?Geraru; Gamedah, Wilti Dora, Matabaietu, Halsaiya; Bouri Fm., Hatayae Mbr.; Konso (lower); Shungura Fm. Mbs. E3 – G14 (H3 – K); Fejej; Nachukui Fm., Kalochoro – Nariokotome Mbs.; Koobi Fora Fm. Upper Burgi – Okote Mbs.; Kanjera; Marsabit; Kaiso, Peninj; Olduvai Bed I, Lower II; ?Chiwondo Beds; Swartkrans Mbs. 1-3 (and hanging remnant); Gladysvale.

Subspecific diagnosis: See Afar section.

Description:

Eck (1987a) has described in detail the cranial material of *T. o. oswaldi* from the Shungura Fm. Harris et al. (1988) have described the comparatively fragmentary material from the Nachukui Formation, and Leakey (1993) has described the Koobi Fora material.

The sample from the Turkana basin, and Koobi Fora in particular, is the largest and most complete known for *T. oswaldi*, with several relatively complete crania and partial skeletons. The morphology of *T. o. oswaldi* preserved at Koobi Fora is very similar to that known at other sites, including the Afar section, and therefore will not be repeated here.

Many authors have observed in the past that there is a trend towards increasing molar size in *T. oswaldi* (e.g. Jolly, 1972; Delson, 1983; Eck, 1987a; Leakey, 1993). As shown by Leakey (1993) the sample from the Turkana basin shows this trend as well, with specimens from Members E and F of the Shungura Formation being the smallest on average, followed by Member G, then upper Burgi Member of the Koobi Fora Fm., KBS larger, and Okote the largest. It is also apparent from inspection of figure 4.10 that for its age, the sample from the Turkana basin is in the smaller part of the observed range for *T. o. oswaldi* from across Africa. In fact, teeth from the Turkana basin are similar in size to those the ca. 2.5 Ma Matabaietu Formation in the Middle Awash. Interestingly, the crania from Koobi Fora, particularly the upper Burgi Member, are relatively large for their age, however this may be due to the relatively small sample of cranial specimens that are complete enough to measure outside of the Turkana basin.

Theropithecus oswaldi leakeyi (Hopwood, 1934)

Holotype: BM(NH) M14680 from Olduvai Bed IV, Tanzania

Turkana specimens included: NME F413-1, P1001-1, Omo K7 '70 C148, Omo K7 '70 C149, OmoK7 ’71 727, ?KNM-WT 14660, ?WT 17403

Range: 1.65 – 0.25 Ma

Turkana range: 1.36 – 1.0 Ma

Distribution: Ternifine; Thomas Quarries; Asbole, Andalee, Bodo, Dawaitoli, Hargufia; Konso (upper); Shungura Fm., Mbr. L; Nachukui Fm., Nariokotome Mbr. Olorgesailie; Kapthurin; Olduvai Beds Upper II – IV, Masek; Nyeri; Hopefield; Gladysvale.

Subspecific diagnosis: See Afar section.

Description:

The sample of this subspecies from the Turkana Basin is small and fragmentary. It does little more than document the presence of the taxon in the basin. The isolated teeth are typical of the genus in morphology, but show more developed enamel complexity, with the increased folding and “vertical ridges” of later *Theropithecus*. The only M_3, Omo K7 ’70 C148, in particular is large with deeply excavated and flattened notches. The other molars are smaller, but still within their expected range given their age.

Theropithecus (Omopithecus) Delson, 1993

(= or including *Dinopithecus* Broom, 1937: Arambourg, 1947, in part. *Simopithecus* Andrews, 1916: Freedman, 1957, in part. New and unnamed subgenus: Szalay and Delson, 1979).

Type species: *Theropithecus brumpti* Arambourg, 1947

Other included species: ?*Theropithecus baringensis* Leakey, 1969

Subgeneric Diagnosis:

This diagnosis largely follows that of Delson (1993) and the description for *T. brumpti* from Eck and Jablonski (1987) and Leakey (1993). The rostrum is more like that of *Papio* than *T. (Theropithecus)* in several features. The dorsal surface is flattened, and the nasals are not prominent above its surface, yielding a paracoronal cross-section that is approximately trapezoidal, except for the lateral projections of the maxillary ridges. Distinct maxillary ridges and fossae are present, particularly in the males. The nasal aperture is convex in lateral view. The zygomatic bone is broad with a large anteroinferior expansion. The zygomatic arch proper is deep and triangular in cross-section, and typically the inferior surface is curved forward at the anterior part of the arch, into the "handle-bar" shape. The mandibular symphysis is deep and vertical in profile, and often "squared" in appearance. The mental ridges are well developed and sinusoidal. The lateral surface of the corpus has a deep and extensive fossa. On the proximal humerus, the greater tuberosity is typically lower than the humeral head.

Theropithecus brumpti (Arambourg, 1947)

(= or including *Dinopithecus brumpti* Arambourg, 1947, in part. *Simopithecus* Andrews, 1916: Freedman, 1957, in part. *Theropithecus*: Jolly, 1972, in part).

Holotype: MNHN OMO 001 from the Shungura Formation, (probably Member G), Ethiopia.

Turkana specimens included: see Delson et al., 1993 (except for specimens transferred here to *T. o. darti*).

Range: 3.4+ – 2.0 Ma

Distribution: Shungura Fm Mbs. B10-G13, ?Mbr. A, ?Usno Fm.; Koobi Fora Fm., Lokochot, Tulu Bor Mbs.; Nachukui Fm. Lomekwi, ?Lonyumun Mbs.

Specific diagnosis: As for subgenus.

Description:

The Turkana basin is the only region where fossils unambiguously allocated to this species have been recovered. The extensive collections from the Shungura Formation have been thoroughly described by Eck and Jablonski (1987). That from the Nachukui Formation has been described by Harris et al. (1988). These two collections, along with that from Koobi Fora, have been discussed by Leakey (1993). The small sample of *Theropithecus* from the Lonyumun level at Lothagam has also been assigned to this species by Leakey et al. (in press), but it consists largely of isolated teeth, and therefore must be considered tentative. Krentz (1992; 1993) has described the long bones of *T. brumpti*. Given that these samples are well described, it would be redundant to do so here. This description will briefly summarize the most important morphological aspects of the species

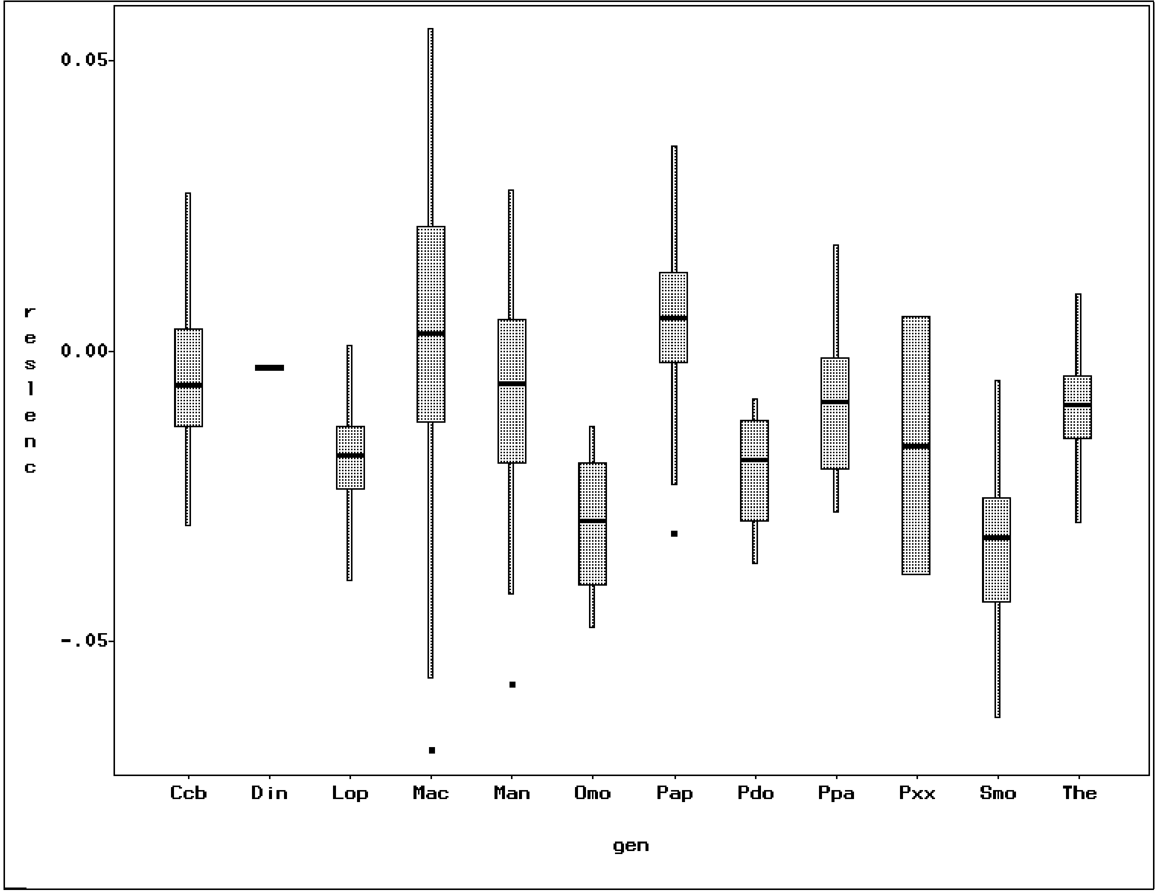
Cranium and mandible

The cranium of *T. brumpti* is marked by a large number of unique, and almost certainly derived, features. Most of these are mentioned in the diagnosis above, and are also discussed in more detail by Eck and Jablonski (1987) and Leakey (1993). The most striking feature of the cranium is clearly the large and anteriorly curved zygomatic arches. The functional significance of these appears to be related to providing mechanical advantage to the masseter during oblique chewing motions of the mandible (Delson and Dean, 1993; Jablonski, 1993) on a face with an absolutely long rostrum. The enlarged zygoma also provides a large site for attachment of the masseter, and resists the stresses generated by this enlarged muscle. This unique zygomatic morphology is present in both sexes and in juveniles as well.

The rostrum is also distinctive. It has extensive postcanine and suborbital fossae, and long well marked maxillary ridges. The dorsal surface of the rostrum is flattened, and the maxillae often meet one another in the midline, thereby covering the nasals at the proximal end of the rostrum. This feature also occurs in some individuals of *P. h. anubis*.

The rostrum of *T. brumpti* is clearly absolutely long. It is also long relative to the length of the neurocranium (see figure 4.5), being relatively longer than that of both *T. gelada* and *T. oswaldi*, but still relatively shorter than that of *Papio* and *Mandrillus*. However, as has been pointed out by many authors (for a review see Ravosa and Profant, 2000) the rostrum has a positively allometric scaling relationship with the neurocranium in cercopithecines. When rostral length is regressed on cranial size, *T. brumpti* has a rostrum that is actually relatively shorter than that of *T. gelada*. In other words, *T. brumpti* actually has a relatively short rostrum for a papionin of its size (see figure 5.1), and is actually more similar to other species of *Theropithecus* than to *Papio*. As discussed by Delson and Dean (1993), the cranium is not as airorhynch as that of *T. gelada* and *T. oswaldi* nor is it as klynorhynch as that of *Papio*.

Figure 5.1 Residual length of glabella to rhinion after regression against centroid size. Labels as for figure 4.3.



Dentition

The dentition of *T. brumpti* is the most important evidence for placing this species as a member of the genus *Theropithecus*. It does differ in a few aspects from that of other *Theropithecus*, particularly *T. oswaldi.* The incisors of *T. brumpti* are not well known, but the available evidence suggests that they are not as reduced as those of *T. oswaldi,* but similar to those of *T. gelada* in relative size (Eck and Jablonski, 1987). The male canines are large and similar in size, relative to the molars, to those of *Papio* (Eck and Jablonski, 1987). Related to this, the P_3 mesiobuccal flange is long. Relative to the size of the M_3

the mesiobuccal flange is longer than that of *T. oswaldi*, including *T. o. darti* (see figure 5.2).

The molars and premolars show all of the specializations that characterize the genus. The crowns are high, the cusps are columnar, and when worn produce complex enamel folds on the occlusal surface. Similar to *T. oswaldi*, there is a trend towards larger molar size observable in *T. brumpti* (see figure 5.3), although given the smaller sample sizes and more restricted temporal range, this can be determined with less certainty.

Figure 5.2 P_3 mesiobuccal flange length / M3 anterior width. Man = *Mandrillus*; Pap = *Papio (Papio)*; Pdo = *Paradolichopithecus*; Tbg = *?T. baringensis*; Tbr = *Theropithecus baringensis*; Tgl = *T. gelada*; Tod = *T. o. darti*; Tol = *T. o. leakeyi*; Too = *T. o. oswaldi*; Twe = *?Theropithecus* from WEE.

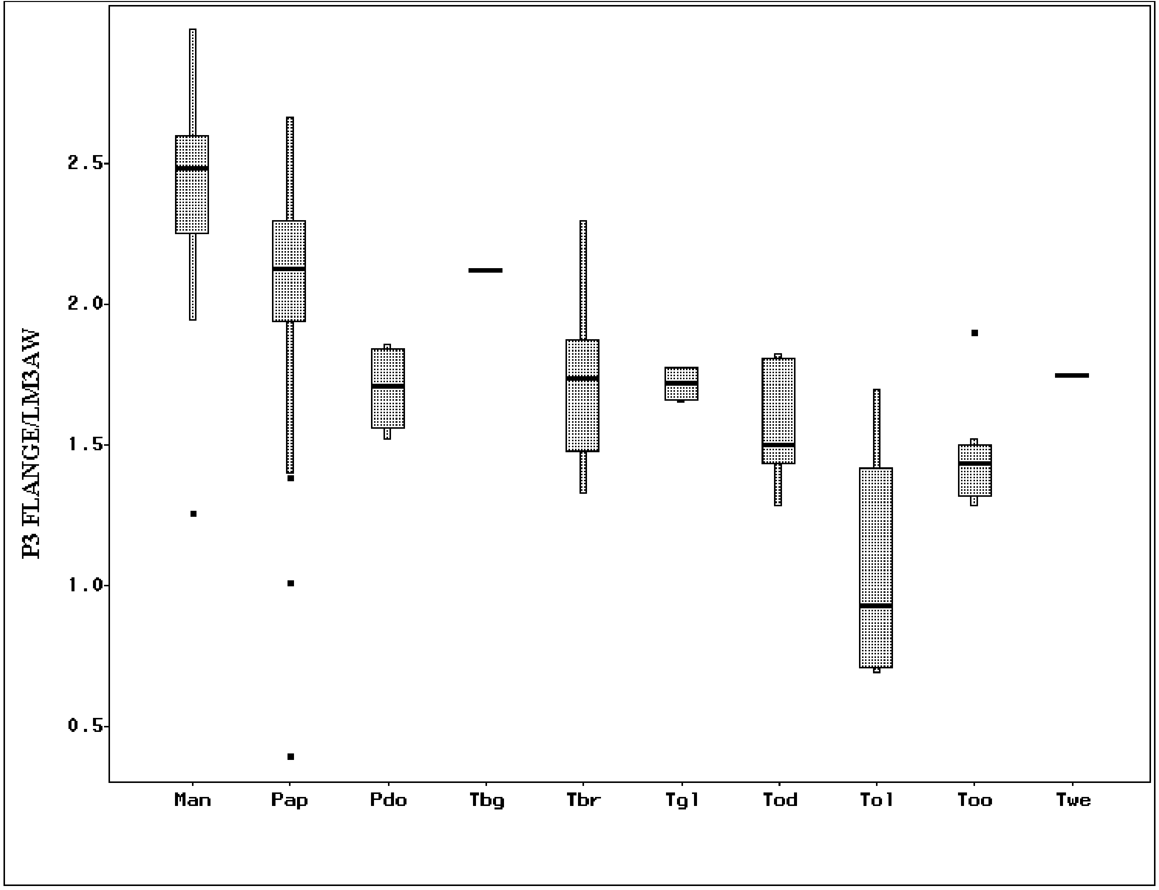
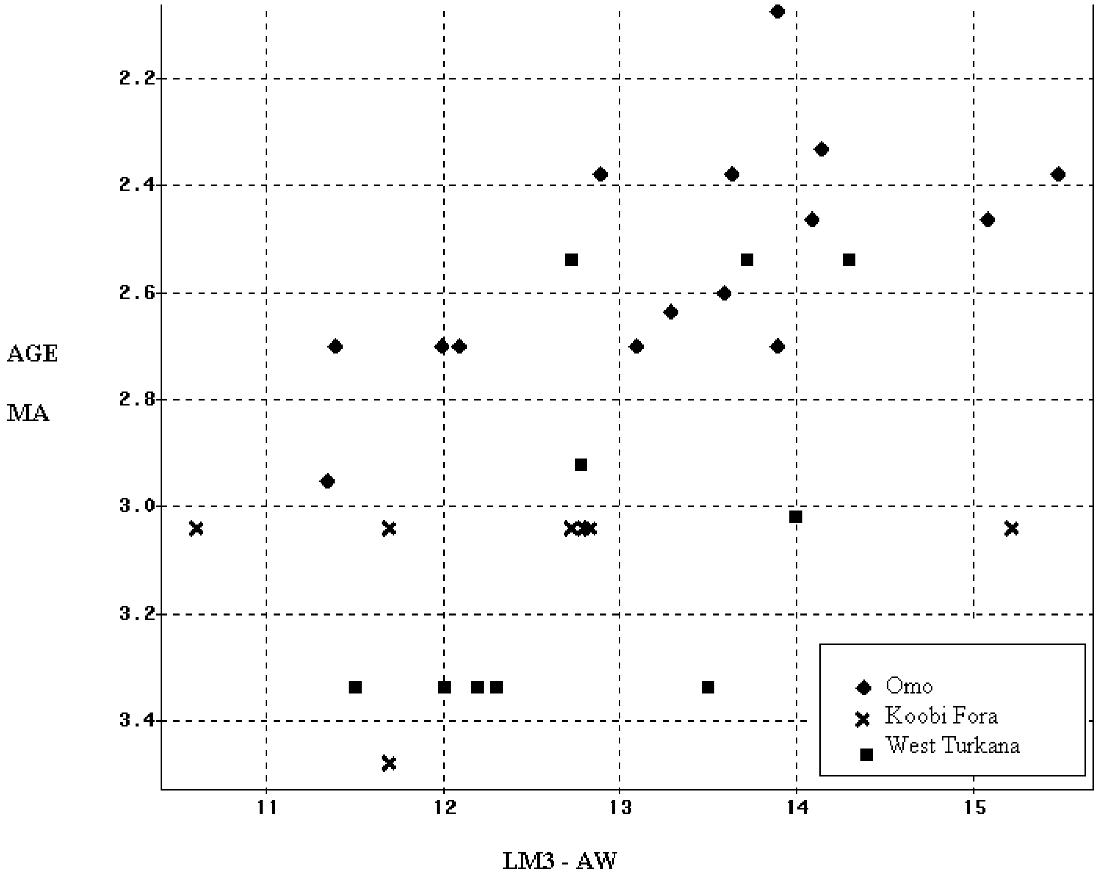


Figure 5.3 M_3 mesial breadth of *T. brumpti* plotted against time in Ma.

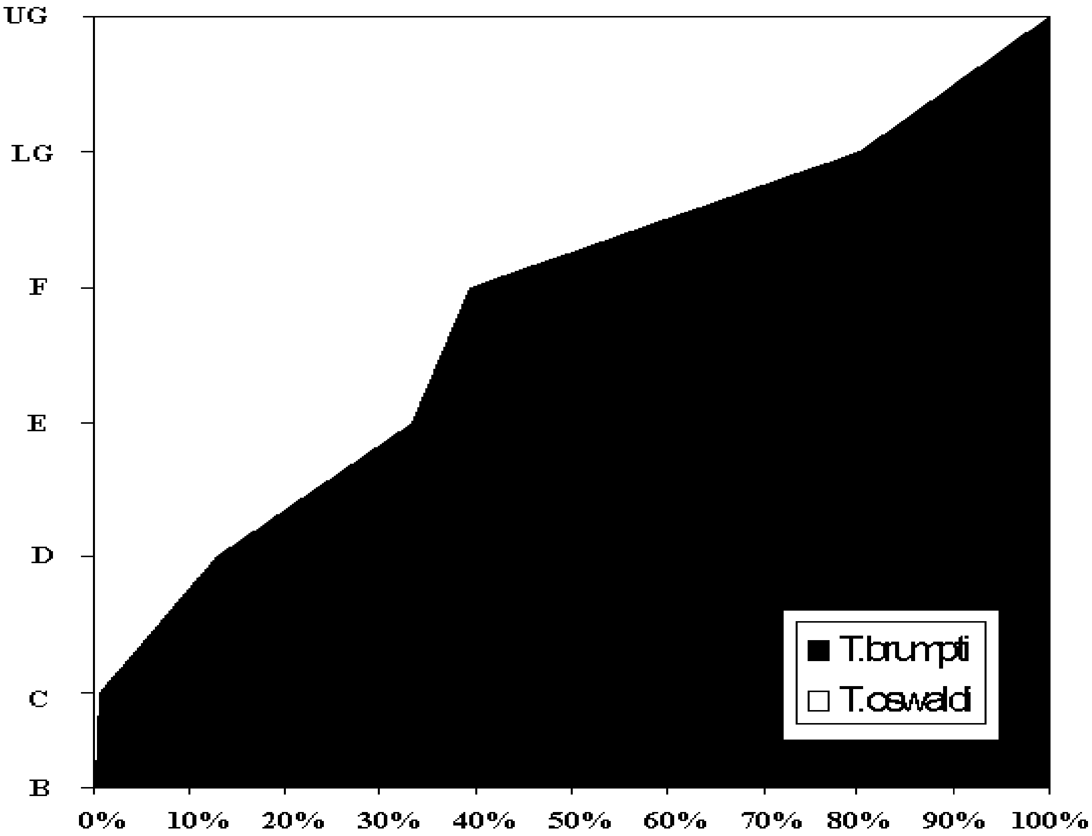


Remarks:

There is still considerable disagreement about the relationship of *Papio baringensis* Leakey, 1969 and *Papio quadratirostris* Iwamoto, 1982 to *T. brumpti*. Eck and Jablonski (1984; 1987) transferred the holotypes of both of these species *Theropithecus*, and argued that they are more closely related to *T. brumpti* than they are to *T. oswaldi* or *T. gelada*. Delson and Dean (1993) provide an alternative view and criticism of Eck and Jablonski’s arguments. For this analysis, the most important question is the position of the holotype of *P. quadratirostris* from the Usno Formation. This specimen has been tentatively included with the large papionin from the Shungura Formation. See the section on *P. (D.) quadratirostris*.

There is a large sample of *Theropithecus* dentition from the Turkana basin that cannot be allocated with any confidence to either *T. brumpti* or *T. oswaldi* based on morphology. The material from sediments 2.0 Ma and younger is most likely all *T. oswaldi*. From this date back to its first appearance at about 3.6 Ma both lineages are present, and this material is best left unassigned to species. Earlier than about 2.3 Ma *T. brumpti* is clearly the more abundant species (see figure 5.4) and most of the isolated *Theropithecus* dentition is likely to represent *T. brumpti* (Eck, 1987; Leakey, 1993).

Figure 5.4 Relative abundance of *T. oswaldi* compared to *T. brumpti* in the Shungura Formation. Members are plotted on the Y-axis in chronological order from oldest (bottom) to youngest (top). The X-axis shows the relative abundance of T. oswaldi. Totals from Delson et al., 1993.



Subfamily Colobinae Blyth, 1875

Genus *Rhinocolobus* Leakey, M.G. 1982

(= or including Colobinae gen. et sp. nov. Leakey and Leakey, 1973; Leakey, 1976; Eck, 1976, 1977; cf. Genus et sp. nov. Omo Leakey and Leakey, 1973. Colobinae gen. et sp. nov. 1. Szalay and Delson, 1979)

Type species *Rhinocolobus turkanaensis* Leakey, M.G. 1982

Generic Diagnosis: See Afar section.

Rhinocolobus turkanaensis, Type Species

Holotype: NME Omo 75 1969-1012 from Shungura Fm. Lower Mb. G.

Turkana specimens included: See Leakey, 1982; 1987.

Range: 3.4 - 1.88 Ma (3.59 – 1.39 including isolated teeth)

Distribution: Shungura Fm. E – G (plus isolated teeth from A – G, K,L); Usno Fm.; Koobi Fora Fm., upper Burgi Mbr. (plus isolated teeth from Lokochot – Okote Mbs. and tentatively identified mandible fragment from Lokochot Mbr.); Hadar Fm. Sidi Hakoma - Denin Dora Members.

Specific diagnosis: As for genus.

Description:

Other than in the relatively few specimens from the Afar region, all material identified as *Rhinocolobus turkanaensis* is from the Koobi Fora, Shungura and Usno

Formations. The Turkana basin material of this distinctive taxon has been thoroughly described by Leakey (1982; 1987) and Leakey and Leakey (1973a). It will therefore be discussed here only briefly. In overall cranial size *Rhinocolobus* is significantly larger than all extant colobines, similar to *P. chemeroni* and *Cercopithecoides*, but smaller than *Paracolobus mutiwa*. In dental size it is smaller than all *Paracolobus mutiwa* and *P. chemeroni*, similar to *Cercopithecoides williamsi* and cf. *Paracolobus* sp. from Laetoli, and significantly larger than all extant colobines.

The most distinctive features of *Rhinocolobus* are concentrated in the face. These include the very airorhynch face, with a profile that is concave from glabella to nasospinale. This profile is quite unique among the Colobinae, and in some aspects similar to that of *T. gelada*. Along with these features is the projecting glabellar region and prominent brow ridge. The nasals are extremely short, and the piriform aperture makes up most of the length of the rostrum. Also similar to *T. gelada*, it opens more dorsally than anteriorly. The mandibular symphysis is deep, and has a median mental foramen (in the Turkana sample only). The corpora are deep and thin, and in profile view, the corpus deepens posteriorly. The gonial region is typically expanded as well.

There is a fragmentary partial skeleton of *Rhinocolobus* known from Koobi Fora, which was discussed by Birchette in the context of his thesis on *P. chemeroni*. In most features where *Rhinocolobus* could be compared with the other large fossil colobines, it showed the greatest expression of features associated with arboreal postures and locomotion (Birchette, 1982).

Remarks:

The sample of *Rhinocolobus* from the Turkana basin is reasonably large, with both sexes represented by relatively complete cranial specimens, as well as some associated postcrania. The fragmentary material from the Afar depression is similar in most features, including the deep mandible and symphyseal shape, as well as the size of the dentition. The one difference between the two samples is the absence of a median mental foramen in the Afar material. Of the postcrania, only the distal humerus can be compared between the two, and they are strikingly similar. The humeri from both samples clearly are both from large colobines, which show fewer adaptations for terrestrial posture and locomotion than do those of *Paracolobus* or *Rhinocolobus*.

Also of note is that all of the best cranial material from the Turkana basin is from the interval between 2.4 and 1.88 Ma. This is substantially younger than the Afar material, which is concentrated near 3.4 Ma.

Genus *Paracolobus* Leakey, R.E.F. 1969

Type species *Paracolobus chemeroni* Leakey, R.E.F. 1969

Other included species: *P. mutiwa* Leakey, M.G. 1982; cf. *P. sp. nov.* Leakey and Delson, 1987.

Generic Diagnosis: See Afar section.

Paracolobus mutiwa, Leakey, M.G. 1982

Holotype: KNM-ER 3843 from the upper Burgi Member of the Koobi Fora Formation.

Turkana specimens included: See Leakey, 1982; 1987; Harris et al., 1988.

Range: 2.74 – 1.88 Ma (3.4 –1.88 including isolated teeth).

Distribution: Shungura Fm., Mbs. C-G (plus isolated teeth from B, Basal Members and the Usno Fm.); Koobi Fora Fm., Upper Burgi Member; Nachukui Formation upper Lomekwi Member.

Specific diagnosis:

This diagnosis follows that of Leakey (1982). *P. mutiwa* is a species of *Paracolobus* that is distinguished from *P. chemeroni* by a large range of cranial and mandibular characters. The rostrum is relatively deep in the dorso-ventral plane, with vertically oriented sides, marked by maxillary fossae, and in the male a maxillary ridge. The mandibular corpus is deep and thin. It is substantially deeper than that of *P. chemeroni*. The gonial area is expanded in the males, and there is a distinct ridge inferior to the M_3 in the lingual surface of the corpus. The dentition of *P. mutiwa* is similar to or even slightly larger in size than that of *P. chemeroni*.

Description:

The taxon has been thoroughly described by Leakey (1982; 1987) and Harris *et al*. (1988). The present description will therefore be brief. Facially, the large and tall muzzle and deep mandible produce what is probably the largest known colobine. Dentally, *P. mutiwa* is the largest known colobine, except for some *C. kimeui*. There is a well-preserved partial skeleton of a male from the Nachukui Formation that is similar in overall size to the *P. chemeroni* skeleton.

The face is unique among the Colobinae. The rostrum is long and boxy, and quite tall dorsoventrally. That of the male is not complete preserved, but shows maxillary ridges, and much of the superior surface of the piriform aperture appears to be rugose. The zygomata are flattened anteriorly, and deep dorsoventrally, a trait more typical of cercopithecines. The zygomatic process of the maxilla is positioned relatively far posteriorly.

The only specimen to preserve the anterior portion of the mandible is WT 16827. The symphysis is squared in profile, and may be marked by modest mental ridges, another feature rare among colobines, though present in *Procolobus verus*. There may also be a corpus fossa, but this may be due to distortion. Both transverse tori are well developed, and the inferior projects posteriorly to the distal end of the P_4. The corpus is deep, and deepens posteriorly in all preserved specimens. There is some variability in the height of the ramus, and the verticality of its anterior border. That of L35-59 is lower than that of WT 16827 even though the corpora are the same depth and the rami are the same length anterioposteriorly. The teeth of *P. mutiwa* are typical for the Colobinae in their morphology. Of note is that the distal lophid of the M_3 is typically narrower than the mesial, and the P^3 has a large and prominent protocone. Finally, the specimen from West Turkana shows an interesting molar wear pattern, where the M2 and M3 are more worn than the M1. Whether or not this pattern is typical of the species is impossible to tell as there are no other specimens which are complete enough and worn enough to evaluate this.

Several elements of the postcranium have been preserved in the skeleton from West Turkana (Harris et al., 1988). The postcrania are similar in some aspects of their morphology to those of *P. chemeroni*, but *P. mutiwa* appears to have a relatively shorter humerus, and possesses a hip and thigh more similar to extant cercopithecines than to *P. chemeroni* (Ting and Ward, 2001).

Genus *Cercopithecoides* Mollet, 1947

Type species: *Cercopithecoides williamsi* Mollet, 1947

Other included species: *C. kimeui* Leakey, M.G. 1982; *C. sp. nov.* Leakey et al., in press.

Generic Diagnosis: see Afar section.

Cercopithecoides williamsi, Mollet, 1947

(= or including: *Parapapio jonesi* Broom, 1940, in part. *Parapapio coronatus* Broom and Robinson, 1950. *Brachygnathopithecus peppercorni* Kitching, 1952, in part. *Cercopithecoides molletti* Freedman, 1957. *Papio sp.* Eck, 1976; 1977, in part.)

Holotype: UWMA MP 3 (203) from Makapansgat Formation, Member 4

Turkana specimens included: NME Omo 33 '68 369; specimens from Koobi Fora listed in Leakey, 1982.

Range: 3 – 1.5 Ma.

Turkana range: 2.3 – 1.88 Ma

Distribution: ?Shungura Fm. Member F.; Koobi Fora Formation Upper Burgi Member; Leba, Makapansgat, Sterkfontein, Swartkrans, Kromdraai, Bolt’s Farm, Drimolen, Specific diagnosis:

This diagnosis is largely taken from that of Freedman (1957) and the descriptions from Szalay and Delson (1979) and Leakey (1982). *C. williamsi* is a species of *Cercopithecoides* larger in cranial and dental size than all extant Colobinae, but significantly smaller than *C. kimeui*. It is also substantially larger than the new species of *Cercopithecoides* from Lothagam. It is distinct from *C. kimeui* in its shorter more rounded neurocranium. The supraorbital torus is more projecting, particularly in the sagittal plane, and is separated from the vault by a deeper ophryonic groove. The mandible is similar in overall morphology to that of *C. kimeui*, but less robust with smaller *prominentia laterales*. The molars are typical in morphology for the Colobinae, but different from *C. kimeui*, in possessing tall cusps, well developed shearing crests, and a low amount of basal flare.

Description:

The material from Koobi Fora has been described by Leakey, 1982. The partial skeleton ER 4420 was described by Birchette (1981) and extensively discussed in his description of *P. chemeroni* (1982). In dental and cranial size, the Koobi Fora material is significantly smaller than *C. kimeui*, but similar to most *C. williamsi* from South Africa. It is larger than all extant colobines, except for some of the largest individuals of *Semnopithecus entellus*.

The preserved cranial morphology is generally similar to that of most individuals from South Africa. The brow-ridge is projecting and separated from the neurocranium by an ophryonic groove. The neurocranium is globular, with temporal lines that do not form a sagittal crest, and post-orbital constriction is modest. The face is broad with a shallow midface, as is normal in colobines. The rostrum is relatively narrow. The rostrum shows a similar level of anterior projection to *Colobus* (see figure 4.11), and the zygomatic process is positioned above the M^2. In superior view, the premaxillae are “squared” anteriorly between the canines. The mandibular symphysis is shallow and vertical. It is pierced by a median mental foramen. In lateral view, the corpus is shallow and deepest under the M1 where there is a distinct inferior lateral bulge. The ramus is low and long in the anterioposterior plane. The gonial region is not expanded.

The dentition is more typical of the subfamily than is that of *C. kimeui*. The molars retain high cuspal relief and sharp transverse lophs seen in most colobines. Some specimens of *C. williamsi* show the same wear pattern seen in *C. kimeui*, in which the occlusal surface wears to a relatively planar surface. In older individuals wide dentine expose is common with enamel generally only retained on the periphery, often exposing a pattern similar to *Theropithecus*. Typically, colobine molars retain their shape and preserve effective shearing crests even at advanced stages of wear.

In its postcranium, *C. williamsi* shows more adaptation to terrestrial locomotion than any other known colobine in every feature studied by Birchette (1981; 1982). In fact, if the partial skeleton were not associated with indisputably colobine cranial material, it would probably have been identified as *Theropithecus* (Birchette, 1982).

There is a single specimen from the Shungura Formation, Omo 33 ’68 369 from Member F, which is tentatively assigned to this taxon. This specimen has not previously been described, and since it is the first specimen of this genus described from the Omo, it will be discussed in more detail. It is the right half of a mandibular corpus from just lateral to the symphysis to the M_3, with the ramus missing. The margin is preserved from the anterior end to the middle of M_2. Of the teeth, the $M_{2\text{-}3}$ are present, as are the roots of the P_3-M_1, and a small portion of the canine alveolus. Dental dimensions for Omo 33 ’68 369 are given in table 5.3. The corpus is shallow and broad. In profile it is deepest under the M_1/M_2 contact where it bulges inferiorly. Thus, the inferior margin is distinctly concave-down in profile. The mental foramen is large and singular, and appears relatively far anterior due to the small size of the incisive region and symphysis. The corpus under the molars is large, but the area for the anterior dentition is quite reduced, yielding a wide, squared off symphysis. There is a broad extramolar sulcus and a marked oblique line. The ramus would have obscured most of the M_3 in lateral view. The molars are broad and quadrate. The M_2 is worn to a single large enamel lake. The M_3 is also worn into a pattern similar to that of worn molars of *Theropithecus*. The enamel can be seen to be thin. The overall wear of the molars is similar to that of *Cercopithecoides* mandibles from both East and South Africa. The M_2 is worn lower buccally than lingually, but the bucco-lingual pattern of wear is actually somewhat sigmoidal. The M_3 is worn similarly, but the deepest part of the wear seems to shift more lingually so that it is towards the midline of the tooth. Additionally, the deepest part of wear seems to be one continuous trough or wear band from anterior to posterior across both teeth, implying some sort of anterioposterior motion of the mandible during chewing. While the molars are heavily worn, they possess relatively deep lingual notches. The roots of the premolars indicate that the P_3 did not have an elongated mesiobuccal flange implying that this specimen may be female. The area for the anterior dentition, particularly the incisors, is far smaller than would be expected in any known cercopithecine.

Remarks:

Cercopithecoides williamsi is the most widely distributed African fossil colobine, both temporally and geographically. Whether all of this material represents a single biological species is beyond the scope of this dissertation, however there is considerable variation in cranial morphology both within southern Africa, and between East and South Africa. In any event, *C. williamsi* as currently recognized is far more common and widespread in southern Africa than it is in East Africa, where it is only known from Koobi Fora, and tentatively from the Omo. It could also possibly be found in the Afar region (see cf. *Cercopithecoides* sp. indet. in the Afar section). *C. kimeui* on the other hand, is comparatively widely distributed in East Africa (see below), but unknown from southern Africa.

Cercopithecoides kimeui, Leakey M.G. 1982

(= or including cf. *Cercopithecoides* Leakey and Leakey, 1973a. cf. Colobinae Leakey and Leakey, 1973a. *Cercopithecoides* sp. nov. Leakey, 1976; Szalay and Delson, 1979. *?Cercopithecoides* sp(p.) Szalay and Delson, 1979, in part.)

Holotype: NMT 068/6514 from MLK Olduvai Gorge (Middle Bed II)

Turkana specimens included: specimens listed in Leakey, 1982

Range: ~2.4 – 0.8 (3.4 - 0.64) Ma

Turkana range: ~1.9 – 1.64 Ma

Distribution: Olduvai Gorge, Middle Bed II, Masek; <u>Koobi Fora Formation upper Burgi and KBS (plus tentative identifications in the Lokochot and Tulu Bor Mbs.)</u>; Rawi

Formation; and the Pinnacle locality in the Hadar region (and if KL272-1 is this species, then the Upper Bodo Sand Unit)

Specific diagnosis: See Afar Section.

Description:

Within the Turkana basin, *C. kimeui* is only known from the Koobi Fora Formation. This sample has been described by Leakey and Leakey (1973a), and Leakey (1976; 1982). Nearly the entire sample, and all of the most complete specimens, comes from the upper Burgi and KBS Members. Two additional maxillae have also been tentatively identified to this taxon, one from the Lokochot and one from the Tulu Bor Member, which would extend the range considerably. In overall cranial size, *C. kimeui* is one of the largest colobines known, perhaps only being smaller than *P. mutiwa*. In dental size, the teeth are similar to *P. mutiwa* as well.

The cranial morphology of *C. kimeui* has been described in the Afar section. There are, however, several well preserved mandibles from Koobi Fora that preserve more of the mandibular morphology. The mandible is similar to that of *C. williamsi* but more robust. The symphysis is shallow, vertical, lacks mental ridges, and is pierced by a median mental foramen (except for one specimen, ER 976). The corpus is shallow and thick, with a broad extramolar sulcus. In lateral view, the corpus is deepest inferior to M_1/M_2 contact, largely due to the presence of large lateral tubercles. The ramus is low and anteroposteriorly short. The gonial region is unexpanded.

The dentition of *C. kimeui* is unique among colobines. The molars are comparatively low crowned with bunodont cusps and shallow cuspal relief. They also have a large amount of basal flare for a colobine, although less than in most papionins. Although the molars are low crowned in comparison to most colobines, they differ from cercopithecine teeth in that the relative proportion of the total tooth height made up by the cusps is greater. Thus, even though the cusps are low, so is the height of the crown from the cervix to the lingual/buccal notch. Furthermore, the cusps appear to be more widely spaced than are those of cercopithecines, and the cross-lophs more completely developed.

Genus *Procolobus* Rochebrune, 1886-87

(= or including *Piliocolobus* Rochebrune, 1886-87; *Tropicolobus* Rochebrune, 1886-87;
Lophocolobus Pousargues, 1895)

Type species *P. verus* (Van Beneden, 1838)

Other included species: *P. badius* (Kerr, 1792); *P. kirkii* (Gray, 1868).

Generic Diagnosis:

This diagnosis draws most heavily upon the description by Napier (1985) with some modifications based on Strasser and Delson (1987) and Groves (1989). As with *Colobus*, the most diagnostic features of this genus are in the soft anatomy, such as a four chambered stomach, presence of female sexual swellings, and males with separated ischial callosities, as well as a lack of the *Colobus* laryngeal specializations. As a result this diagnosis will focus on the hard tissues. *Procolobus* is a small to mid-sized African colobine, with *P. verus* being the smallest extant colobine, and *P. badius* and *P. kirkii* similar in size to *Colobus*, *Libypithecus*, and significantly smaller than *Cercopithecoides* (other than the new species from Lothagam), *Rhinocolobus*, and *Paracolobus*.

The interorbital distance is broad, unlike *Nasalis, Libypithecus,* and *Rhinocolobus*. The nasals are short relative to the length of the rostrum, which is distinct from *Nasalis,* but longer than those of *Rhinocolobus* and *Rhinopithecus*. In contrast to *Colobus*, infraorbital fossae are typically present, the supraorbital rim is thick, and perforated by supraorbital foramina. An anteriorly positioned sagittal crest is present, which is distinct from *Colobus*, *Cercopithecoides*, *Rhinocolobus*, and most Asian colobines. The choanae are tall and narrow, unlike those of *Colobus*. The pterygoid fossae are deep and narrow, and generally perforated at their apex. The mandibular corpus is not as deep as that of *Colobus*, and bears large *prominentia laterales*, separating it from *Colobus*, *Rhinocolobus*, and *Paracolobus.* The gonial area is typically not expanded, once again different from *Colobus*, *Rhinocolobus,* and *Paracolobus*.

Procolobus (Piliocolobus) Rochebrune, 1886-87
(= or including *Tropicolobus* Rochebrune, 1886-87)
Type species: *Procolobus badius* (Kerr, 1792)
Other included species: *P. kirkii* (Gray, 1868)

Subgeneric diagnosis:

A subgenus of *Procolobus* significantly larger than *P. (Procolobus)*. It is also distinguished from *P. (Procolobus)* by several features of the pelage and other soft tissue characters. The mandibular symphysis lacks the mental ridges and median mental foramen of *P. (Procolobus)*, and the incisors lack a larger lingual cingulum and tubercle. The M_3 also typically only has five cusps, whereas *P. (Procolobus)* typically has a small tuberculum sextum.

cf. *Procolobus (Piliocolobus)* sp.

Turkana Specimens included: See Leakey, 1987; Leakey, 1976.

(= or including *Colobus sp.* Eck, 1976;1977; Leakey, 1976; Szalay and Delson, 1979)

Range: (?3.0) 1.88 – present

Turkana range: 1.88 – 1.39 Ma

Distribution: Late Pleistocene, Sudan; Andalee; Issee; Shungura Fm. J(or K), L Mbs.; Koobi Fora KBS, Okote Mbs; Lothagam-3?; Kapthurin; Kanam East; Olduvai Beds I,II(M+U), III and above; Taung "Upper".

Description:

The sample of small colobines from the Shungura Formation has been described by Eck (1976) and Leakey (1987). That from Koobi Fora was discussed by Leakey (1976). The Shungura material is composed of a small sample of isolated teeth. Little more can be said of them other than they are in the size range of both modern *Colobus guereza* and *Procolobus badius*, although there is a substantial size range. In the two measurable M_3's the width of the distal lophid relative to that of the mesial is closer to that of *Procolobus* in P997-15b, whereas that of F8-14 is outside of the *Procolobus* range and within that of *Colobus*. However, given the variability in this feature, it cannot be ruled out that these represent a single species. It may well represent the same taxon that is present at Koobi Fora.

Only a small portion of the maxillary morphology is preserved. The rostrum was likely to have been comparatively short, and the zygomatic process was located above the mesial M^2 and distal M^1. The mandible is different from that of *Colobus*, and shows the affinity of this taxon with *P. (Piliocolobus)*. The symphysis is steep and vertical in profile, and lacks a median mental foramen and mental ridges. The corpus has large inferiorly placed *prominentia laterales*. As a result, the deepest part of the corpus is at the level of the M_1. The extramolar sulcus is relatively narrow. The ramus is tall and not back-tilted with the condyle being well above the occlusal plane. The gonial area was likely to have been slightly expanded. Dentally, the Koobi Fora material is intermediate in size between the larger and smaller Shungura specimens. Morphologically, the preserved dentition, which lacks upper incisors, is typical of colobines. Similar to other African colobines, the P^3 protocone is reduced. The distal lophid width in comparison to the mesial is within the range for *Procolobus*.

Genus et species indet. Medium, size A Eck 1977

(= or including Colobinae gen. et sp. indet. Leakey, 1987)

Specimens: See Leakey, 1982; KNM-ER 3041.

Description:

The specimens from the Shungura and Usno Formations are all isolated teeth of a colobine significantly smaller than *Rhinocolobus* but larger than modern *Colobus*

(Leakey, 1987). KNM-ER 3041 is a mandibular corpus fragment of a similarly sized colobine with M_{1-3} and only a small part of the corpus around the molar roots preserved. The dental dimensions for the Omo material are given in Leakey (1987). They are similar in size to both *Kuseracolobus* and the Leadu colobine (cf. *Cercopithecoides* sp. nov. in the Afar Section), but these taxa are indistinguishable dentally. Therefore, it is impossible to assign this material to either taxon. This material is important, however, as it documents the presence of at least one additional colobine species in the Turkana Basin not represented by more complete cranial material. The Omo material is from the Usno Formation and B10 through D5 as well as the lower part of Member G (Eck, 1976; Leakey, 1987). The Koobi Fora specimen is from the Tulu Bor Member, and therefore between 3.4 and 2.68 Ma in age.

Genus et species indet. Large, size B Eck 1977
Turkana Specimens: see Leakey (1987).

Description:

There is a large sample of isolated colobine teeth and other fragmentary remains that cannot be allocated to genus with any certainty. The teeth of this sample are larger than those of Size A above, but are compatible with *Rhinocolobus*, *Paracolobus* and *Cercopithecoides*. Leakey (1987) has listed those from the Omo. They span the range from Members A though K in the Shungura Formation, the Usno Formation, and from the Lokochot through Okote Members of the Koobi Fora Formation. None are known from the Nachukui Formation.

Chapter 6

Comparison between the Afar Depression and Turkana Basin

Introduction

This section will describe and compare several aspects of the cercopithecid fossil records from the Afar Depression and the Turkana Basin. The taxonomy of these samples was described in chapters 4 and 5 respectively and is graphically summarized for each region in figures 6.1 and 6.2. The basic stratigraphy for each of these paleontological regions was discussed in Chapter 2. Both collections and history of their discovery have been discussed in Chapters 3 and 2.

In combination, the collections from these two basins constitute the majority of the Pliocene and Pleistocene East African fossil record for the Cercopithecidae. The record from the Afar depression covered in this study spans the time range from 4.4 Ma to approximately 0.25 Ma. There are several large gaps, notably between approximately 2.9 Ma and 2.5 Ma, and between 2.3 Ma and approximately 1.8 Ma, and finally between 1.8 and 0.6 Ma. This latter gap can be filled to some degree by data from the 1.0 Ma Dakanihylo member of the Bouri Formation (de Heinzelin et al., 1999), which is currently under analysis by H. Gilbert. There are also only very small samples between 4.4 and nearly 3.4 Ma. The record in the Turkana basin covers the time span from approximately 3.5 Ma up through nearly 1 Ma. Two older sites can be added to extend the age further into the Early Pliocene. The site of Kanapoi in the southern Turkana basin ranges in age from 4.17 to 4.12 Ma. While this sample is currently under analysis by M.G. Leakey, a partial faunal list has been published (Leakey et al., 1995) which can be used for some of the comparisons to be undertaken here. Second, Coffing et al. (1994)

Figure 6.1 Temporal Range of Afar Cercopithecidae. Also shown are the species groups discussed in the text, and the chronological representation of the stratigraphic units. Solid boxes show the age range for species based only on confidently assigned material. Hatched boxes show ranges based on more tentatively assigned material. Solid error bars represent geochronological uncertaintly. Dashed lines represent implied ranges across large gaps in the sequence.

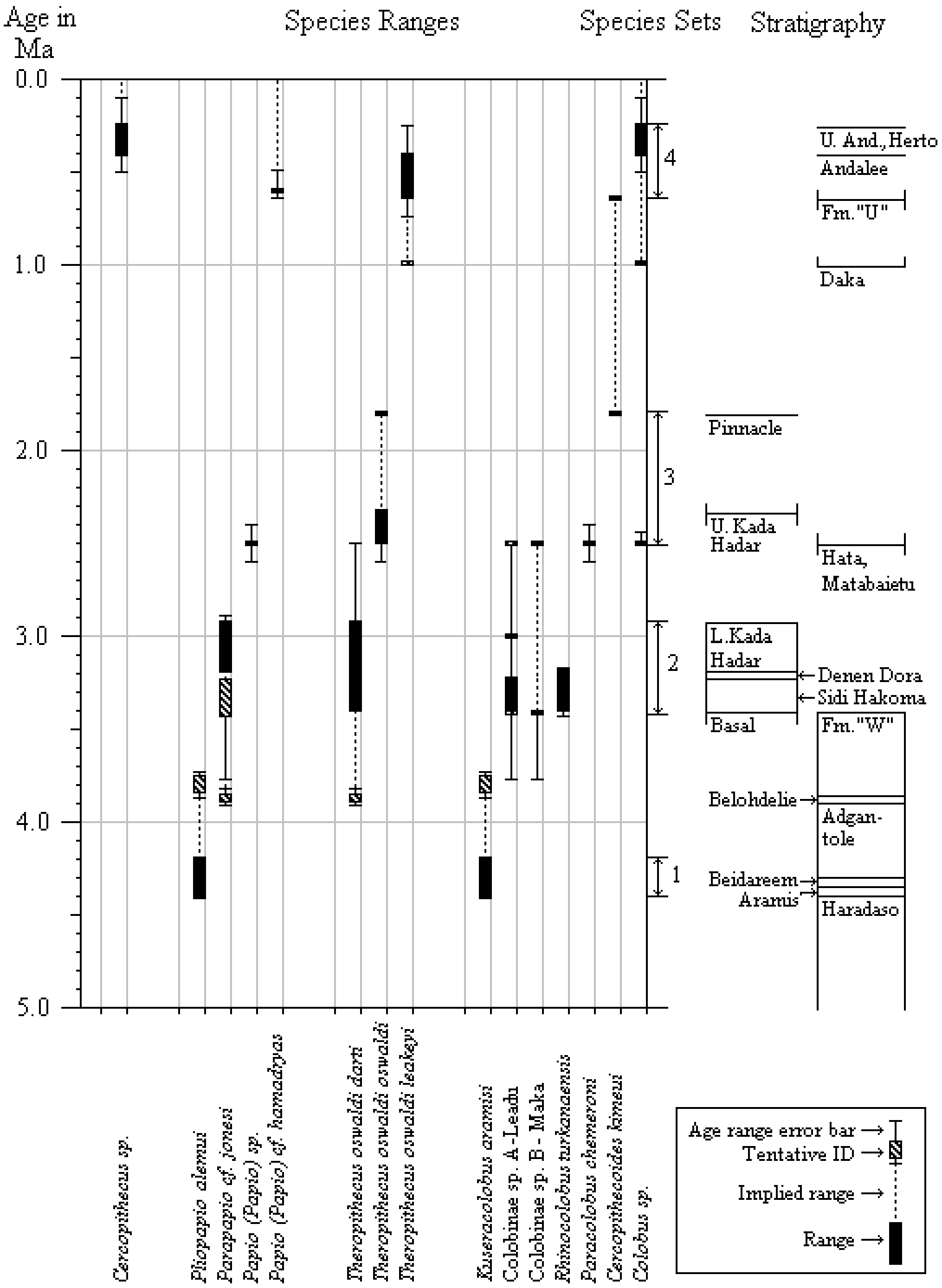
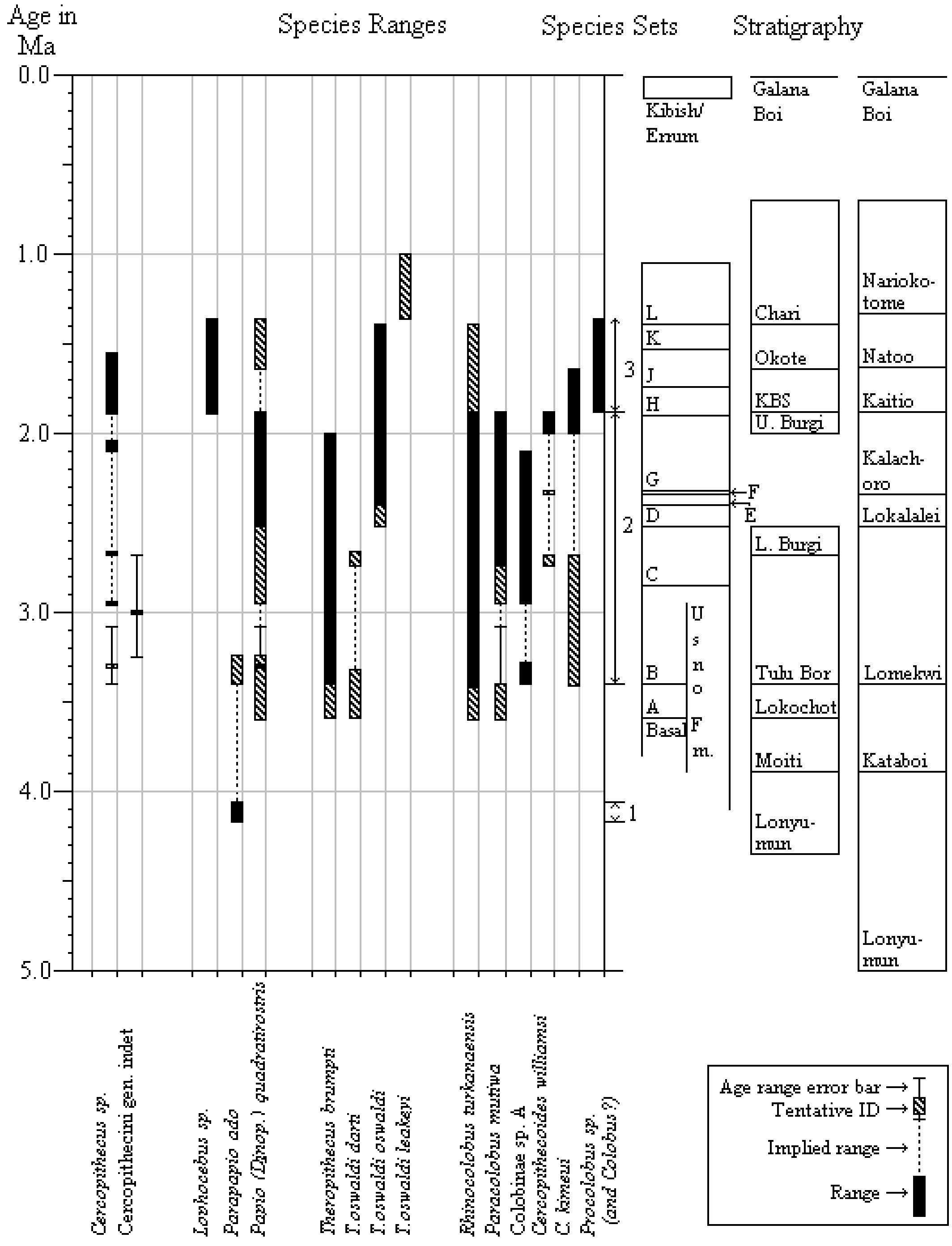


Figure 6.2 Temporal Range of Turkana Basin Cercopithecidae. Symbols as in figure 6.1.



included *Parapapio* spp. and colobines in their faunal list for Area 261 in the Lonyumun Member of the Koobi Fora Formation, dated to 3.9 Ma.

Several aspects of the cercopithecid samples are described for the Afar Depression and for the Turkana Basin. Then comparisons are made among the species present in both samples, followed by comparisons of the genera. Following Delson (1973; Szalay and Delson, 1979) cercopithecids can be grouped into four suprageneric categories based on molar morphology as described in chapter 2. These categories are colobines, cercopithecins, papionins other than *Theropithecus*, and *Theropithecus*. While all of these groups are not holophyletic, they are useful as they are diagnosable based on isolated teeth and can therefore be applied to a much larger proportion of the sample than is the case in for specifies or genus level designations.

Afar Region

Conservatively, there is a minimum of 13 cercopithecid species in at least 10 genera present in the Afar sample covered here (see Figure 6.1). These species are distributed in a very heterogeneous manner through the represented time span. The most diverse stratum in the sequence has a minimum of 5 species (and probably 6 depending on a tentative identification). Table 6.1 summarizes sample size and number of species in the different Afar strata. Sample size refers here to number of specimens, with associated elements counted as a single specimen. Number of species and sample size for the different Afar sites is illustrated in figure 6.3. There is also considerable turnover of species through the record, with no single taxon being present at all levels. *Theropithecus oswaldi* comes closest to this, spanning the interval from approximately 3.4 through 0.25

Table 6.1 Cercopithecid distribution and diversity in the the Afar depression. Rows represent different stratigraphic levels. The column headings indicate the following: Species lists the most likely number of species, Min Species lists the smallest possible number of species, IND is the number of individuals.

Level	Species	Min Species	IND
Andalee (Upper)	2	2	39
Andalee (Lower)	3	3	158
Bodo	3	2	10
Daka	2	2	14
Pinnacle	2	2	26
UKH	2	2	13
Hata	4	3	37
Matabaietu	3	3	110
MATAHATA	6	5	147
Geraru	1	1	3
Leadu	2	2	4
Kada Hadar	2	2	45
Denen Dora	2	2	158
Sidi Hakoma	4	4	134
Basal	2	2	8
Ahmado	3	3	104
FM "W" Sub SHT	4	4	65
SUBSHT	5	4	73
VT3-CT	2	2	4
Belohdelie	3	2	6
Adgantole	2	2	3
SupraDABT	1	1	3
GATC/DABT	2	2	1027

Table 6.2 First (FAD) and Last (LAD) appearances of for Afar species. FAD and LAD based on confidently assigned specimens. FAD max and LAD min include tentative assignments.

Taxon	FAD	FAD max	LAD	LAD min
Cercopithecus	0.40	0.40	0.25	0.25
Pliopapio	4.39	4.39	4.19	3.75
Parapapio cf. Jonesi	3.40	3.40	2.92	2.92
Papio sp. small	2.50	2.50	2.50	2.50
cf. Papio hamadryas	0.64	0.64	0.64	0.64
Theropithecus oswaldi	3.40	3.89	0.40	0.40
Kuseracolobus	4.39	4.39	4.19	3.75
Rhinocolobus	3.40	3.40	3.18	3.18
Paracolobus chemeroni	2.50	2.50	2.50	2.50
Ceropithecoides kimeui	1.80	1.80	1.80	0.64
cf. Cercopithecoides sp. nov. Leadu	3.40	3.40	3.28	2.50
cf Cercopithecoides sp. indet. Maka	3.40	3.40	3.40	2.50
Colobus sp.	0.40	2.50	0.25	0.25

Ma, and possibly as early as 3.9 Ma. However, this lineage undergoes a considerable amount of change, with three successive chronosubspecies.

First appearance data (FADs) and last appearance data (LADs) for the Afar basin taken from chapter 4 are summarized in table 6.2. These include two sets of appearance data: those based on confidently assigned specimens, and a separate set including ages based on more tentative material. These appearance data are graphically summarized in figure 6.4. It is important to note, that many of the taxa are rare and based on relatively few specimens, so that their first and last appearances are almost certainly not “real.” There are of course first appearances at the beginning of the section, but these clearly represent only the fact that they are at the beginning of the record. There is a second set of first appearances that occur near to the Sidi Hakoma Tuff, where sampling increases after the long gap between Aramis and the sub-SHT level. Vrba (1997) also found turnover in the Afar Bovids between 3.8 and 3.4 Ma. There is a series of LADs at the top of the main part of the Kada Hadar Member as well. A smaller concentration of FADs and LADs also occurs at the 2.5 Ma period. This represents the level of maximum diversity. The large number of appearance data at this level are likely to be due to the large temporal gaps that bound these levels. Thus the pattern of first and last appearances shown in figure 6.4, is likely to be more the result of stratigraphic incompleteness than reflect biotic events in the ancient Afar Basin.

As a result of this turnover, there appear to be four chronological sets of species present. These sets are separated by temporal gaps where there are either no collections of intermediate age, or only very small samples. These sets are shown on figure 6.1 to the right of the stratigraphic ranges. The oldest set, from the Early Pliocene, is exemplified

---

Figure 6.3 Sample size and number of species for stratigraphic levels in the Afar Basin. Left hand scale shows number of individual specimens as in Table 6.1

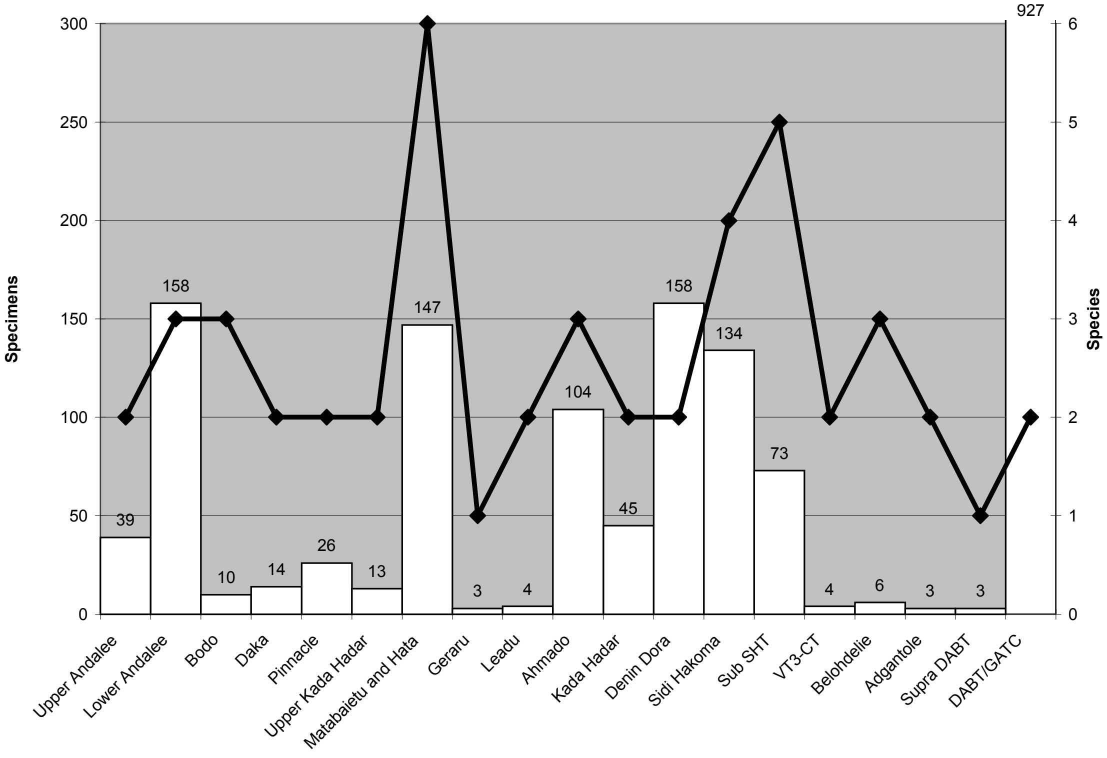
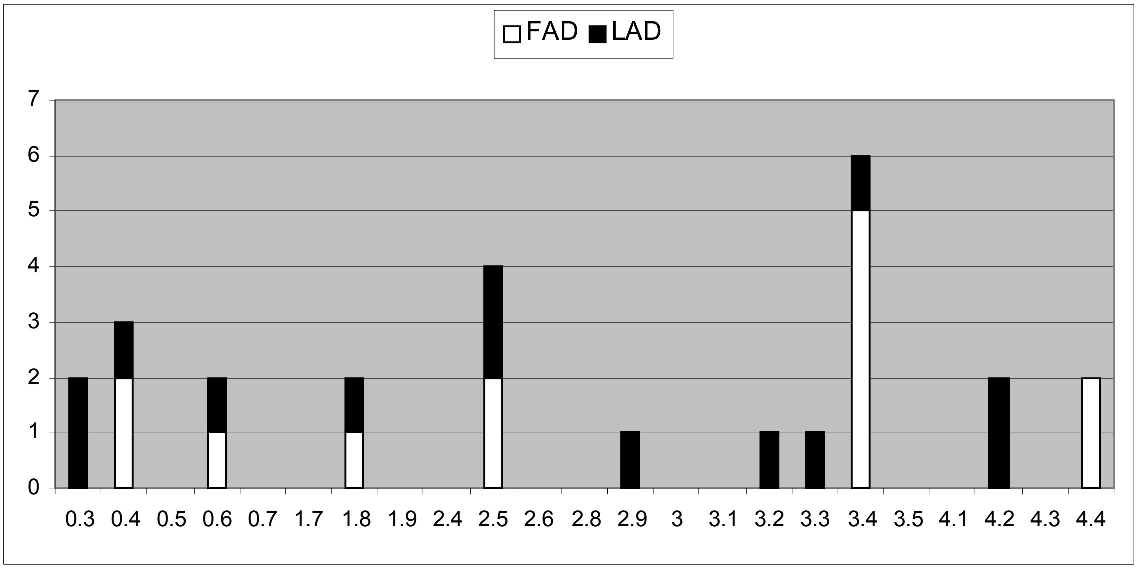


Figure 6.4 First and Last Appearance Data for the Afar cercopithecid species from table 6.2 broken into 100 Kyr intervals.



by the large sample for the Aramis Mbr. of the Sagantole Formation. Small samples of isolated teeth from above the DABT tentatively extend this set to the Adgantole Member of the Sagantole Formation. The sample from above the DABT, however, is very small and consists entirely of isolated teeth, and therefore must be considered tentative. The time span for this set would then be from about 4.4 Ma to 4.2 Ma. There are also a few isolated teeth from the lower part of the informally named Formation "W" of White et al. (1993) that could potentially extend this group up to 3.75 Ma. However, given the large time difference, and the non-diagnostic nature of the fossils, this requires verification from more complete material.

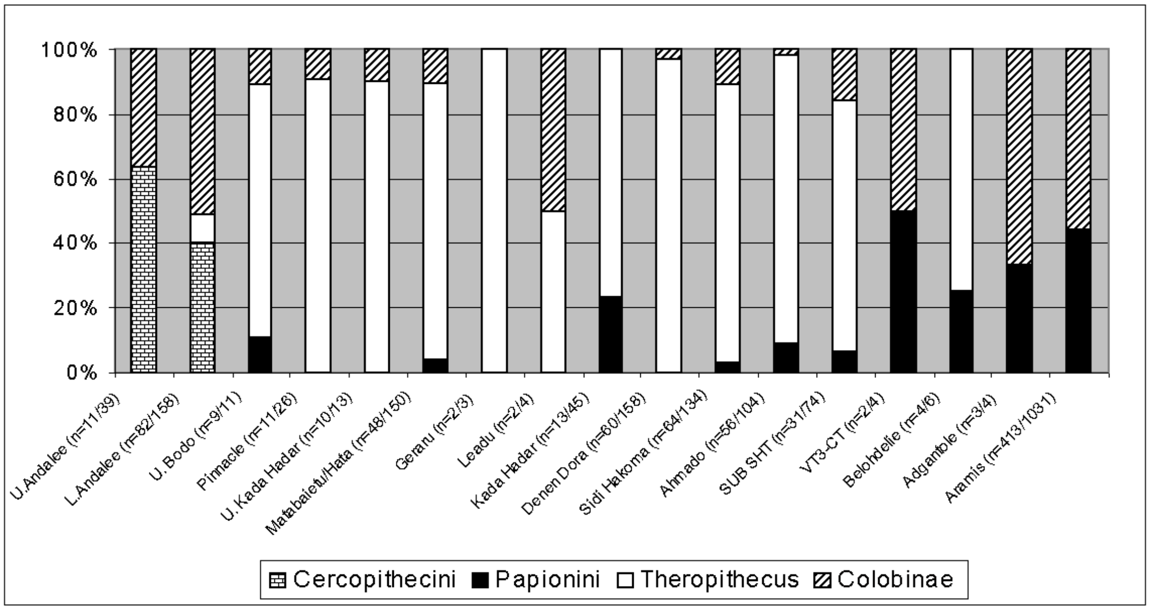
The second set of associated species is typified by the Hadar and Maka assemblages. It is basically early Middle Pliocene in age. In abundance it is dominated by *T. o. darti*. It also includes *Pp.* cf. *jonesi*, cf. *R. turkanaensis*, the Leadu colobine, and cf. *Cercopithecoides* (Maka species). This zone is similar in some respects to the contemporary cercopithecids from the Turkana Basin (i.e. Tulu Bor, Lower Lomekwi, Usno, and Shungura Mbr. B). Similarities include the high abundance of *Theropithecus* (although *T. brumpti* is most common in the Turkana basin) and the presence of a diversity of large colobines, including probably *R. turkanaensis*. In some respects this group is also quite similar to the cercopithecid fauna from Makapansgat, with *Parapapio* cf. *jonesi*, *T. o. darti*, and depending on identification of MAK-VP-1/35 a species of *Cercopithecoides*.

The third set of species is at approximately 2.5 Ma. By far the most abundant taxon is *T. o. oswaldi*. The other taxa are all very rare, most being represented by single specimens. These include the small species of *Papio (Papio)* from Bouri, cf. *Paracolobus* *chemeroni*, cf. *Cercopithecoides* (sp. Maka), a colobine similar in size to the Leadu colobine, and possibly an additional species of colobine similar in size to modern *Colobus*. At approximately the Plio-Pleistocene boundary, but still in this zone (or possibly transitional with the next) there is the site of Pinnacle in the Hadar region. Two species are present, *T. o. oswaldi* and *Cercopithecoides kimeui*, both widespread. They are present in roughly contemporaneous strata in the Turkana Basin and Olduvai.

The fourth species set is a Middle Pleistocene assemblage. This set includes *T. o. leakeyi*, and the modern taxa *P. hamadryas, Colobus* cf. *angolensis* and *Cercopithecus* cf. *aethiops*. Interestingly, *T. o. leakeyi* is actually a comparatively rare member of this group, with the latter two taxa being most common. The exception to this is from the Upper Bodo level, the informally designated Unit “U” of Clark et al. (1994), but samples are small from this time span. It is worth noting that the roughly contemporary Afar site of Asbole has all four of these taxa with a small colobine dominating and abundant *Cercopithecus*. Along with *Theropithecus*, *Cercopithecus* and *Colobus* are common in Early to early Middle Pleistocene sediments from the Gona region (personal observation). Bodo is older than Andalee, possibly by over two hundred Kyr. The difference in the cercopithecid faunas from Andalee and Bodo, however, may be due more to paleoenvironment than to age, with Andalee perhaps representing a more closed paleoenvironment as described by Kalb et al. (1982a).

When the relative abundance of the taxa represented by Delson’s four dental morphologies (i.e. colobines, cercopithecins, non-*Theropithecus* papionins, and *Theropithecus*) in the different strata is studied, three distinctive periods can be recognized (see figure 6.5). The earliest is a period of codominance of colobines and non-

Figure 6.5 Relative abundance of dental groups in Afar Mbs. Numbers in parentheses represent sample sizes. The numerator is the number of specimens identifiable to one of the four categories, and the denominator is the total number of specimens.



Theropithecus papionins. This is an unusually high abundance of colobines for a Pliocene assemblage. Importantly this period is lacking in *Theropithecus* (or at least it is very rare). This time period is essentially equivalent to that represented by the first species set.

The second time period is characterized by a dominance of *Theropithecus*. During this span *Theropithecus* generally approaches an abundance of 80 to 90%. This *Theropithecus* zone runs from prior to 3.4 Ma in the sub-SHT levels through the early Middle Pleistocene. It is equivalent to the second and third species sets, and overlaps the earliest part of the fourth.

The third time period is only in the upper and lower levels of the Andalee Member of the Wehaietu Formation. This zone is characterized by the very high abundance of Cercopithecini, and Colobinae. While colobines are relatively abundant during other periods (e.g. Laetoli) and in other collecting regions (e.g. Laetoli), the abundance of guenons is unique in all of the Pliocene through the Middle Pleistocene. It is likely, however, that this abundance zone represents a facies shift from the older Unit "U" rather than a widespread shift in cercopithecid abundance. Additionally, the cercopithecid sample form Unit "U" is small and its proportions may not be reliable.

Turkana Basin

There is a minimum of fourteen species and nine genera present in the Turkana Basin (see Figure 6.2). These are distributed more evenly through the main portion of the sequence, from approximately 3.4 Ma through about 1.5 Ma, than is the case in the Afar depression. There is still considerable change through the sequence however. While the total number of species is similar in the Turkana basin to the Afar, there are generally more species present at any given time interval, with values ranging from 1 up to possibly 10 species present near the interval of the Tulu Bor Tuff. Table 6.3 lists the number of individuals and the number of species present in the different members found in the Shungura, Koobi Fora, and Nachukui formations.

First and last appearance data for the Turkana basin taken from chapter 5 are summarized in table 6.4. These include both the ranges based on confidently identified material, and those based on more tentatively assigned specimens. There is a group of FADs at the beginning of the record, and a series of LADs at or near the end of the record at about 1.4 Ma. Similar to the situation in the Afar basin, there appears to be a concentration of FADs at approximately 3.4 Ma, near the Tulu Bor Tuff. This is most likely the result of sampling being much better above the Tulu Bor Tuff than below it.

Table 6.3 Cercopithecid distribution and diversity in the Turkana Basin. Row and column headings the same as those of Table 6.2. IND totals marked by an asterisk are from the Analytic catalog of Bobe (1997) and are not for the complete collection. These are shown to give an idea of relative proportion. The total numbers would be larger.

Level	Species	Min Species	IND
L	5	5	26
K	5	5	12
J	3	3	9
H	1	1	19
G (Upper)	4	2	43
G (Lower)	8	7	588*
F	7	7	376*
E	7	6	250*
D	6	6	256*
C	9	8	1091*
B	8	7	246*
A	4	3	7
Usno	8	7	583*
Okote	6	6	122
KBS	7	7	83
Burgi (Upper)	7	7	119
Tulu Bor	8	8	56
Lokochot	4	5	19
Kalochoro-Nariokotome	1	1	15
Lomekwi (Upper)	3	3	34
Lomekwi (Middle)	1	1	5
Lomekwi (Lower)	3	3	41

Table 6.4 First and last appearances for Turkana species. Columns as for Table 6.2.

Taxon	FAD	FAD max	LAD	LAD min
Cercopithecus sp.	2.95	3.30	1.55	1.55
Cercopithecini gen. et sp. indet.	3.00	3.40	3.00	2.68
Lophocebus sp. nov.	1.88	1.88	1.36	1.36
Parapapio ado	4.17	4.17	4.07	3.24
Papio (Dinopithecus) quadratirostris	3.30	3.59	2.00	1.36
Papionini B	2.00	3.59	1.39	1.05
Theropithecus brumpti	3.40	3.59	2.00	2.00
Theropithecus oswaldi	3.40	3.59	1.00	1.00
Rhinocolobus turkanaensis	3.40	3.59	1.88	1.39
Paracolobus mutiwa	2.74	3.59	1.88	1.88
Cercopithecoides williamsi	2.00	2.74	1.88	1.88
Ceropithecoides kimeui	2.00	3.40	1.64	1.64
Procolobus sp.	1.88	1.88	1.36	1.36
Colobinae sp. A	3.40	3.40	2.10	2.10

Finally there is a large cluster of first and last appearances at approximately 2.0 – 1.9 Ma. This may be partially due to two different sedimentary factors. The first is the shift from fluvial to lacustrine sedimentation in the Shungura Formation (de Heinzelin, 1983), causing a drastic decrease in preservation (see Table 6.3). The second is the increased sampling and good preservation of specimens in the Upper Burgi Member of the Koobi Fora Formation after a long gap. However, when both of these units are studied together sampling is good both just before and just after 2.0 Ma, even if there are some ecological differences between East Turkana and the lower Omo Basin. Thus, sedimentation may explain this ca. 2.0 Ma turnover event, but it probably also marks some biological events such as the extinction of *T. brumpti*, *P. mutiwa*, and *C. williamsi*, and the first appearances of *Lophocebus* sp. nov., *Cercopithecus* sp., and *Procolobus* sp. The more homogenous distribution of species in the Turkana basin is reflected in the relatively small number of events between 3.4 and 2.0 Ma.

When the species ranges are studied together, there are three successive sets of cercopithecid species in the Turkana basin. The oldest is typified by Kanapoi where *Pp. ado* is predominant, and a small colobine is also present (Leakey et al., 1995). Fossils from Allia Bay in the Lonyumun Member of the Koobi Fora Formation also have a small papionin as well as some colobines, which date to 3.9 Ma (Coffing et al., 1994). As noted by many previous authors (e.g. M. G. Leakey, 1976; Feibel et al., 1991; Delson, 1984; Delson et al., 1993) *Theropithecus* does not appear to occur below the Lokochot Tuff. Following this, from perhaps as early as 3.6 Ma, but certainly by 3.4 Ma another set of species is most common. *T. brumpti*, *P. (Dinopithecus) quadratirostris*, *R. turkanaensis*, and *P. mutiwa* typify this assemblage. *Cercopithecoides* may also be present, but is only well known from the Upper Burgi member. Rare occurrences of *T. o. darti* and later *T. o. oswaldi*, *Cercopithecus*, Colobinae sp. A, and small papionins also occur in this set. This species set occurs through the Lomekwi Member of the Nachukui Formation, the Tulu Bor Member of the Koobi Fora formation, and members B through Lower G of the Shungura Formation. This set basically occupies faunal zones B and C of Harris (1983) from Koobi Fora. The upper part of the Burgi Member yields an assemblage which is transitional between the second and third species sets.

The youngest set of cercopithecid species represented is early Pleistocene in age. It is typified by *T. oswaldi*, *C. kimeui*, *Lophocebus* sp. nov., *Cercopithecus* sp. and cf. *Procolobus (Piliocolobus)* sp. One important absence is *T. brumpti*, which makes its last appearance at approximately 2.0 Ma. This group occurs in the KBS and Okote Members of the Koobi Fora Formation and the Shungura Formation above G13, particularly members K and L. Samples from the upper members of the Nachukui Formation are small and so far contain only *T. oswaldi*, and are therefore likely to represent the same species set. This group is equivalent to the *Metridiochoerus andrewsi* and *Metridiochoerus compactus* faunal zones of Harris (1983).

The relative abundance of Delson's four dental types in the Turkana Basin show a pattern that is generally similar to that of the Afar Depression. There is an early period that is equivalent to the first species set. It occurs at Kanapoi and possibly Allia Bay (Leakey et al., 1995). In this period, non-*Theropithecus* papionins are the most common cercopithecid. Exact data are not available, but it is clear that colobines are rare, and *Theropithecus* and Cercopithecini are absent.

From the Lokochot Member, and especially the Tulu Bor Member through the Okote Member of the Koobi Fora Formation, the Lomekwi through Nariokotome members of the Nachukui Formation, and members A through upper G of the Shungura Formation, *Theropithecus* predominates (Figures 6.6 – 6.8). The relative abundances in Mbs. J-L of the Shungura Fm. may be different, but given their small sample sizes, this is difficult to interpret. This period is equivalent to the second and third species sets. It is worth noting, however, that the dominant species of *Theropithecus* in the early part of the Turkana basin is *T. brumpti*. In the Afar Basin and in the Turkana Basin after about 2.3 Ma *T. oswaldi* is the dominant species of *Theropithecus*. Colobines and non-*Theropithecus* papionins are generally present but of low abundance throughout the section, and guenons are very rare, and often absent.

Figure 6.6 Relative abundance of dental groups in the Shungura and Usno Formations.

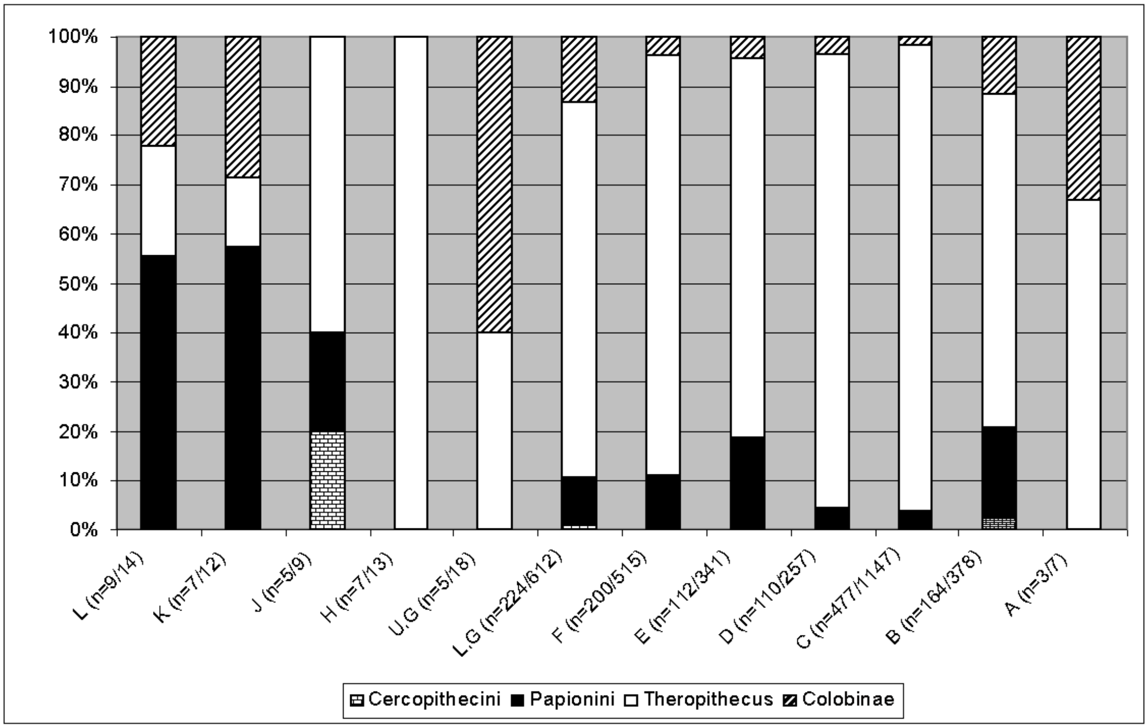


Figure 6.7 Relative abundance of dental groups in the Koobi Fora Fm.

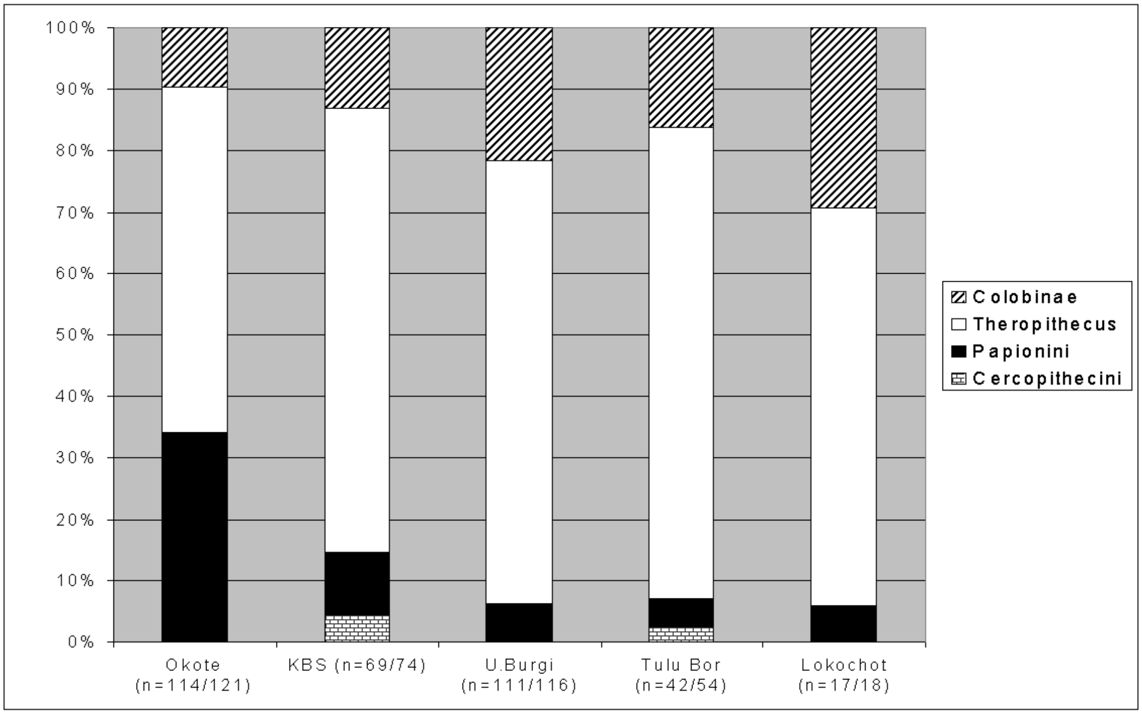
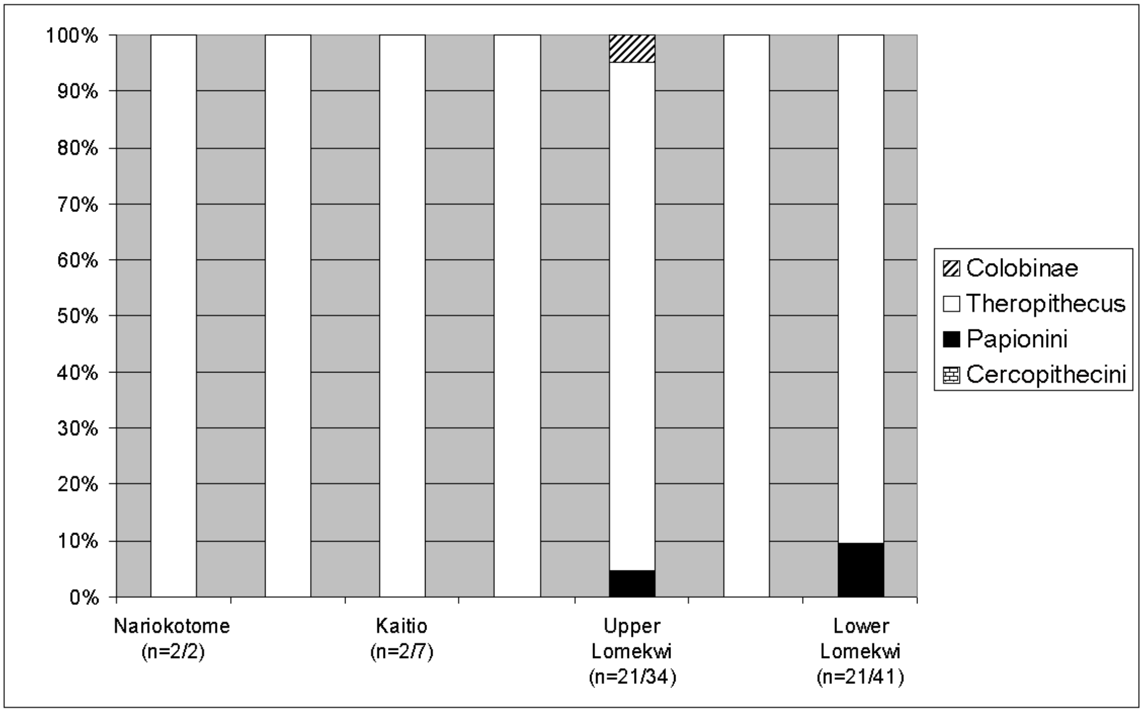


Figure 6.8 Relative abundance of dental groups in the Nachukui Fm.



Specific level comparisons

Of the thirteen species present, two are almost certainly conspecific with those from the Turkana basin. (Table 6.5 presents presence/absence by region). These are *Theropithecus oswaldi* and *Cercopithecoides kimeui*. Both of these taxa are represented by comparatively well preserved crania in both regions, and these are strikingly similar. Only *T. o. oswaldi* is well represented in the Turkana Basin. The remains of *T. o. darti* and particularly those of *T. o. leakeyi* are quite fragmentary. In addition to these two, *Rhinocolobus turkanaensis* is probably shared between the two regions, based on the mandibular material from Hadar. Certainty about the Afar identification requires the recovery of facial material, which is highly distinctive in this taxon. There are four additional species that are possibly shared between the two basins. These cannot be known with more certainty due to a lack of diagnostic material at one or either of the basins, but there is enough to suggest a possible connection. Each of these is discussed individually below.

Cercopithecus sp. from Andalee cannot be positively identified in the Turkana basin, largely due to the fragmentary nature of the material from the latter region. It is definitely not conspecific with Cercopithecini gen. et sp. indet. and is not likely to be conspecific with the specimens of *Cercopithecus* from the Shungura Formation that are similar in size to *C. nictitans*. However, the larger *Cercopithecus* from the Shungura Formation, and the *Cercopithecus* from the KBS member of the Koobi Fora Formation is similar in dental size to that from Andalee. That said, it does not mean that they are conspecific, only that they may be.

Table 6.5 Presence of taxa in the Afar and Lake Turkana Regions. X = present, ? = possibly present, and cf. for tentatively assigned material. See text for further explanation.

Taxon	Afar Depression	Turkana Basin
Cercopithecus cf. *aethiops*	X	?
C. sp - "*C. nictitans*-sized" – if distinct		X
Cercopithecini gen. et sp. indet.		X
Pliopapio alemui	X	
Parapapio ado		X
Pp. cf. *jonesi*	X	
Lophocebus sp. nov.		X
Papio (Dinopithecus) quadratirostris		X
P. (Papio) sp. Small	X	
P. (Papio) cf. *hamadryas* ssp.	X	
Papionini sp. B		X
Theropithecus (Omopithecus) brumpti		X
T. (Theropithecus) oswaldi darti	X	X
T. (Theropithecus) o. oswaldi	X	X
T. (Theropithecus) o. leakeyi	X	?
Kuseracolobus aramisi	X	
Rhinocolobus turkanaensis	cf.	X
cf. *Paracolobus chemeroni*	X	
Pc. mutiwa		X
Cercopithecoides williamsi		X
Cs. kimeui	X	X
cf. *Cs*. sp. Maka	X	
cf. *Cs*. sp. nov. - Leadu	X	?
Colobus cf. *angolensis*	X	?
Procolobus (Piliocolobus) sp.		X

Colobus cf. *angolensis* from Andalee could be conspecific with some of the material tentatively assigned to *Procolobus* from the Omo. The Omo material is entirely composed of isolated teeth and is all of a similar size to that from Andalee. The material from Koobi Fora on the other hand has morphological differences that most likely place it in a separate genus from the Andalee material. The large colobine mandible, MAK-VP-1/35, is tentatively assigned to *Cercopithecoides* and does not represent *C. kimeui*, but is close in dental size to *C. williamsi* from Koobi Fora and the Omo. While it does differ to some degree in corpus morphology, there is insufficient material to determine if this difference is enough to rule out conspecificity. Finally, there is a small series of colobine teeth from the Omo and gnathic remains from Koobi Fora, which is similar in dental size to both *Kuseracolobus aramisi* and the Leadu colobine, which could potentially represent one of these two species. Given the age of the Turkana material, and the other associated cercopithecid taxa, it is more likely to represent the Leadu colobine than *K. aramisi*. Thus there is a minimum of two shared species, and probably at least three of them. Additionally, there are potentially four more shared species for a possible total of seven, approximately half of the total for each basin.

There are also six species present in the Afar basin that appear not to be shared with the Turkana basin. However, there is always the possibility that isolated teeth, particularly from the Omo, may represent one of these taxa. These include *Pliopapio alemui*, *Parapapio cf. jonesi*, the small species of *Papio* from Bouri, cf. *P. hamadryas*, *Kuseracolobus aramisi*, and *cf. Paracolobus chemeroni*. The possibility of *Pl. alemui* and *K. aramisi* being present in the Turkana basin has been discussed by Frost (in press).*Parapapio* cf. *jonesi* appears to be absent, unless ER 1562 does in fact represent this species, as discussed by Delson (1984). See the section for *Theropithecus oswaldi darti* in Chapter 5 for further discussion. There is no evidence for *P. hamadryas* in the Turkana basin, and there is no evidence for the presence of *P. chemeroni* either (Leakey and Leakey, 1973a; Leakey, 1976; 1982; 1987; Harris et al., 1988).

There are at least seven species from the Turkana basin that are not shared with the Afar depression. These include Cercopithecini gen. et sp. indet. (the talapoin-sized species), *Parapapio ado*, *Lophocebus* sp. nov., *Papio (D.) quadratirostris*, *T. brumpti*, *P. mutiwa*, and cf. *Procolobus (Piliocolobus)* sp. The small cercopithecin is unique in the

African fossil record, and predates the Afar *Cercopithecus* by approximately 2.5 Myr. It is smaller in dental size than would be expected for the species represented by small humerus WEE-VP-1/6. Both *T. brumpti* and *P. mutiwa* have only been recovered from sediments of the Turkana basin. *Parapapio ado* appears to be known only from Laetoli and Kanapoi, but may also be represented by some of the specimens allocated to Papionini sp. size A from the Turkana basin. It is absent so far in the Afar region. There is no evidence for the presence of either *Lophocebus* or *Cercocebus* in the Afar region. Kalb et al. (1982a) included *Dinopithecus* cf. *ingens* in their species list for the Matabaietu Fm., but this material was assigned to *T. o. oswaldi* in this analysis. While *Procolobus (Piliocolobus)* was not found in the Afar sample, this taxon was included in the species list of Alemseged and Geraads (2001) for the Afar site of Asbole. If this diagnosis is correct, then this species may be shared with the Afar sample.

The difference between the Afar and Turkana cercopithecid faunas during the Middle and Late Pliocene was greater than is the case now. In the Afar depression today, there are three species of cercopithecids present, including a hypbrid zone between two subspecies of *Papio hamadryas*: *P. h. anubis*, *P. h. hamadryas*. The other two species are *Cercopithecus aethiops*, and *Colobus guereza*. In the Omo valley there are four species of cercopithecid present: *Cercopithecus aethiops*, *Cercopithecus neglectus*, *Papio hamadryas anubis*, and *Colobus guereza*. (Kingdon, 1971; Napier, 1981; 1985). Thus three out of four taxa are shared between the two basins. It is not clear at what point the two regions became more similar from their greater difference during the Early and Middle Pliocene, but during "Pinnacle" time, approximately 1.8 Ma, both of the Afar species present are known in the Turkana Basin. However they are only two of the eight species known from the Turkana Basin at this time. The modern Afar and Turkana faunas are, however, less different from one another than the either is from the West African Tai Forest in Ivory Coast, or Bioko Island, where none of the same species are found. Overall, the difference between the fossil cercopithecid assemblages of the Turkana and Afar Basins is generally similar to the difference between Kibale Forest in Uganda and Ipassa Makokou Reserve in Gabon. These two forests have eight and nine species of cercopithecids respectively, but only share two species: *Lophocebus albigena* and *Colobus guereza*. Both regions include moist forest, but lie in different regional primate communities (Oates, 1996). While there are many difficulties comparing two fossil basins and two modern forests, perhaps this level of difference is analagous to the situation in the Pliocene between the Afar and Turkana Basins.

When the sequence of FADs and LADs from each basin are compared, they show several similarities, but also some important differences. First, preservational factors are important in both records, with FADs and LADs found at the oldest and youngest levels respectively. Additionally, both show a cluster of first appearances around 3.4 Ma. This is partly due to an increase in sample size in both regions following long periods represented by small samples. While this event is probably largely caused by taphonomic factors, there is likely to be at least one significant biological event. This is the appearance *Theropithecus* in both assemblages. While the *T. oswaldi* lineage may first appear as early as 3.89 Ma in the Afar basin, it seems to become an important member of most East African faunas around 3.4 Ma, and this is preserved in both basins. The other events in the two basins do not appear to be synchronous. This is probably in large part caused by differences in regional preservation or environments.

Generic level comparison

At the generic level, however, the two samples are more similar. Of the 10 potential genera from the Afar basin, four are also found with reasonable certainty in the Turkana Basin. These are *Cercopithecus*, *Papio*, *Theropithecus*, and *Cercopithecoides*. All four of these genera are represented by clearly identifiable cranial and gnathic remains in both regions. *Paracolobus* and *Rhinocolobus* are probably shared as well. The identifications of both of these genera in the Afar basin are based on mandibular and humeral remains, but these taxa are best diagnosed in the rostrum. Their presence in the Afar basin is therefore likely, but not as certain as the four genera above.

There are also several genera that are potentially shared between the two regions. The first of these is *Parapapio*. *Pp. ado* has been identified at Kanapoi in the southern part of the Turkana basin, but the generic status of this species is still uncertain, due to the lack of known facial material (see chapter 5 for discussion). If its allocation to *Parapapio* is shown to be correct, then this genus would occur in both regions (given the presence of *Pp.* cf. *jonesi* in the Afar Depression).

While *Pliopapio* cannot be positively identified in the Turkana basin (Frost, in press), it cannot be ruled out completely either. The mandible WT 16752 and the fragments ER 3122 and 3027, as well as several isolated teeth identified as Papionini sp. A could possibly represent this taxon, although they are as likely to represent other taxa such as *Parapapio*. A similar situation applies to the Afar genera *Kuseracolobus* and *Colobus* (see Frost, in press for a discussion of *Kuseracolobus* distribution). Both of these genera are represented by fairly large samples of craniodental remains in the Afar region.

Isolated teeth from the Shungura and Usno identified as Colobinae sp. A in Chapter 5 could possibly represent this species. Also, some of the material identified as *Colobus* sp. from the Shungura formation could possibly be conspecific with *Colobus* sp. from Andalee. If the Leadu colobine were demonstrated to represent a genus other than *Cercopithecoides* it could still possibly represent a shared taxon with the Colobinae sp. A dental material from the Turkana basin.

There are no taxa from the Afar depression that are definitely lacking in the Turkana basin, but the probability is high that at least some of the above four genera are absent in the Turkana Basin. In particular, the possibility that *Kuseracolobus* or *Pliopapio* is represented in the Turkana basin seems remote given the relatively large age difference and the possible differences in environment between Aramis (WoldeGabriel et al., 1994) and deposits in the Turkana Basin closest in age (Coffing et al., 1994; M.G. Leakey et al., 1995; Wynne, 2000). Finally, there are two genera, *Lophocebus* and *Procolobus*, in the Turkana basin that do not appear to be represented in the Afar basin. On the other hand, Alemseged and Geraads (2001) listed *Procolobus* among the four genera of monkeys found at Asbole, in the Afar depression. If this identification proves to be correct, then it would indicate that this genus is shared after all, but is apparently not present in the sample included in this thesis.

Higher level comparison

When comparisons are made using the relative abundance for the four dental groups, the two basins are quite similar for most of the Middle Pliocene through Early Pleistocene. Figures 6.5 – 6.8 show the relative proportions of these groups from the different regions. Data for the different formations of the Turkana basin have not been pooled as taphonomic, sample size, and collection differences make them not entirely comparable. Proportions from the Omo members A though H are from Bobe (1997) and only include the sample from the American contingent of the International Omo Expedition. Those from the Nachukui Formation are from Harris et al. (1988), and those from Koobi Fora are from M. G. Leakey and R. E. F. Leakey (1973a; 1976), M. G. Leakey (1976), Delson et al. (1993), and personal observation.

To facilitate this comparison, a correspondence analysis was performed using the abundance data for the four dental categories from the different stratigraphic units. Correspondence analysis is an ordination technique, similar to principal components analysis, designed for frequency data of nominal variables (Greenacre, 1993). Correspondence analysis is performed on a contingency table where frequencies are given for both row and column variables. In this case, the four dental categories are the rows, and the geologic units are the columns, and each cell represents the relative abundance of a particular dental taxon in a specific geologic unit. Due to large differences in sample size, a second table was also created where raw abundances were converted into relative abundances by dividing the values for each unit by the sample size for that unit. The data were then entered into matrices with the four suprageneric groups as rows and the different members as columns. A correspondence analysis was then performed on these contingency table using NTSYSpc 2.1 (Applied Biostatistics, 2000). This analysis produces a bi-plot where both nominal row and column variables are plotted. Results for the raw abundance data and the relative abundance data are qualitatively similar, but the latter shows a larger scatter of values. As a result figures 6.9 and 6.10 show only the results from the table using relative abundances.

From earlier than 3.4 through 1.5 Ma both basins are dominated by *Theropithecus*, which typically comprises more than 75% of the sample in any given unit. Both non-*Theropithecus* papionins and colobines are rarer, but constantly present in both basins. *Cercopithecus* is absent from the Afar depression until the Pleistocene (with the possible exception of the Wee-ee humerus) and is extremely rare in the Turkana basin. This dominance of *Theropithecus* for the majority of stratigraphic units in both basins is shown by the large cluster of points in the central left side of figures 6.9 and 6.10 near the point for *Theropithecus*, reflecting low scores on dimension 1. It is worth reiterating that, while these proportions are similar, the species making them up are often different. For example in the Afar basin *T. oswaldi* is the most common cercopithecid, whereas in the Turkana basin *T. brumpti* predominates though about 2.3 Ma (Member F), and is absent after about 2.0 Ma.

Prior to about 3.6 Ma, the two regions are quite different. *Theropithecus* is generally absent in both regions. That is where the similarities end. In the Afar region, most of the 3.75 Ma and older sequence has too few specimens to yield reliable abundances, but in the Aramis member there is a very large sample. At Aramis colobines are predominant, or at least co-dominant with non-*Theropithecus* papionins. The distinctiveness of the Aramis sample in its colobine proportion can be seen in its isolated position near the center of figure 6.10. For the Turkana basin, quantitative data are not available from Pliocene sites older than 3.6 Ma. However, it is clear from the discussion of Leakey et al. (1995) that *Pp.* aff. *ado* from Kanapoi is very common, and colobines

Figure 6.9 Scatter plot of first and second axes of correspondence analysis of dental group relative abundance. '■' indicate taxa, '●' for Afar units, '+' for Omo, 'X' for Koobi Fora, and '*' for Nachukui. The abbreviations are as follows: Uand = Upper Andalee Mbr.; Land = Lower Andalee; Bodo = Upper Bodo Beds; Pinn = Pinnacle; UKH, KH, DD,SH, Bas = Upper Kada Hadar, Main Kada Hadar, Denen Dora, Sidi Hakoma, and Basal Mbs, of the Hadar Fm.; Mat = Matabaietu Fm.; Hata = Bouri Fm., Hata Beds; Ahm = Ahmado; Sub SHT = Formation W below the Sidi Hakoma Tuff; VT3-CT = Formation W between the VT3 and CT; Bel, Adg, Ara = Belohdelie, Adgantole and Aramis Mbs., Sagantole Fm.; A-K = Shungura Fm.; UG, LG = Upper and Lower G, Shungura Fm.; Ok, KBS, Ubg, TB, Lk = Okote, KBS, Upper Burgi, Tulu Bor, and Lokochot Mbs., Koobi Fora Fm., Unach = Kalochoro through Nariokotome Mbs., Nachukui Fm., LL,ML,UL = Lower, Middle and Upper parts of the Lomekwi Mbr of the Nachukui Fm.

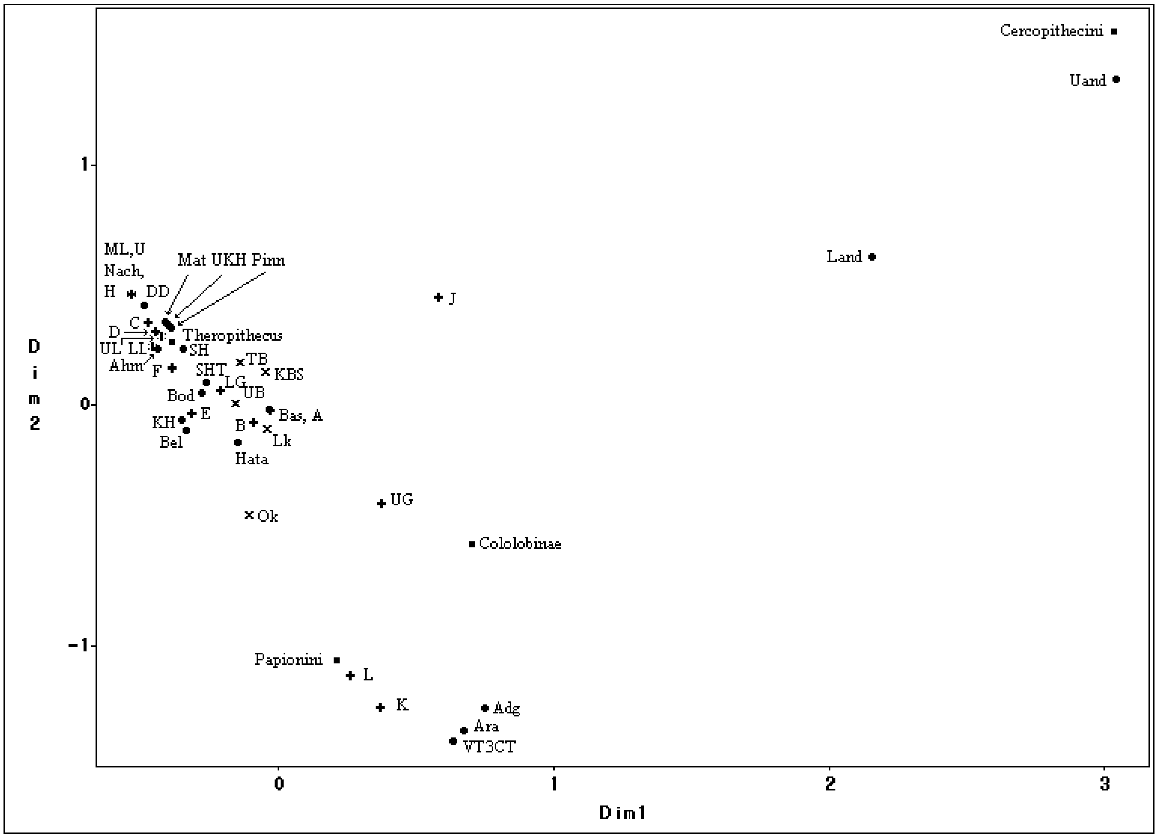
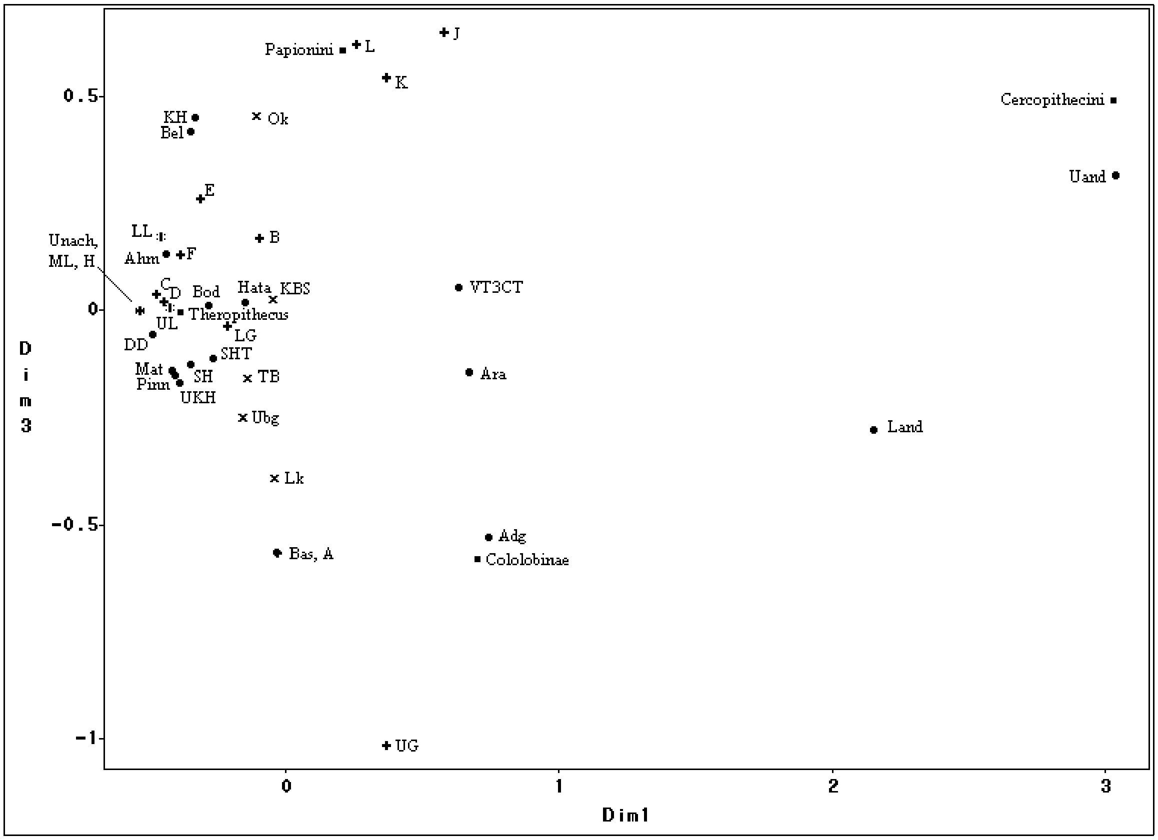


Figure 6.10 Scatter plot of first and third axes of correspondence analysis. Symbols as for figure 6.9.



very rare, being represented by only a few specimens. Papionins other than *Theropithecus* also predominate in the 3.9 Ma sediments at Allia Bay (Coffing et al., 1994;Bobe pers. com.). While the two basins appear quite different during this early time period, it should be kept in mind that this is essentially a comparison between a single site in the Afar Basin with two (Kanapoi, Allia Bay) in the Turkana. As a result, these differences may not be as pronounced on a region-wide scale. Additionally, the Turkana sites are separated by 220 and 500 Kyr from Aramis, respectively.

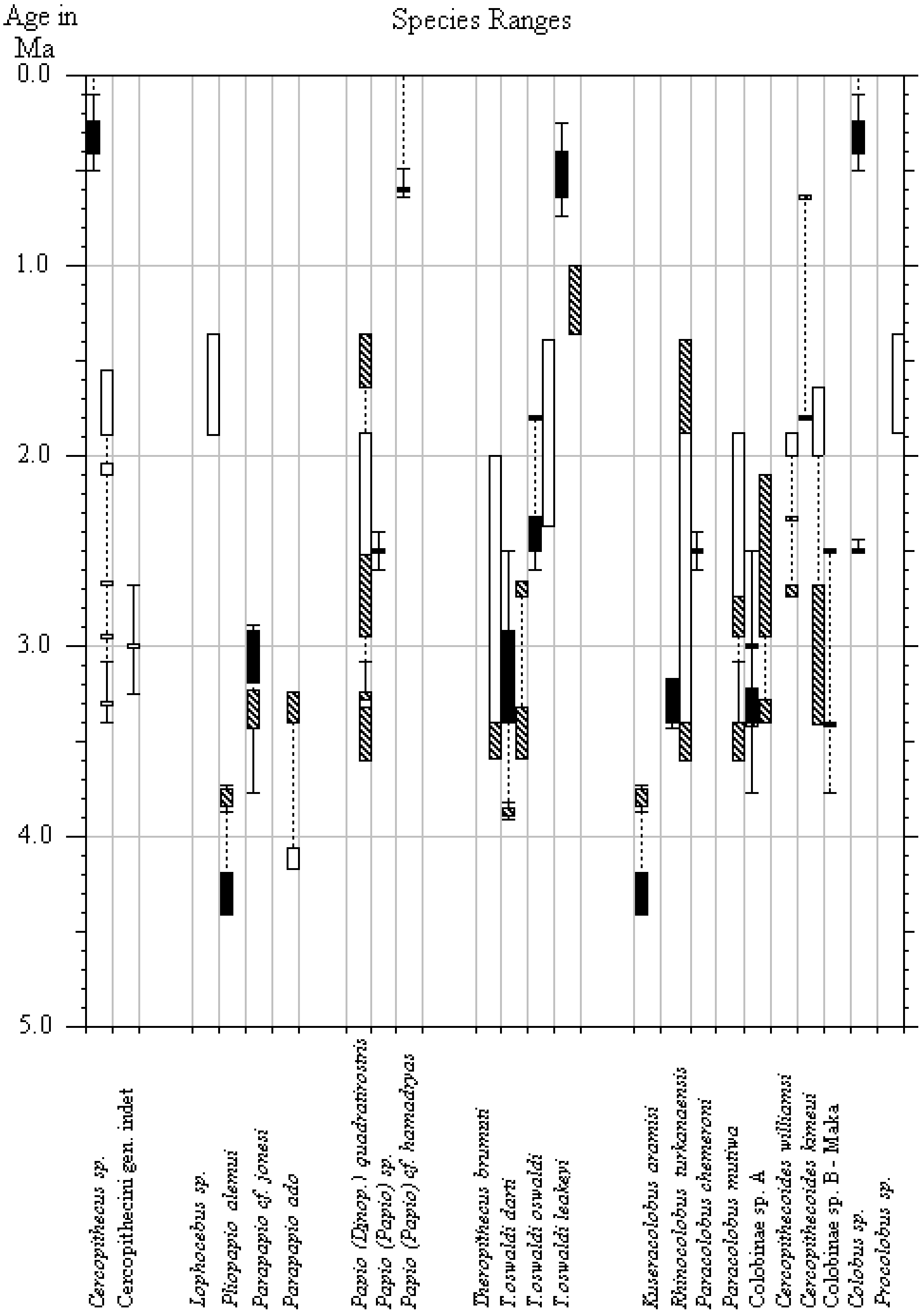
Samples of middle Pleistocene age are only present in the Afar depression. The Upper Bodo unit shows a pattern of abundance similar to other horizons dominated by

Theropithecus, but the Lower and Upper deposits of the Andalee Mbr. of the Wehaietu Fm. are clearly very different. *Theropithecus* is rare and absent (respectively) from these beds, which are dominated by colobines and cercopithecins. In fact, the Andalee Mbr. deposits (and other Pleistocene sites in the Afar region, such as Asbole) may be unique in Africa for the high proportion of cercopithecins. This distinctiveness is clearly shown by their high scores on both dims 1 and 2 on figure 6.9.

Summary

At the specific level the Afar Depression and the Turkana Basin are quite distinct. Of at least 13 species in the Afar Depression and 14 in the Turkana basin, approximately only half are possibly shared. The most likely number, however, is probably smaller than this and could be as few as 2. There are four chronological species sets in the Afar depression, and three in the Turkana Basin (see figures 6.1 and 6.2). Figure 6.11 shows the species ranges for both basins. In each basin, there is an Early Pliocene set represented by Aramis and Kanapoi for the Afar and Turkana Basins respectively. In each basin there is also a Middle Pliocene set, in both cases exemplified by the appearance of *Theropithecus* as well as a diversity of colobines. In the Afar Depression, the third species set is early Late Pliocene in age, whereas in the Turkana basin the third set is latest Pliocene and Early Pleistocene in age and is exemplified by the appearance of several more modern forms. Thus the two basins differ significantly in the timing of the turnover between their second and third species sets. This occurs between 2.9 and 2.5 Ma in the Afar Basin, but at ca. 2.0 Ma in the Turkana Basin. Modern forms appear in the Afar Depression in the fourth species set, which is Middle Pleistocene in Age.

Figure 6.11 Species ranges for the Afar and Turkana basins. Afar ranges are shown as black boxes and are on the left side of species columns. Turkana ranges are shown as white boxes and are on the right side of species columns. Others symbols as for figure 6.1.



Periods with comparatively large numbers of first and last appearance data occur at the boundaries of these species sets. They show little synchrony between basins, except around 3.4 Ma, and are probably driven to a large extent by differential preservation in the two regions. There may be evidence for a turnover event in the Turkana Basin around 2.0 – 1.9 Ma, between the second and third species sets. This same change may be marked by the appearance of *C. kimeui* at the Pinnacle site in the Afar Basin. Additionally, there is turnover between the four species sets of the Afar Depression as well, but it is not possible to tell whether these are rapid or gradual events due to the large gaps between groups.

At the generic and suprageneric levels, however, the cercopithecid records of the two regions are quite similar to one another. Of the 10 genera present in the Afar Basin, 4 are shared with a high degree of confidence based on well-preserved diagnostic material in both basins. These are *Cercopithecus*, *Papio*, *Theropithecus*, and *Cercopithecoides*. *Rhinocolobus* and *Paracolobus* are probably shared as well, based on mandibular material from the Afar Basin, but require the recovery of better material for confirmation. *Parapapio* is also shared, provided *Pp. ado* is a member of this genus. The remaining Afar genera could possibly be shared, but there is no diagnostic material to support this. *Lophocebus* and *Procolobus* are known from the Turkana basin, but are not present in the Afar sample.

In the proportions of Delson's four suprageneric dental groups used here the Afar and Turkana Basins are very similar, with *Theropithecus* dominating both assemblages between about 3.4 and 1.0 Ma. In this respect, both are similar to other collections from East Africa, such as Olduvai Gorge (Jolly, 1972; Leakey and Leakey, 1973b). This dominance of *Theropithecus* may represent a widespread East African phenomenon, but is quite distinct from broadly contemporary South African sites, where the genus is either absent or rare (Freedman, 1957; 1961; 1965; Eisenhart, 1974; Delson, 1984; Brain, 1982; Benefit, 1999). Prior to 3.4 Ma, the Afar and Turkana basins seem to differ from one another, with high relative abundance of colobines at Aramis and a high proportion of non-*Theropithecus* papionins at Kanapoi (Leakey, et al., 1995) and Allia Bay.

The two regions are not directly comparable after approximately 1.0 Ma, due to an absence of material from the Turkana basin. In the Afar, the Middle Pleistocene unit "U" at Bodo and other areas is similar to earlier sites where *Theropithecus* predominates. The younger Middle Pleistocene levels in the Andalee Member, however are distinctive in their high proportion of Colobines and Cercopithecins.

When all of the data are considered together, it appears that the two basins are quite distinct from one another in the Early Pliocene in all aspects. There appears to be turnover in both basins sometime prior to 3.4 Ma, where there is a shift in proportions as well as the first appearances of several species. This period of turnover is also marked in the bovids from the Middle Awash (Vrba, 1997). From this period through about 1.8 Ma in the Afar basin and 1.4 Ma in the Turkana basin, *Theropithecus* dominates, and the two regions are more similar to one another above the species level, but still distinctive at the species level. There is turnover between the second and third species groups in the Afar basin sometime after 2.9 Ma but before 2.5, whereas in the Turkana basin there is appears to be turnover at approximately 2.0 – 1.9 Ma. After this period, the Turkana basin becomes more similar to the Afar basin, it is during this period that most of the definitely shared taxa occur. There are still some taxa that are not shared at this time. The fourth

Afar species group has no direct comparison in the Turkana basin. This group is middle Pleistocene in age, and shows a shift in abundance as well as species representation from earlier periods, although these changes are not all synchronous. When this species group appears is impossible to say as there is a large gap from approximately 1.8 Ma to 0.64 Ma, however Vrba (1997) does note a shift in bovid species between about 1.0 Ma and 0.64 Ma.

Chapter 7

Discussion and Conclusions

The primary objective of this thesis was to systematically describe the fossil cercopithecids from the Afar depression of Ethiopia, from localities younger than 4.4 Ma. A second objective of this dissertation was to compare the evolutionary pattern of the Afar cercopithecids with that from the Turkana Basin. Describing the Afar cercopithecids included determining how many species were represented in the sample, and their taxonomic affinities. As briefly summarized in chapter 2, most of the paleontological collecting sites within the Afar depression are well controlled chronologically (see figure 2.5 and table 3.1). For most taxa, this allowed relatively precise determination of their first and last appearances within the different strata of the basin (see figure 6.1).

The evolutionary pattern described from the Afar Basin was compared with that from the Turkana Basin in order to put it into a larger context. The Turkana Basin was chosen because it is the only other African paleontological collecting region that covers approximately the same time period as the Afar Basin and also has an extensive cercopithecid fossil record. Importantly, most of the fossils are from known stratigraphic contexts with good chronological control allowing comparison of species ranges, and other evolutionary patterns.

Cercopithecidae of the Afar Depression

The cercopithecid fossil record from the Afar depression was described in chapter 4. It adds considerably to what is known of African Pliocene and Pleistocene cercopithecid evolution. Thirteen fossil species were found through the sequence, representing approximately 10 genera. A minimum of three and possibly four species are new. At least two of these species are also in new genera. In addition to increasing the number of known taxa, the sample also provides new information about many previously known species. It extends both the geographic and temporal ranges of several different species, and for some it includes morphological and anatomical regions unknown from other localities. Additionally, the Afar sample includes strata that are of ages not well sampled elsewhere in Africa, such as the interval near 4.5 Ma. Various findings about the species are described individually below, in systematic order by tribe and age within tribe. *Theropithecus* is placed at the end of the papionins because of it represents a separate morphology (one of Delson's four [1973] dental groups) from the other papionins.

Cercopithecini

Cercopithecus sp.

As discussed by Leakey (1988), there are very few fossils of *Cercopithecus* known, and those are fragmentary. The sample from Andalee and Issie, which is of Middle Pleistocene age, is one of the best, with several maxillary and mandibular specimens, as well as some tentatively assigned postcrania. This sample has a few features that indicate that it may represent the extant species *C. aethiops*, which occurs in the Afar region today. However, given the difficulty of diagnosing species of *Cercopithecus* based on osteological and dental characters this must be considered very tentative.

Papionini

Pliopapio alemui

Pliopapio alemui represents a newly identified genus and species, known with certainty only from the Afar basin. There are similarly sized papionin teeth and jaw fragments from several East African sites, while these can not be positively identified as *Pl. alemui*, they also can not be completely ruled out (Frost, in press). This is a small papionin that lacks the two most diagnostic features of *Parapapio*: it clearly possesses an anteorbital drop and a distinct ophryonic groove, both of which are characters shared with *Papio*, *Mandrillus*, *Theropithecus*, *Paradolichopithecus*, *Gorgopithecus*, and some species of *Macaca*. However, *Pliopapio* lacks the diagnostic derived features of any of these latter genera.

Parapapio cf. *jonesi*

Represented by a well-preserved partial cranium and a second more fragmentary face, *Parapapio* cf. *jonesi* from Hadar is the only definite Pliocene occurrence of the genus in East Africa. It does appear to occur, based on a partial face, at the late Miocene site of Lothagam (Leakey et al., in press). *Parapapio* is represented by as many as four species in South Africa, and is often the most abundant Pliocene cercopithecid there. In East Africa on the other hand, *Parapapio* (along with papionins other than *Theropithecus* in general) is comparatively rare. *Parapapio* has been mentioned at several East African sites. *Pp. ado* from Laetoli and Kanapoi (Leakey and Delson, 1987; Leakey et al., 1995) was placed in the genus *Parapapio* largely due to a lack of mandibular corpus fossae, a feature shared with other genera (e.g. *Papio (Dinopithecus)*, *Pliopapio*, and some

Macaca). *Pp. ado* and *Pp. whitei* were described in the Lomekwi Member of the Nachukui Formation by Harris et al. (1988). In this analysis the Nachukui "*Pp. ado*" material was identified as a small papionin other than Laetoli *Pp. ado*, whereas the "*Pp. whitei*" was identified as representing a large papionin of unknown genus. The Hadar specimens are the only *Parapapio* fossils from the Pliocene of East Africa identified on the basis of facial material, and therefore the only occurrence of this genus in East Africa during the Pliocene that is securely established.

Papio (Papio) sp. A.

The small species of *Papio (Papio)* from Bouri may represent a new taxon, but more material is required to evaluate this possibility. There are a few small forms of *P. (Papio)* known: *P. izodi*, *P. hamadryas* "angusticeps" and the extant *P. h. kindae*. The Bouri specimen is distinguished from these in the morphology of its maxillary ridges, and to some degree its nasals. It is not clear, however, how much taxonomic weight should be assigned to these features, given their variability in extant subspecies of *Papio hamadryas*.

The Bouri specimen is also one of the earliest occurrences of the subgenus in the fossil record. Dated to just over 2.5 Ma the Bouri species is roughly contemporary with the first appearance of *P. (Papio)* in South Africa at Sterkfontein, where both *P. izodi* and *P. h. robinsoni* are present. In East Africa, two specimens from the Upper Laetolil Beds, a distal end of a humerus and a dP^4, were tentatively termed cf. *Papio* by Leakey and Delson (1987), and could possibly represent *P. (Papio)*. This diagnosis was largely based on the large size of the material and the adaptations for terrestrial locomotion in the humerus. It is impossible to tell whether this material represents *P. (Dinopithecus)* or *P. (Papio)*, or any other large papionin. The *?T. baringensis* holotype from the Chemeron was originally described as *P. baringensis* (Leakey, 1969). If it does not represent *Theropithecus* it could potentially be a species of *Papio*, but it lacks some features of *P. (Papio)*, such as relatively deep maxillary fossae, larger incisors, and a posteriorly positioned sagittal crest.

cf. *Papio hamadryas* ssp.

This species is tentatively identified from a single molar fragment from Unit “U” at Bodo. Morphologically this specimen is could be any large papionin other than *Theropithecus*. It has been tentatively assigned to this species based on the identification of more complete material at the site of Asbole, which is close to Unit “U” in age and located fewer than 25 kilometers North of Andalee (Alemseged and Geraads, 2001).

Theropithecus oswaldi

There are a large number of well-preserved cranial and post-cranial specimens of the *Theropithecus oswaldi* lineage known throughout Africa. The material from the Afar, however, adds a substantial amount of new information. If the specimens from the Belohdelie Member of the Sagantole Formation do in fact represent *Theropithecus* then they would mark the first occurrence of the genus at nearly 3.9 Ma. This would make *Theropithecus* the first extant papionan genus to appear in the fossil record. It would also then be the second extant catarrhine genus to appear, after *Macaca*.

As discussed by Eck (1993) the sample of *T. o. darti* from Hadar greatly increases what is known of the early part of this lineage, particularly of the postcranium and male cranial morphology which is not well represented at Makapansgat. The large sample from Hadar contributes to understanding of the variability in this taxon. For instance, it can be seen in figure 4.10 that the size range of the molars is about twice as large at Hadar as it is at Makapansgat. Additionally, the material from the Middle Awash, from below the Sidi Hakoma Tuff slightly extends the range represented by relatively complete cranial material back to greater than 3.4 Ma. There is also a large collection of *T. o. oswaldi* with several partial crania and some stratigraphically associated postcrania. This sample is important as much of it represents some of the oldest members of this subspecies known. It shows that the features used to separate *T. o. darti* from *T. o. oswaldi* had evolved by 2.5 Ma, at least in this sample.

In spite of a near pan-African distribution, and common occurrence at several sites, there is no well-preserved cranial material of *T. o. leakeyi* outside of the Afar basin. The sample from Unit “U” includes four partial crania, one being nearly complete. This allows a much better assessment of the phylogenetic relationships of the lineage as a whole. Analysis of this sample confirms that many of the trends observable between *T. o. darti* and *T. o. oswaldi* continue on into the Middle Pleistocene and also shows that some of the features found in *T. o. darti* that have been used to separate it at the specific level from *T. o. oswaldi* are also present in *T. o. leakeyi*. The latter implies that these features are either variable within the lineage, or that *T. o. oswaldi* is not a direct intermediate between the other two. It is also clear that the difference between *T. o. darti* and *T. o. oswaldi* is no greater than the difference between *T. o. oswaldi* and *T. o. leakeyi*. Given the large number of morphological trends, and otherwise similar morphology among these three groups it seems unlikely that they represent distinct evolutionary branches. They appear to be best recognized as a widely distributed and geographically variable taxon, not unlike modern *Papio hamadryas*, that shows a considerable amount of anagenetic morphological change through time as well.

Colobinae

Kuseracolobus aramisi

As with the other species from the Aramis Member, *Kuseracolobus aramisi* represents a new and unique genus and species. It can not be positively identified at any other Pliocene sites. There are, however, similarly sized colobine dental fragments from several areas, including Laetoli and older strata at Koobi Fora and the Omo, that cannot be ruled out as representing *K. aramisi* (Frost, in press). It is intermediate in size between the large Pliocene and Early Pleistocene genera and the extant forms, and it displays an interesting mosaic of features relative to the other known fossil colobines.

cf. *Rhinocolobus turkanaensis*

Several mandibular fragments, a deformed maxilla, and possibly a distal fragment of a humerus, all from Hadar, have tentatively been assigned to this species. It is primarily known from the Koobi Fora and the Omo, where it is represented by well preserved crania and mandibles. Unfortunately, the most diagnostic features of this genus are in the rostrum. However, the Afar mandibles are a very close match to those from the Turkana Basin. Furthermore one of the characteristics that separates *Rhinocolobus* from the other large colobine genera is that it shows more adaptations for arboreal locomotion. If the humerus is correctly assigned, then it strengthens the diagnosis of *Rhinocolobus* as it also shows similar adaptations for arboreal locomotion.

cf. *Paracolobus chemeroni*

The species of *Paracolobus* have an interesting distribution. Not including isolated teeth and small fragments that have been tentatively assigned to this genus, *P. chemeroni* is only known from the Tugen Hills, and has been tentatively identified in the Afar Depression. The very distinctive taxon *P. mutiwa* is only known from the Turkana Basin. A possible third, unnamed species is only known from Laetoli. Its possible identification from the Afar depression would be only the second identification of *P. chemeroni*. It is only known from a single mandible from the Matabaietu Formation. This species is better diagnosed on facial features, and positive identification will have to await cranial material. The mandible, however, is a very good match for that of the holotype. It is more robust than mandibles of *Rhinocolobus* but not nearly as deep as are those of *P. mutiwa*. The teeth are similar in size as well. The age of approximately 2.5 Ma for the Matabaietu Formation is not much younger than the age of 3.0 Ma given by Gundling and Hill (2000) for the holotype of *P. chemeroni*.

Cercopithecoides kimeui

The presence of *C. kimeui* at Hadar greatly extends the known geographic range of this species. It was originally described at Koobi Fora and Olduvai Gorge, and has also been recovered from the Middle to Late Pliocene site of Rawe (Ditchfield et al., 1999;

personal observation). Hadar is thus the northern-most occurrence of this species, yielding a distribution that ranges from Northern Tanzania to Northern Ethiopia. The morphological similarity of the Hadar cranium with the female cranium KNM-ER 398 from Koobi Fora is so strong that there can be little doubt they are conspecific. The occurrences at Hadar, Koobi Fora and Olduvai are largely semi-contemporaneous. The Koobi Fora material ranges in age from roughly 1.9 to 1.64 Ma. There is a single maxillary fragment with heavily worn P^4-M^1 from the Lokochot Member that Leakey (1982) identified as this species. Given its fragmentary nature and worn teeth this must be considered tentative, but if correct then this would extend the range back to more than 3.4 Ma. The type specimen from Olduvai is from Middle Bed II, and therefore between 1.65 and 1.52 Ma. The Hadar material is likely to date to approximately 1.8 to 1.6 Ma, which fits well with the above two sites. The specimen from Rawe is somewhat older than these, probably between 2.4 and 2 Ma (Ditchfield, et al., 1999). There is also a tentatively identified isolated lower molar from Bed III at Olduvai, which would extend the range up to perhaps 1.2 Ma. If the isolated upper molar from Unit “U” at Bodo is correctly allocated, then it would greatly extend the range of this taxon up to 0.64 Ma. As this is an isolated tooth, and it does lie so far out of the known range for this taxon, its identification must be treated very cautiously.

cf. *Cercopithecoides* sp. nov.

This medium-sized colobine from Leadu and Hadar has been recognized as representing a new species for years, but is as yet not formally named, and has gone by the label “Colobine A” (Eck, 1976; 1977; Szalay and Delson, 1979; Delson, 1984; 1994).

It is smaller in dental and postcranial size than *C. williamsi* from Koobi Fora, but is similar in some aspects of its morphology. These include the relatively short rostrum that is somewhat “squared” in superior view. It is also similar to the Koobi Fora material in that it seems to show a number of adaptations in its post-cranium that indicate a more semi-terrestrial locomotor behavior than is the case in most extant colobines, as well as in *Rhinocolobus* and possibly *Paracolobus*. It also shows a number of differences from the Koobi Fora material that merit specific distinction. These include smaller size, a less projecting lower face, a deeper mandible (although still fairly shallow), lack of a median mental foramen, and adaptations for terrestriality that are not as strongly developed.

cf. *Cercopithecoides* sp. indet.

This taxon is represented by a single mandibular fragment from Maka. There is also an edentulous mandibular corpus fragment from the Hata Member of the Bouri Formation that is probably the same species. It may also be represented by some of the isolated teeth and postcrania identified as Colobinae size B. This material documents the presence of a second large colobine species in sediments near in age to the Sidi Hakoma Tuff, as it is clearly distinct from the mandibles of cf. *Rhinocolobus turkanaensis*. Additionally, if the generic of the mandible from Bouri is correct, then it documents the presence of a second colobine species (distinct from cf. *Paracolobus chemeroni*) at ca. 2.5 Ma.

Colobus sp.

Most Pliocene and earlier Pleistocene localities preserve only a few fragmentary specimens of *Colobus*. One exception is a relatively complete cranium of *Colobus* reported from the later Pleistocene of Sudan by Simons (1967). However, the sample from Andalee is the largest and most complete of this genus from a single site in the Middle Pleistocene. The fact that it represents a species other than *Colobus guereza* is interesting, as *C. guereza* is the only species of colobine that occurs in Ethiopia today.

Additional Comments

Of the approximately thirty species of Pliocene and Pleistocene cercopithecids known in sub-Saharan Africa, few occur in both East and South Africa. If the tentative assignment of the *Parapapio* material to *Pp. jonesi* proves to be correct, then this would be one of only three such pan-African species. The two others are *Theropithecus oswaldi* (including all three subspecies) and perhaps *Cercopithecoides williamsi*. There is little doubt about the conspecific nature of the material from Swartkrans and Hopefield with East African *T. o. oswaldi* and *T. o. leakeyi* respectively, but *T. o. darti* from Makapansgat and Hadar may be somewhat more distinct from one another. There is some doubt as to whether the *C. williamsi* from Koobi Fora represents the same species as is present at in Southern Africa. Some of the concern is related to the postcrania. Ciochon (1993) identified several postcranial elements from Sterkfontein and Bolt’s Farm as colobine. As *C. williamsi* is the only colobine species documented at these sites, these elements were assigned to *C. williamsi*, but they showed adaptations consistent with the arboreal locomotion of modern colobines. On the other hand, the *C. williamsi* partial skeleton from Koobi Fora shows adaptations for terrestrial locomotion that are more strongly developed than in any other colobine (Birchette, 1981; 1982). A revision of the South African material is required to evaluate whether specific distinction is warranted between the Koobi Fora material and some or all of the South African samples.

Phylogenetic analyses were not performed as a part of this dissertation. However, the material described here has implications for cercopithecid phylogeny. Among the papionins, the phylogenetic positions of *Parapapio* and *Pliopapio* have ramifications for the evolutionary history of the remaining genera. It is well accepted that *Macaca* is the sister taxon to the sub-Saharan papionin genera. *Parapapio* is typically placed as the sister taxon to all other papionans. If this position is correct, then *Pliopapio* may be derived relative to *Parapapio*, but possibly the sister taxon to all of the remaining genera. This phylogenetic arrangement means that *Lophocebus* and *Cercocebus* independently lost the anteorbital drop and ophryonic groove and convergently returned to morphology more like that of *Parapapio* (but with deep suborbital fossae, and more flaring molars). Another possibility would be that *Pliopapio* is only the sister taxon to the *Papio/Theropithecus/Lophocebus* group. This would require *Mandrillus* to convergently develop the anteorbital drop and an ophryonic groove. Alternatively, if the unique facial morphology of *Parapapio* is not primitive, but instead is a derived feature relative to the African papionin morphotype, then *Pliopapio* may be closer to the base of the African papionin radiation. This position requires the lineage that gave rise to *Pl. alemui* extend back to before 7 Ma, because of the presence of *Parapapio* in the lower Nawata Formation at Lothagam.

Within the larger fossil colobines from Africa there appear to be two groups: one long-faced and the other shorter-faced. The long-faced group is composed of *Paracolobus* and *Rhinocolobus*. In addition to large size and long faces, this group is further diagnosed by having mandibular corpora that are deep and narrow in breadth, that deepen posteriorly, are flared at gonion (except less in *P. chemeroni*, but greatly in *P. mutiwa*), and have tall rami. This group is further distinguished from the second group by being generally more arboreal. The short-faced and terrestrial group is composed of East African *Cercopithecoides* and likely cf. *Cercopithecoides* from Leadu. This second group, along with South African *Cercopithecoides*, shares a mandibular morphology that includes a shallow but broad corpus, a shallow and vertical symphysis, and a short but deep ramus with a relatively unexpanded gonion. The preserved facial morphology of *K. aramisi* is quite different from that of the *Paracolobus*/*Rhinocolobus* group, but the mandible is different from that of the *Cercopithecoides* group. Therefore, its position relative to these two groups is ambiguous. Furthermore, the relationship of all of these fossil forms to the extant African colobines is unclear.

Comparison with the Turkana Basin and its Implications

As noted above, the second goal of this dissertation was to compare the evolutionary pattern of the Afar cercopithecids with that from the Turkana Basin. In order to make the records from these two basins comparable (through the eyes of a single reviewer), the sample from the Turkana Basin was analyzed in chapter 5. This sample contained at least 14 species from 9 genera. In general, the Turkana Basin record was more diverse in terms of number of species present at a given time horizon. The evolutionary pattern for the Turkana Basin is graphically summarized in figure 6.2. In chapter 6 the two records were compared. The two regions shared only two species based on secure identifications: *Theropithecus oswaldi* and *Cercopithecoides kimeui*. They also probably share a third species, *Rhinocolobus turkanaensis*. Other species could not be positively identified in both regions.

In the Afar sequence, the cercopithecid species could be organized into chronological sets: one in the Early Pliocene, a second in the early Middle Pliocene, a third in the late Middle to Late Pliocene, and a fourth in the Middle Pleistocene. In the Turkana Basin there were three such sets of species: an Early Pliocene set, a Middle Pliocene set and a Late Pliocene to Early Pleistocene set. In the Afar Basin the transition between the Early Pliocene and Middle Pliocene set occurred sometime before 3.4 Ma. The Middle Pliocene set is present by the time represented at Maka below the Sidi Hakoma Tuff, and possibly as early as 3.85 Ma depending on the identifications of the fossils from the Belohdelie Member. In the Turkana basin this transition appears to have occurred between 3.6 and 3.4 Ma, roughly by the time of the Lokochot Member. The transition between the second and third sets in the Afar Depression took place sometime between 2.9 and 2.5 Ma. This is a period that Vrba (e.g. 1985; 1995) has discussed as one of marked turnover among bovids in Africa. In the Afar Basin, however, the apparent transition may be explained by the 400 Kyr gap between the top of the lower part of the Kada Hadar Member, and the Matabaietu Formation. Due to this gap it is impossible to tell whether this transition was gradual or rapid. In the Turkana basin, the transition between the second and third groups occurs much later: between 2.0 and 1.8 Ma, with little turnover between 3.4 and 2.0 Ma. This lack of synchrony between the two basins makes it less likely that the turnover in the Afar cercopithecids was a direct response to a rapid global shift in climate. The transition between the third and fourth species groups occurred sometime between approximately 1.8 and 0.64 Ma, and marked the appearance of more modern species.

At the generic level it was found that four of the ten genera represented in the Afar sample were shared with the Turkana Basin. These are *Cercopithecus*, *Papio*, *Theropithecus*, and *Cercopithecoides*. Additionally, *Paracolobus* and *Rhinocolobus* are also probably shared, pending more diagnostic material from the Afar Region. Whether or not *Parapapio* is shared between the two basins depends on the generic status of *Pp. ado*. If it is a species of *Parapapio* then this genus would be shared between the two basins (see description in chapter 5 for more discussion). The remaining Afar genera could not be positively identified in the Turkana basin. *Colobus* may have been shared, but this possibility is only supported by isolated teeth. *Pliopapio* and *Kuseracolobus* seem less likely to be shared between the two basins, but the possibility can not be completely ruled out. Two genera from the Turkana Basin appear to be absent in the Afar Depression: *Lophocebus* and *Procolobus*.

At a coarser scale, when the relative abundance of the four dental groups of Delson (1973) were studied, it was found that there were three distinct periods in the Afar region: Early Pliocene, Middle Pliocene to early Middle Pleistocene, and finally later Middle Pleistocene. The Early Pliocene period is distinct in its high proportion of colobines. This abundance, however, is based on the site of Aramis and stratigraphically equivalent sites in the Sagantole and Kuseralee catchments, and may not be representative of the whole time span, as the sequence from above Aramis though 3.75

Ma (i.e. between the DABT and CT) has only yielded very small samples. The second period is marked by a predominance of *Theropithecus*. The difference in abundance between the second and third periods represents a large increase in the abundance of colobines, and a uniquely high proportion of cercopithecins. This transition, however, is most likely to represent a facies shift between Unit "U" and Andalee, and not necessarily a larger scale change.

The shift in relative abundance prior to 3.4 Ma is also found in the Turkana Basin. Prior to the Lokochot Member and Member A, the Turkana basin has a high abundance of non-*Theropithecus* papionins with colobines more rare, and an absence of *Theropithecus* or cercopithecins. This pattern is also different from the Early Pliocene pattern in the Afar basin, which has more abundant colobines. By between 3.6 and 3.4 Ma the two basins are more similar in their relative abundances, with *Theropithecus* predominating. The Turkana basin is slightly different in the occasional presence of cercopithecins during this interval.

Both basins have shifts in their relative abundances prior to 3.4 Ma. They also both show transitions between different species sets at this time. Both also seem to shift to abundance regimes dominated by *Theropithecus*. It is also at this time that the first species present in both areas appear (*T. darti* and possibly *R. turkanaensis*). This synchrony may simply be due to the increased sampling in both basins relative to earlier times. However, there does appear to be a real, perhaps pan-East African change. In addition to the Afar and Turkana Basins, *Theropithecus* is absent from most sites older than 3.4 Ma, such as Laetoli (Leakey and Delson, 1987), the Apak Member of the Nachukui Formation at Lothagam (Leakey et al., in press), and the lower part of the

Chemeron Formation (Gundling and Hill, 2000). The exception may be Belohdelie where two mandibles are identified as possibly representing *Theropithecus*, but with molars that have only partially developed the derived morphology of the genus. *Theropithecus* has also been reported from Lothagam as early as 4.5 – 4 Ma (Patterson, 1970; Delson, 1993), but Leakey et al. (in press) have indicated that this material is most likely younger than this based on faunal grounds. Most sites from about 3.4 Ma and younger in East Africa generally contain *Theropithecus* (Delson et al., 1993).

When the Afar and Turkana records are examined together, there are a large number of first and last appearances sometime before 3.4 Ma, between 2.9 and 2.5 Ma (mostly based on Afar species not present in the Turkana Basin), and between 2.0 – 1.9 Ma (mostly based on Turkana species not present in the Afar Basin). There is also a major shift in abundance data at both basins prior to 3.4 Ma. Relative abundances of the four dental groups are approximately constant between 3.4 and 1.5 Ma in both basins. A major climatic change has been described at just older than 2.5 Ma (e.g. Shackleton, 1984; Denton, 1999), but none have been documented at ca. 3.4 or ca. 2.0 Ma. Therefore the timing of the major evolutionary events in the combined cercopithecid evolutionary pattern for these two regions is not closely tied to major climatic events. On the other hand, it appears that preservational bias and/or local paleoenvironmental and tectonic factors are more likely causes for the timing of these events. It should be pointed out that there are several problems associated with using the cercopithecid record for this purpose.

Comparison between the Afar and Turkana Basins reveals that they have similarities, but also a large number of differences. These differences highlight the regional variability in Africa during the last 4.5 myr and caution against making generalizations about whole continents or parts of continents based on evidence from individual basins, even very well sampled and understood collections, such as that from the Turkana Basin. These regional differences also make studying and comparing different assemblages far more interesting.

Plate 1. Specimens of Cercopithecus sp. Top Left: KL191-87 lateral view; Middle Left: KL191-87 ventral view; Bottom Left: KL191-105 lingual view, Top Right: KL191-58 occlusal view; KL191-58 lateral view.

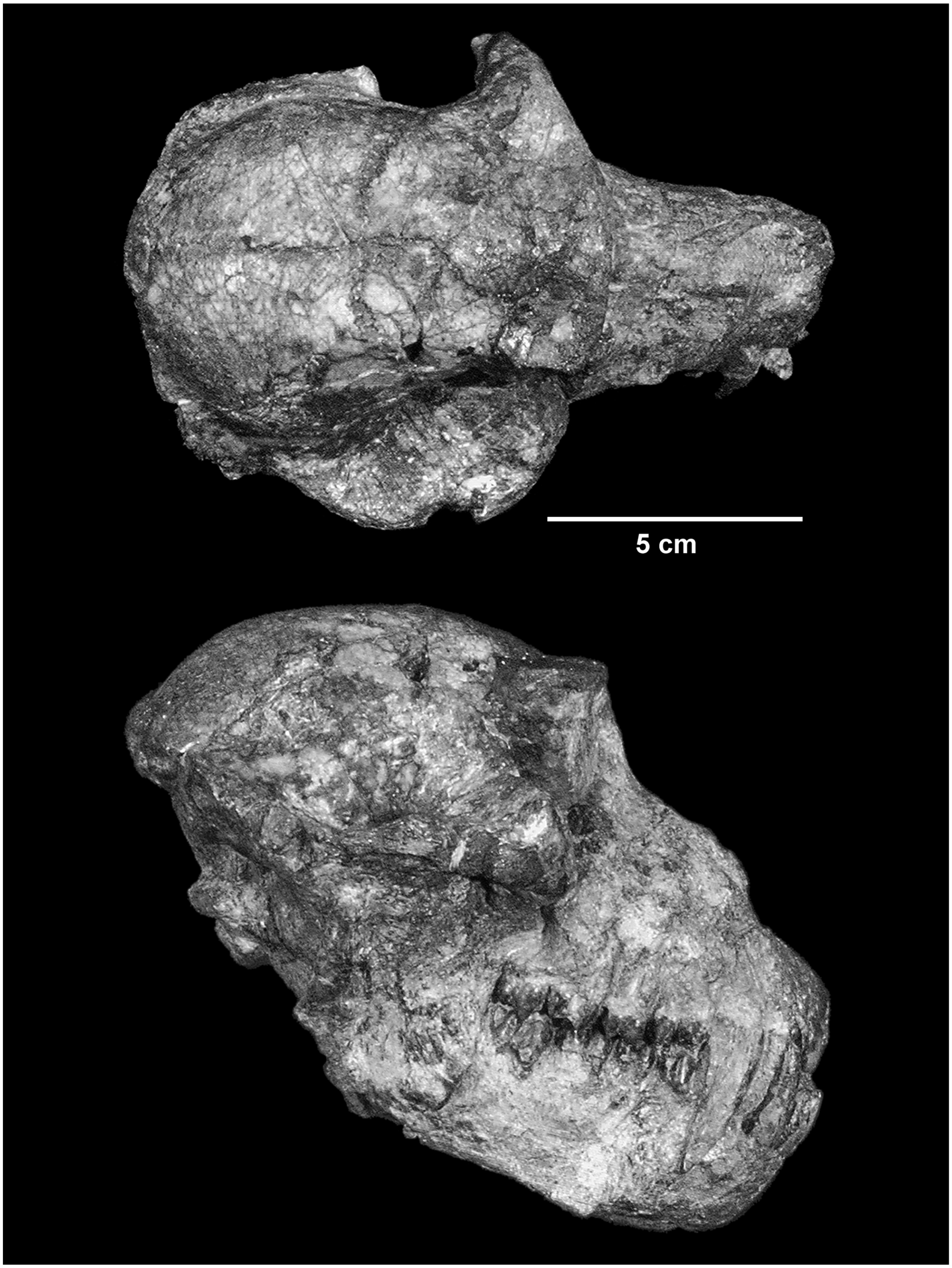


Plate 2. Holotype of Pliopapio alemui ARA-VP-6/933. Top: dorsal view; Bottom: right lateral view.

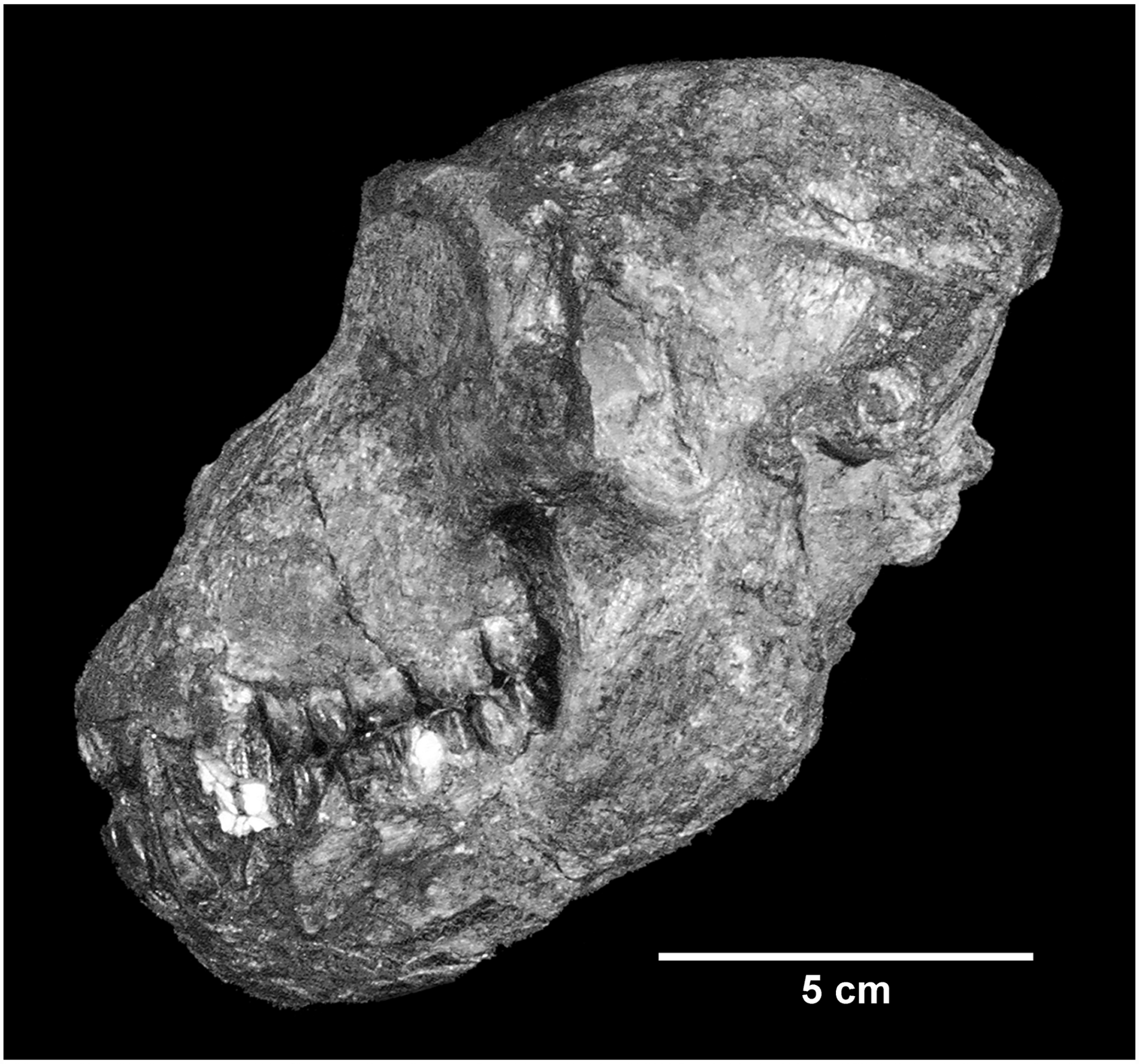


Plate 3. Holotype of Pliopapio alemui ARA-VP-6/933. ARA-VP-6/933 left lateral view.

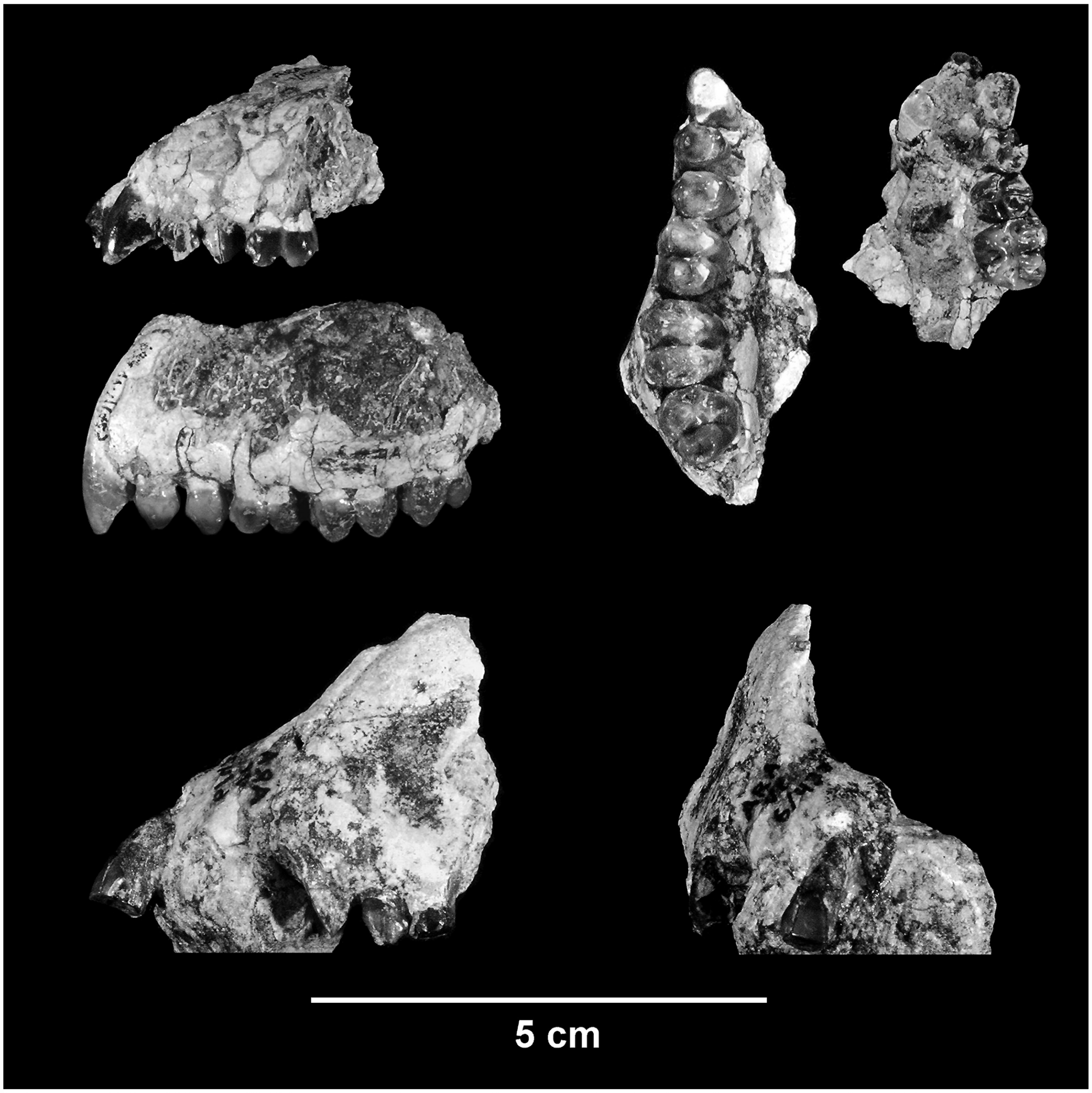


Plate 4. Maxillae of Pliopapio alemui. Counterclockwise from top left: ARA-VP-1/1007 lateral view, ARA-VP-1/1723 (reversed), ARA-VP-6/437 lateral view (reversed), ARA-VP-6/437 frontal view, ARA-VP-1/1007 occlusal view, ARA-VP-1/1723 occlusal view.

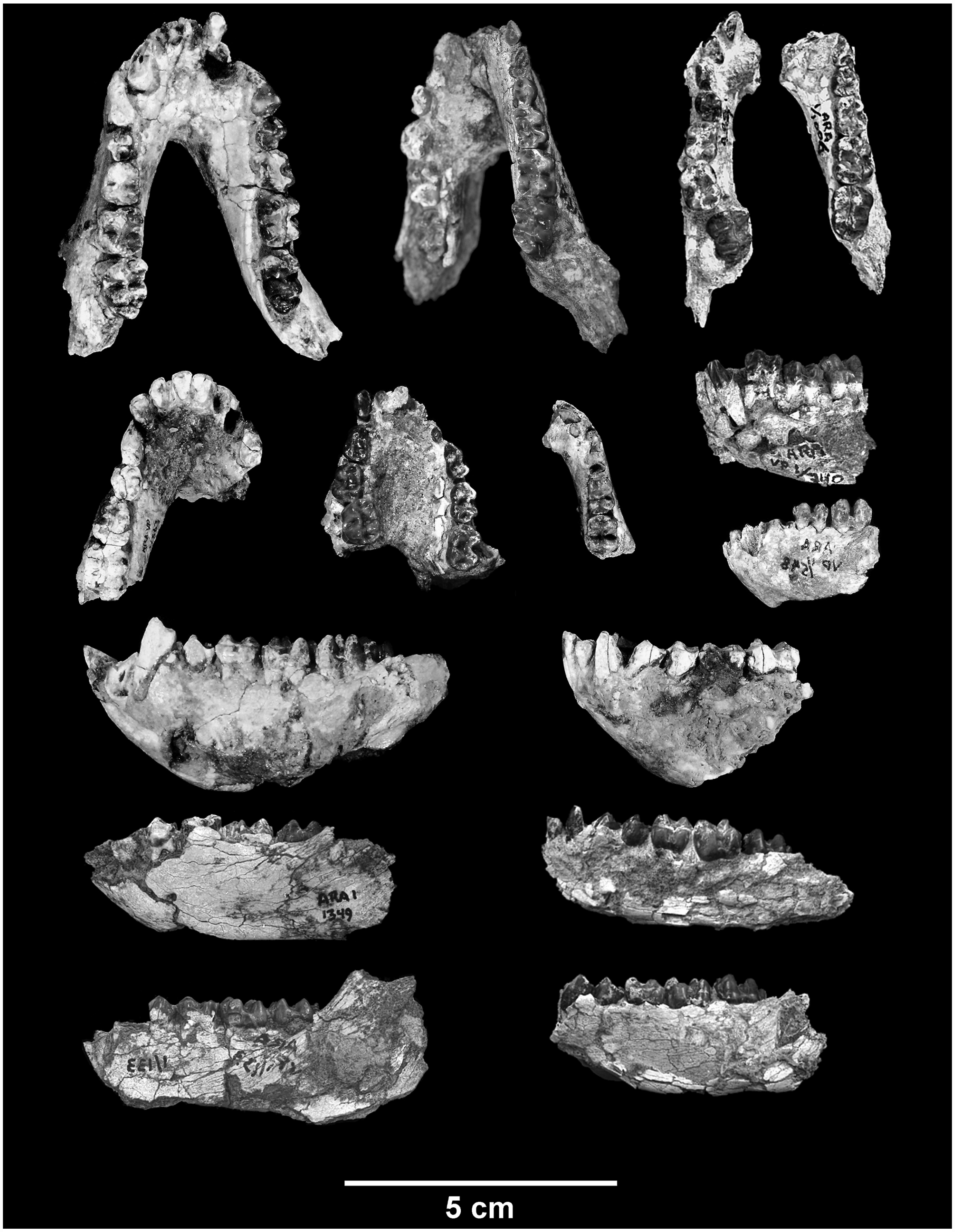


Plate 6. Mandible of Pliopapio alemui. Top row left to right: ARA-VP-1/73, ARA-VP-1/133, ARA-VP-1/1006 (two pieces). 2nd row: ARA-VP-1/563, ARA-VP-1/740, ARA-VP-1/548, ARA-VP-1/740, ARA-VP-1/548 (reversed). 3rd row: ARA-VP-1/73, ARA-VP-1/563. 4th row: ARA-VP-1/133 left corpus (1349 is an old number), ARA-VP-1/1006 left corpus. Bottom row: ARA-VP-1/133 right corpus, ARA-VP-1/1006 right corpus.

Plate 6. Male Parapapio cf. jonesi AL363-1a. Top: dorsal view; Bottom: lateral view.

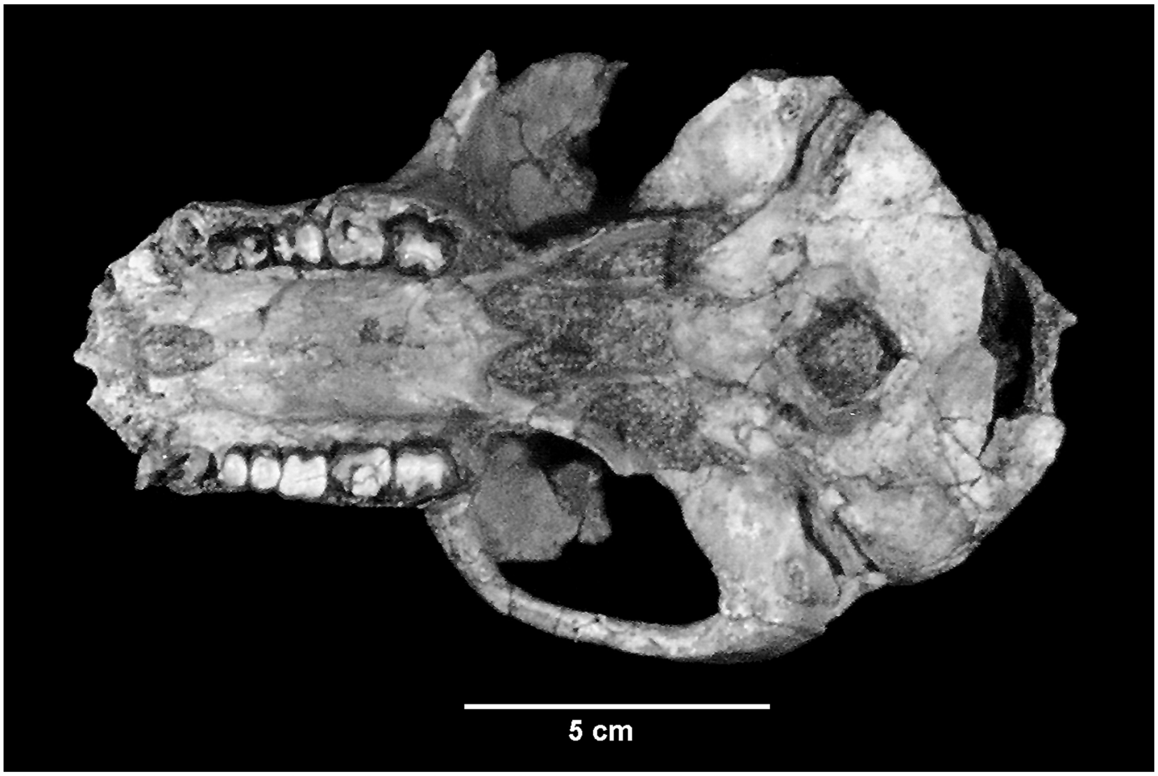


Plate 7. Male Parapapio cf. jonesi AL363-1a. Ventral view.

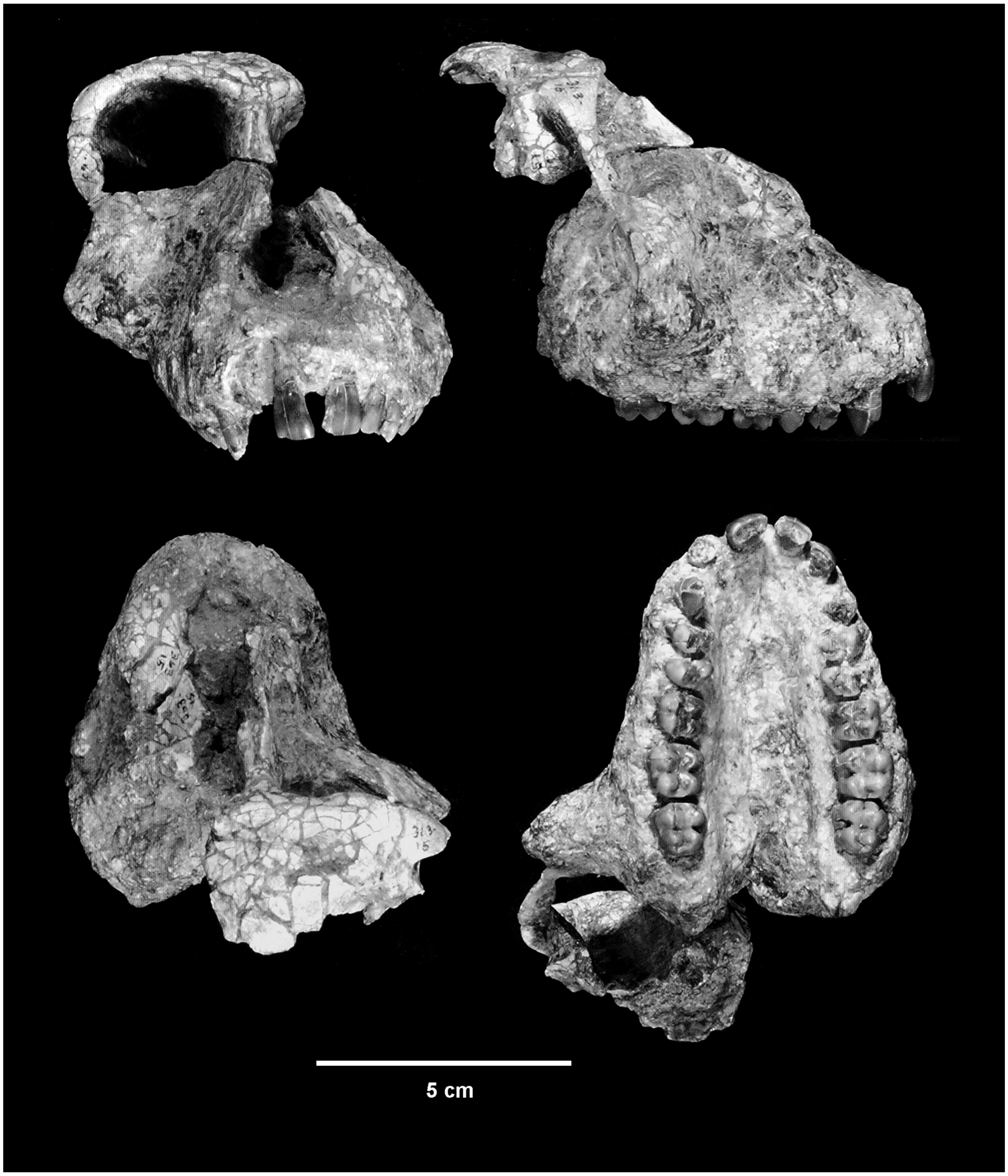


Plate 8. Female Parapapio cf. jonesi AL363-15a. Top: frontal and right lateral views; Bottom: dorsal and ventral views.

Plate 9. Mandibles of Parapapio cf. jonesi. Top row left to right: AL363-1b dorsal view, AL363-15b dorsal view. Center: AL363-15b lateral view. Bottom: AL363-1b lateral view.

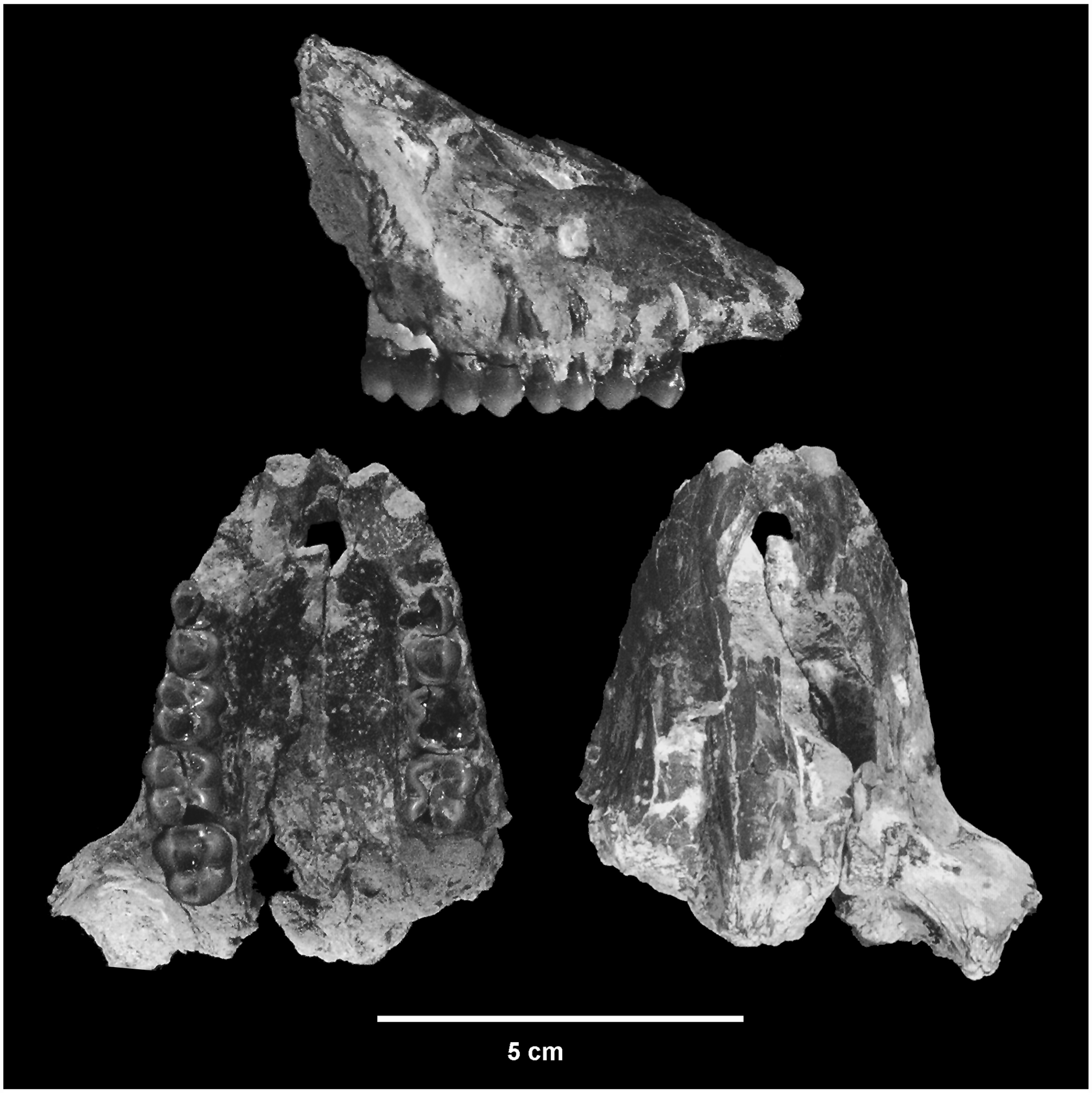


Plate 10. Papio sp. BOU-VP-12/9. Top: right lateral view. Bottom let to right: ventral and dorsal views.

Plate 11. Papionin mandible WIL-VP-1/2. Top: occlussal view. Center: lateral view. Bottom: lingual view.

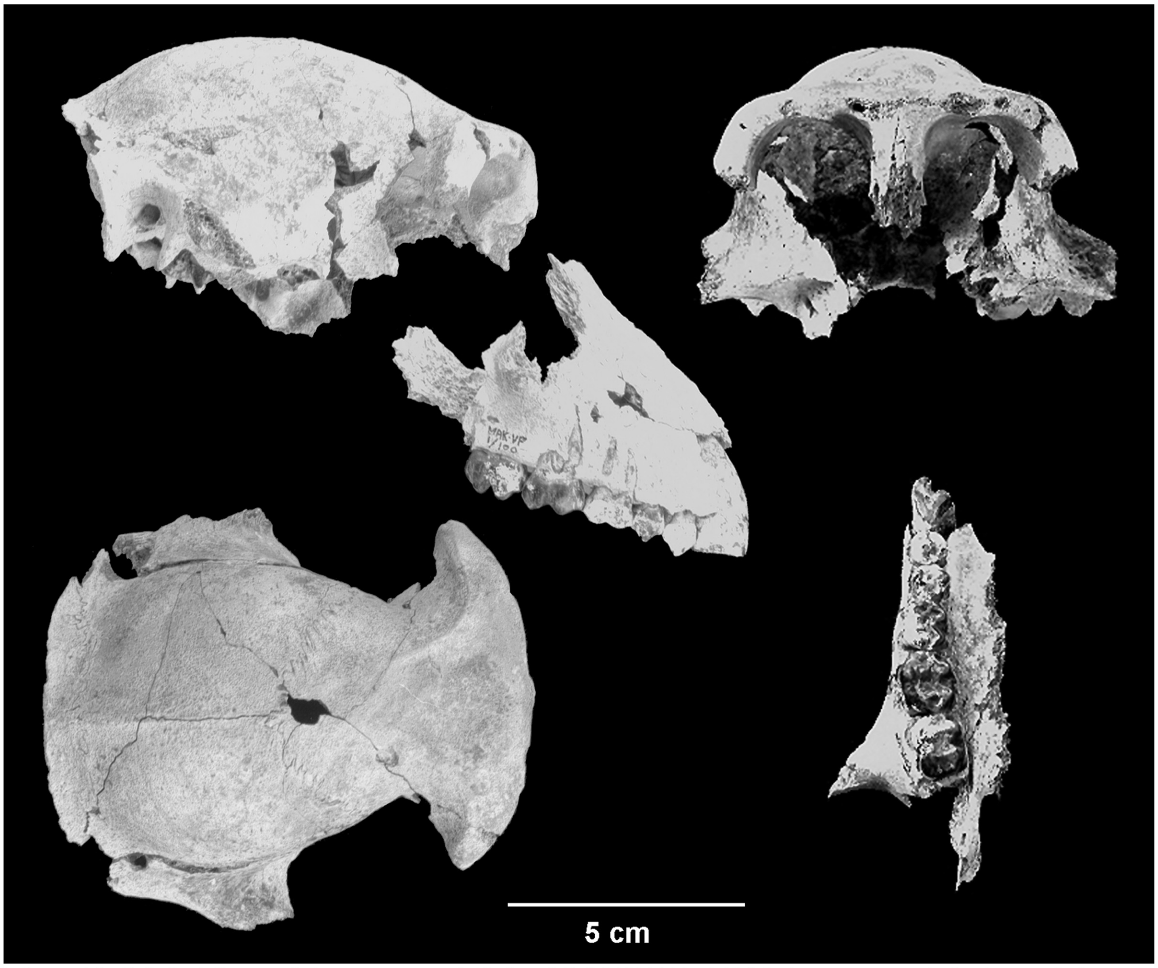


Plate 12. Male Theropithecus oswaldi darti MAK-VP-1/100. Top row: right lateral (two pieces) and frontal view. Bottom: dorsal view calvaria only; occlussal view maxilla only.

Plate 13. Male Theropithecus oswaldi darti AL412-1. Top: dorsal view. Bottom: left lateral view.

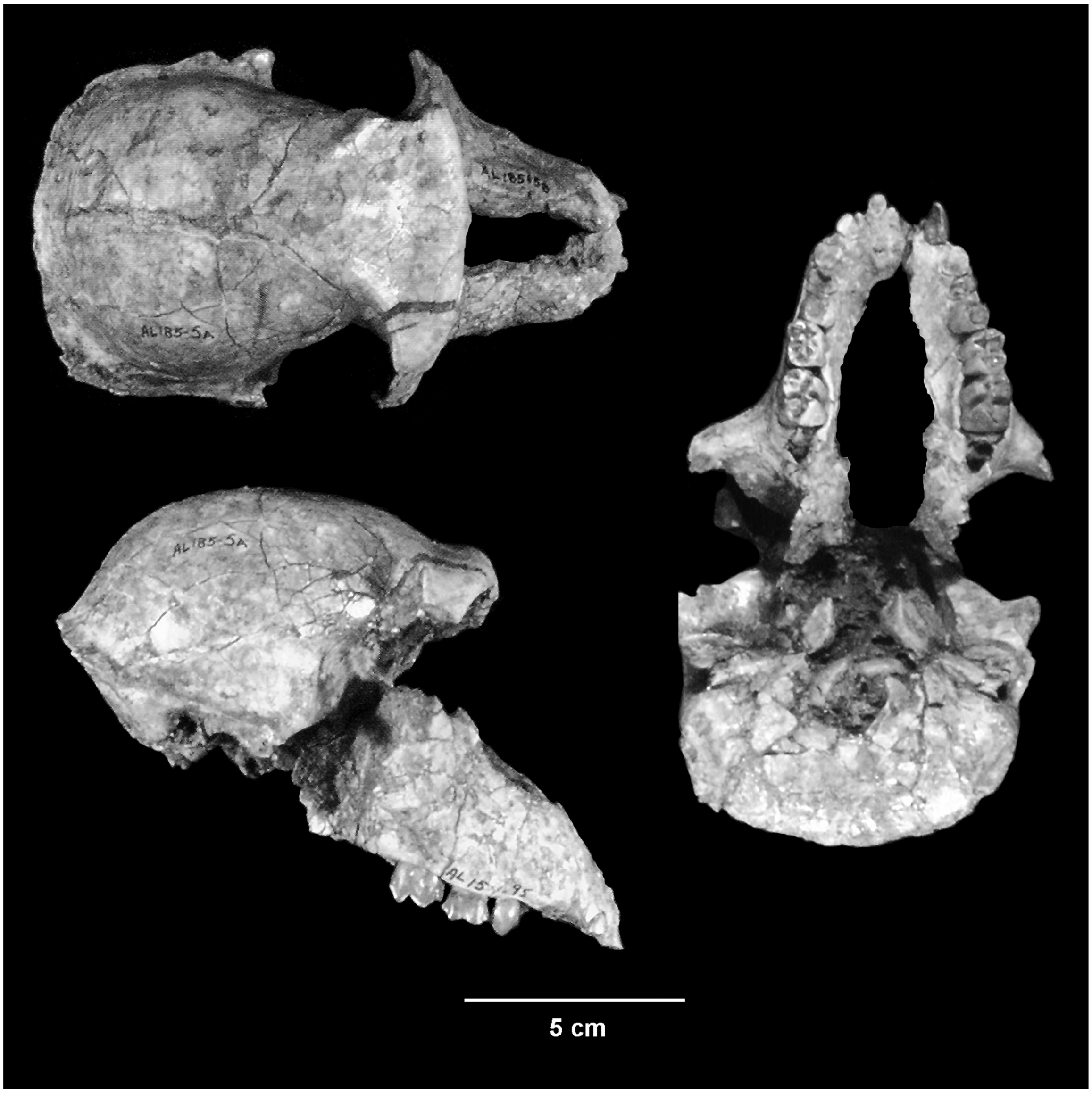


Plate 14. Female sub-adult Theropithecus oswaldi darti AL185-5a-b/AL154-95. Clockwise from top left: dorsal, ventral and right lateral views.

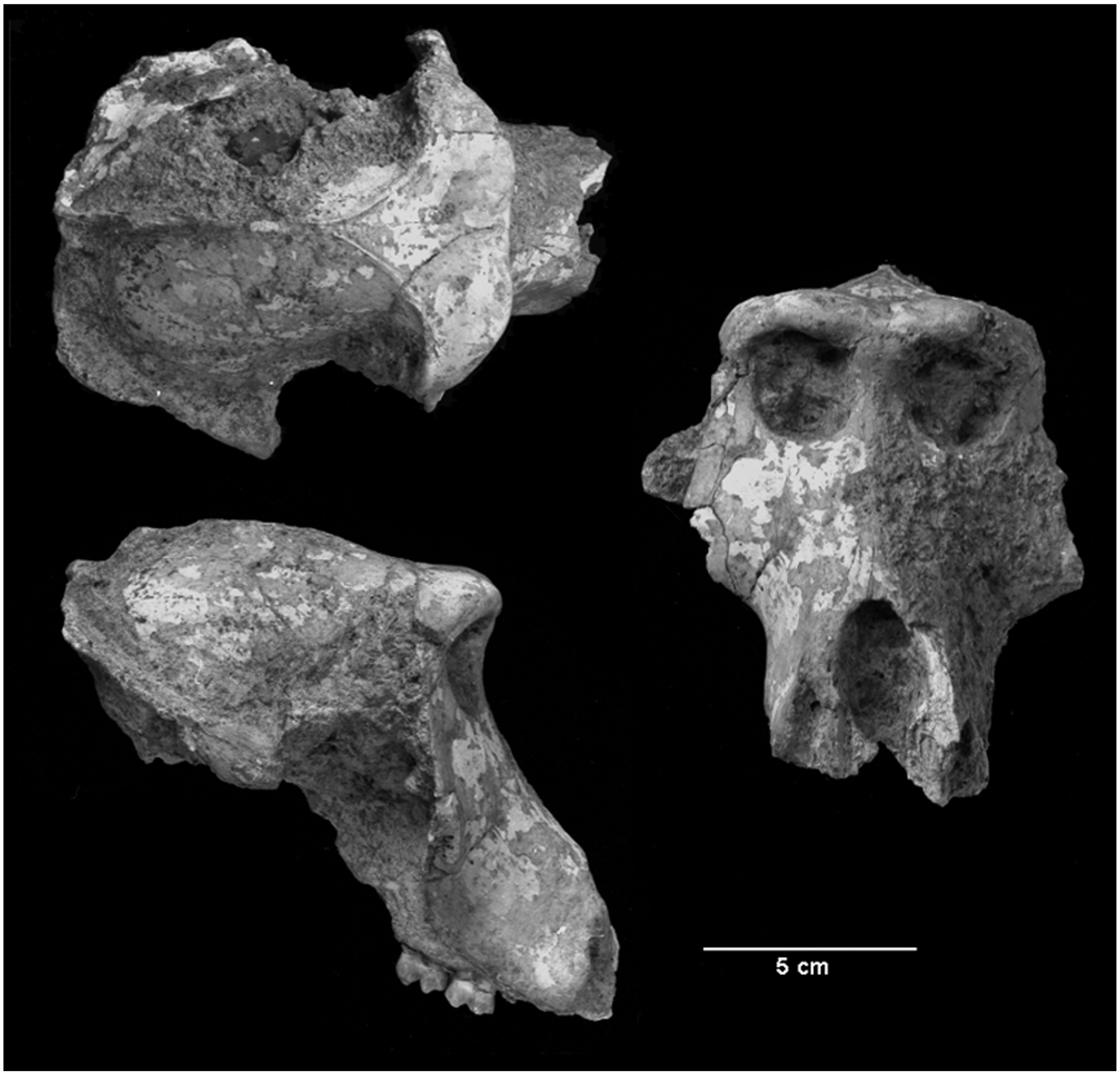


Plate 15. Male Theropithecus oswaldi oswaldi KL157-1. Clockwise from top left: dorsal, frontal, and right lateral views.

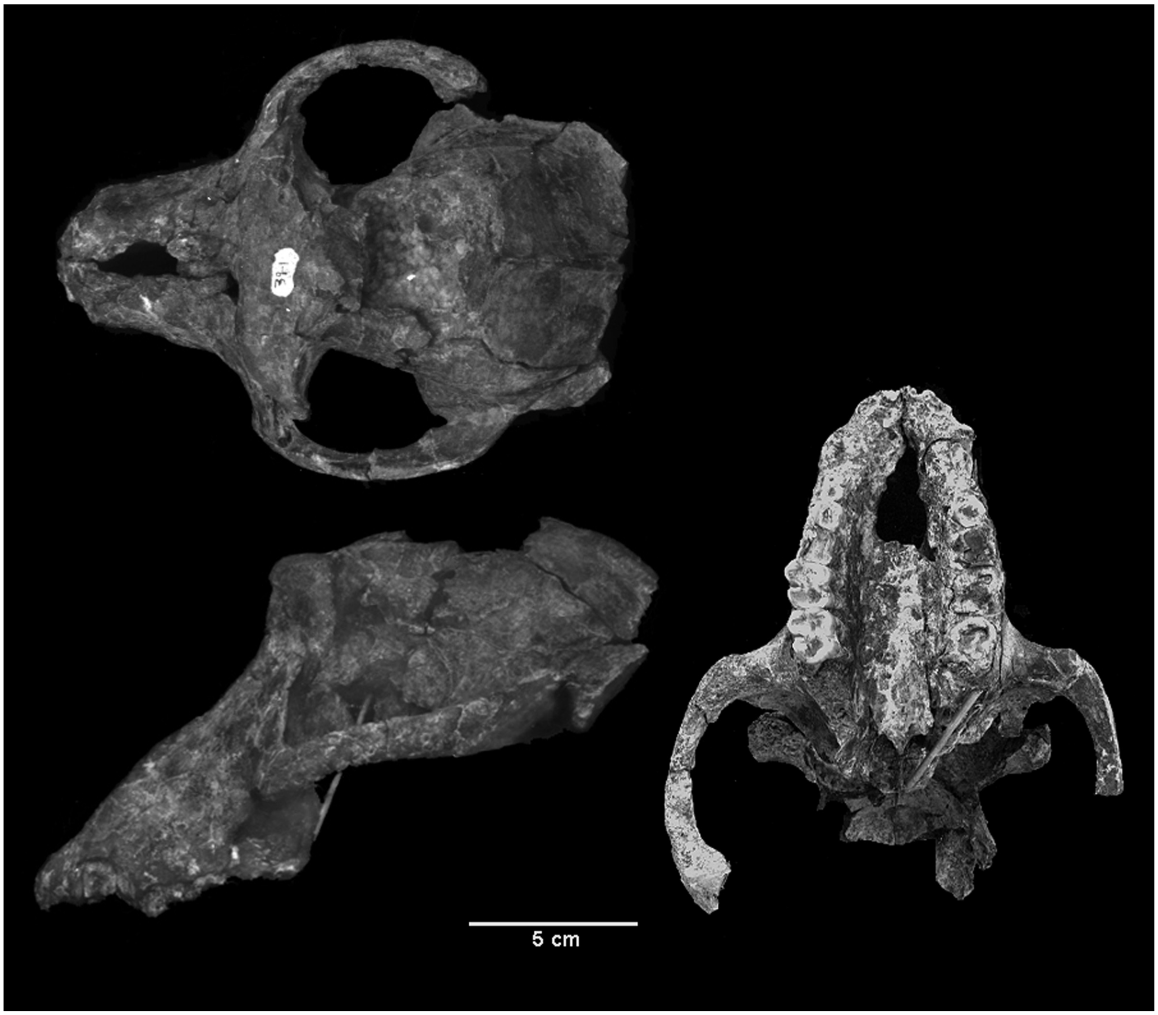


Plate 16. Male Theropithecus oswaldi oswaldi KL39-1. Clockwise from top left: dorsal, ventral (face only), left lateral views.

Plate 17. Female sub-adult Theropithecus oswaldi oswaldi KL38-1. Top: left lateral view. Bottom: ventral view.

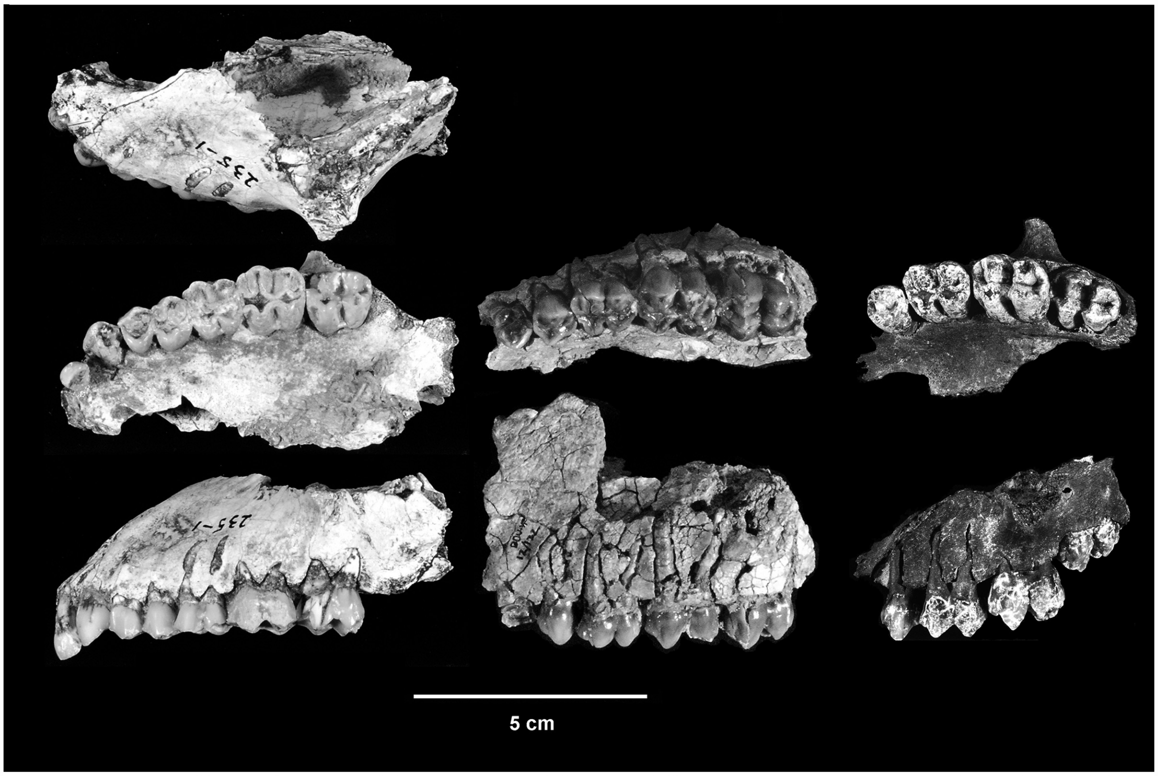


Plate 18. Maxillae of Theropithecus oswaldi oswaldi. Top row: KL235-1 dorsal. Middle row left to right: KL235-1 ventral view, BOU-VP-12/132, WIL-VP-2/15.

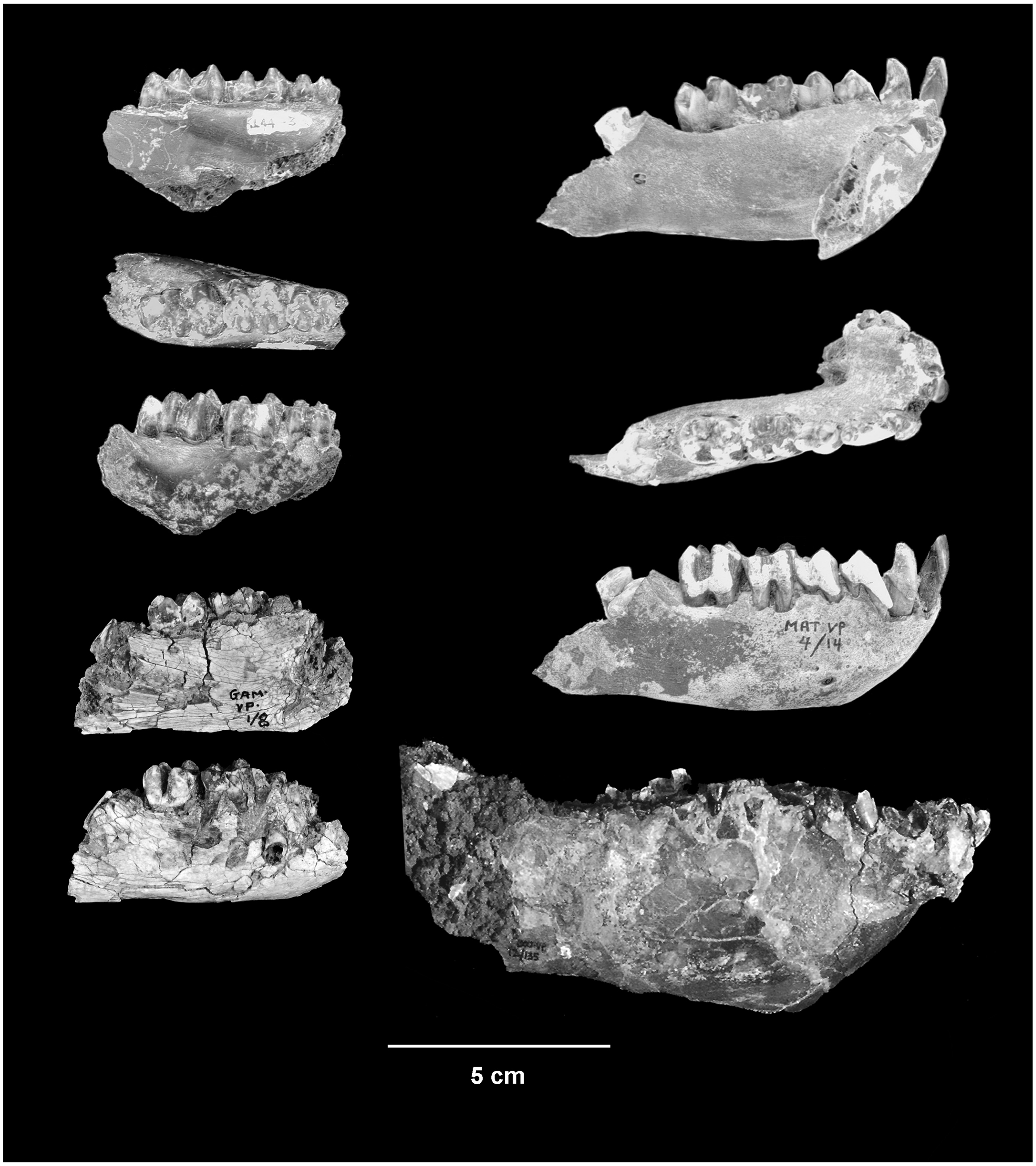


Plate 19. Mandibles of Theropithecus oswaldi oswaldi. Anticlockwise from top left: KL44-3 lingual view; KL44-3 occlussal view; KL44-3 lateral view; GAM-VP-1/8 lingual view; GAM-VP-1/8 lateral view; BOU-VP-12/135 lateral view; MAT-VP-4/14 lateral view; MAT-VP-4/14 occlussal view; MAT-VP-4/14 lingual view.

Plate 20. Male Theropithecus oswaldi leakeyi KL337-1. Clockwise from top left: dorsal, frontal, and ventral views.

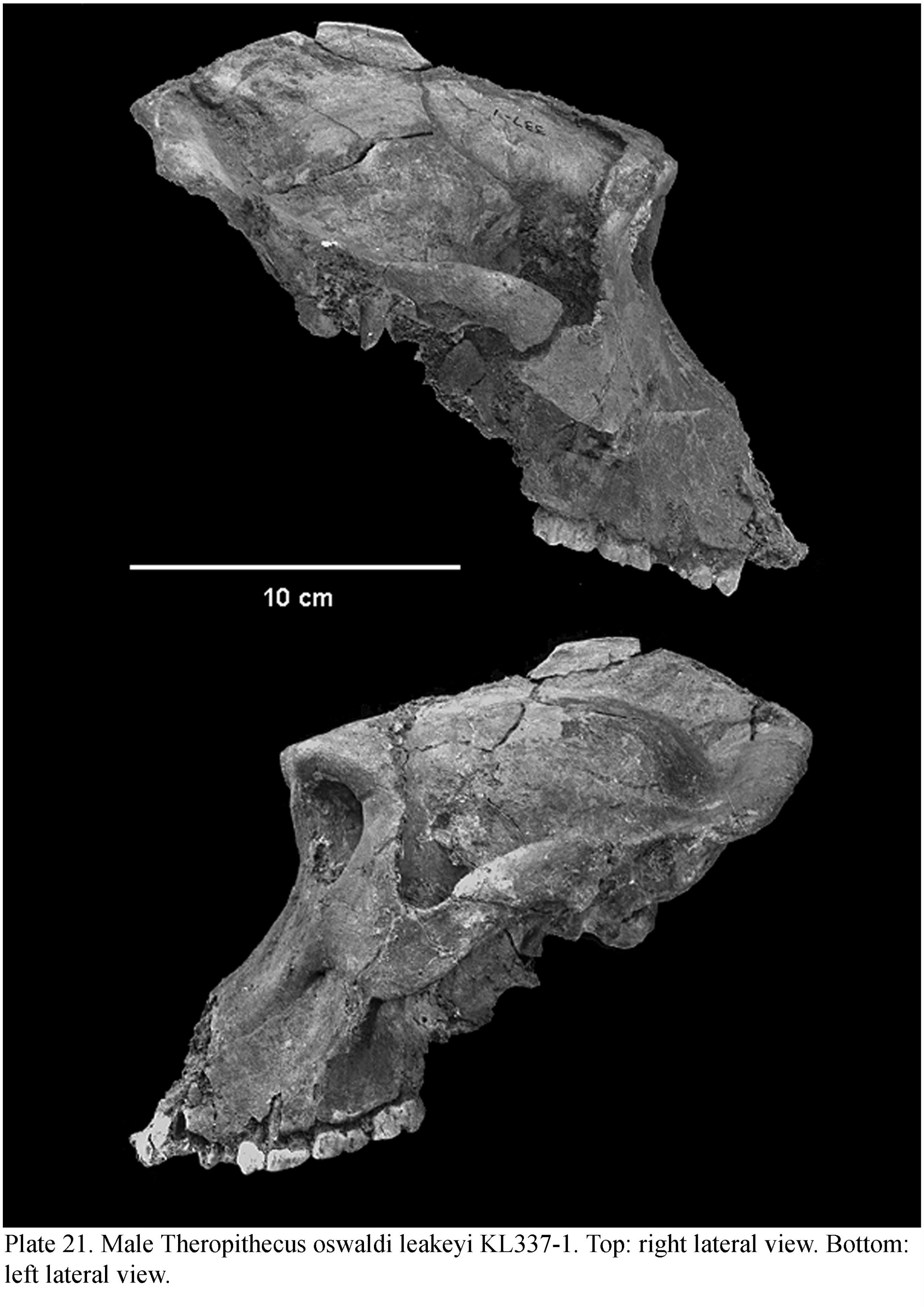


Plate 21. Male Theropithecus oswaldi leakeyi KL337-1. Top: right lateral view. Bottom: left lateral view.

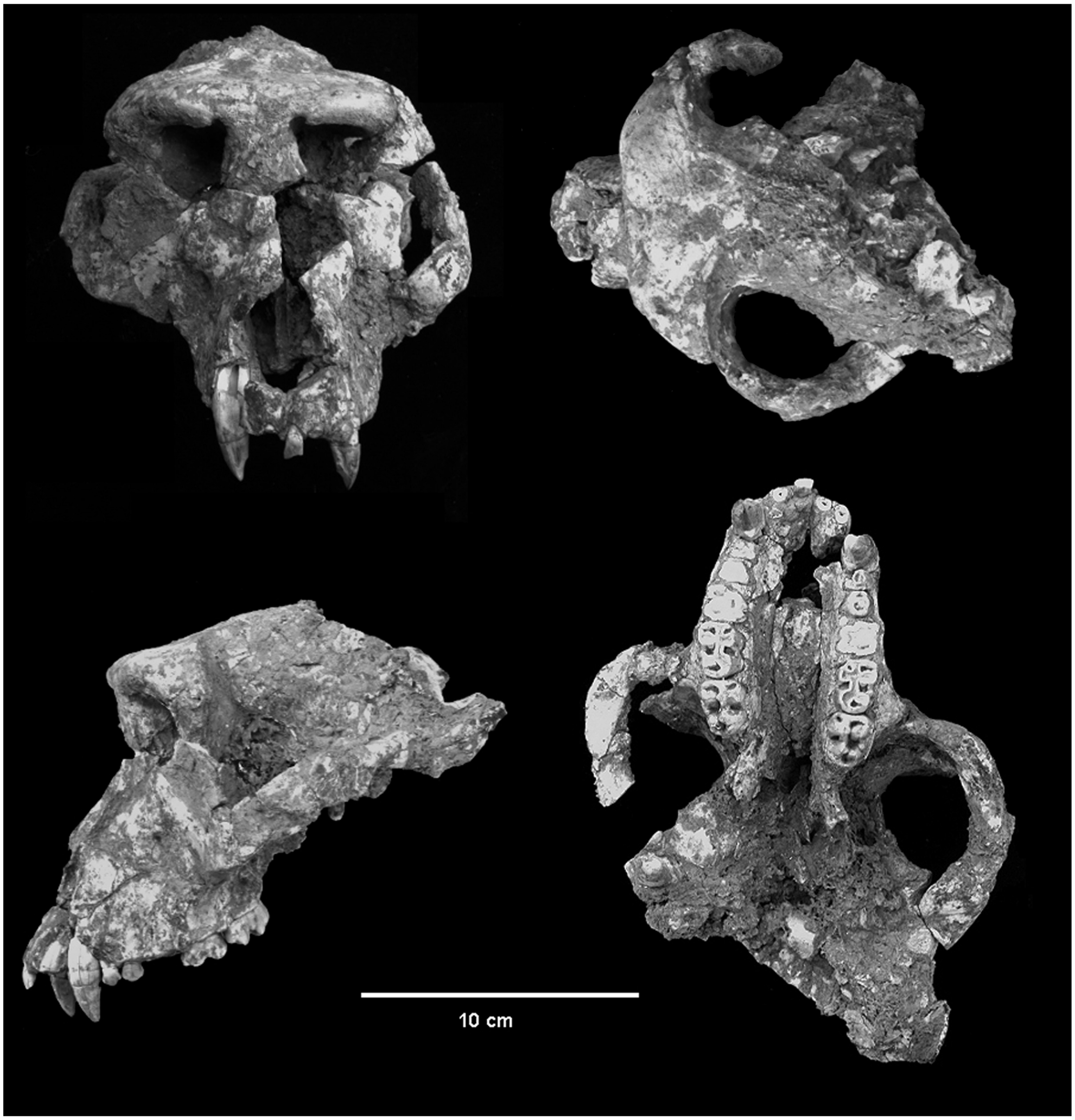


Plate 22. Male Theropithecus oswaldi leakeyi HAR-VP-1/1. Clockwise from top left: frontal, dorsal, ventral, and left lateral views.

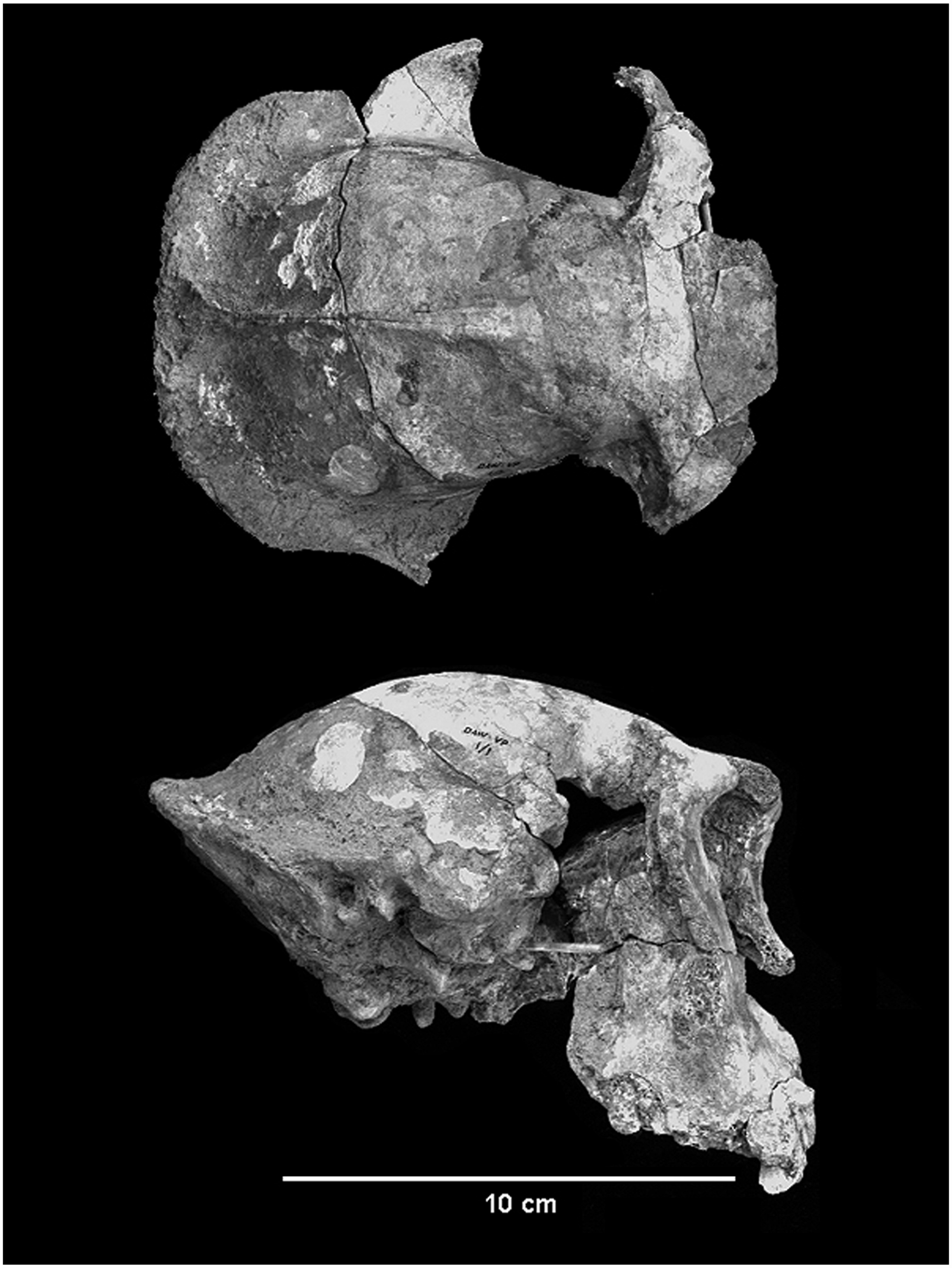


Plate 23. Female Theropithecus oswaldi leakeyi DAW-VP-1/1. Top: dorsal view. Bottom: right lateral view.

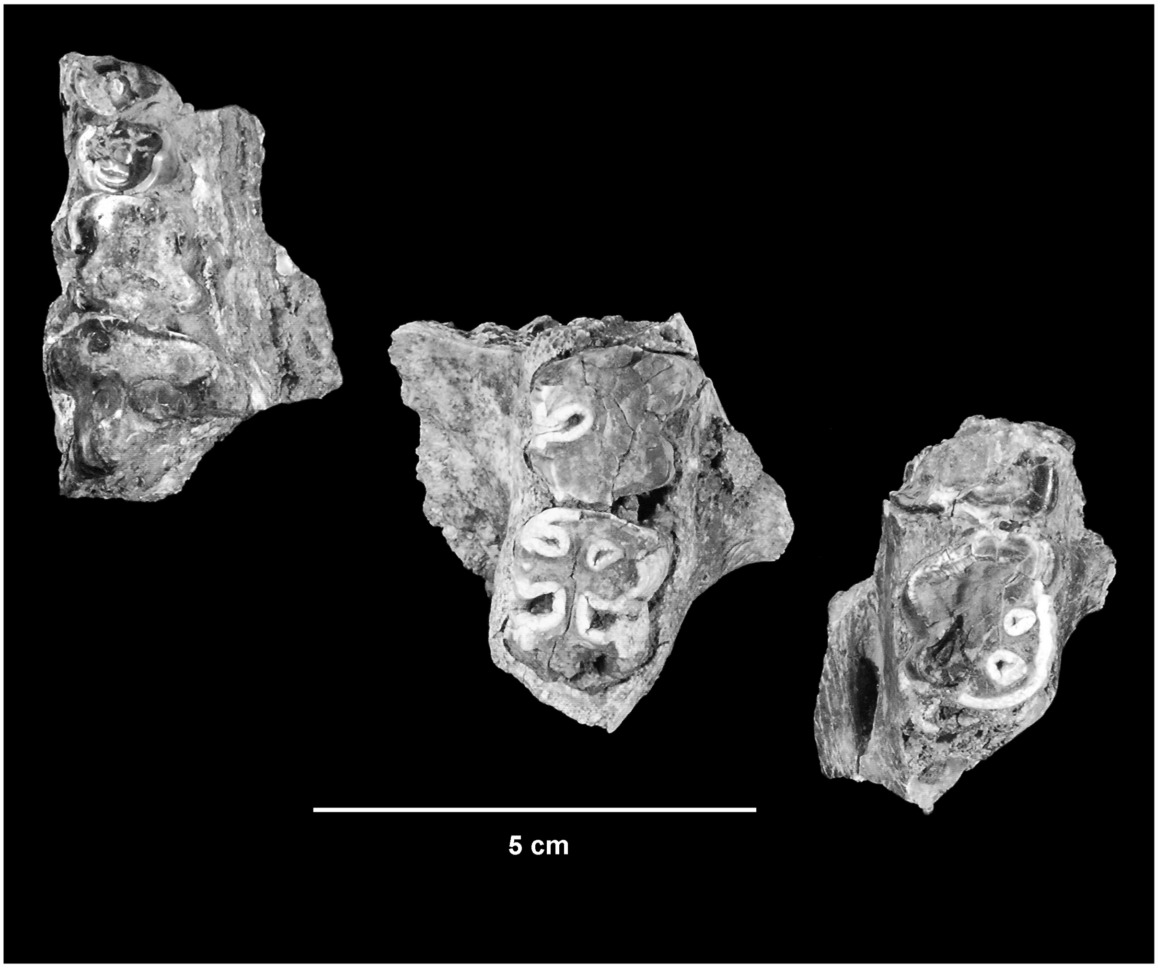


Plate 24. Maxillae of Theropithecus oswaldi leakeyi. Left to right: KL189-34; BOD-VP-1/4; KL6-8.

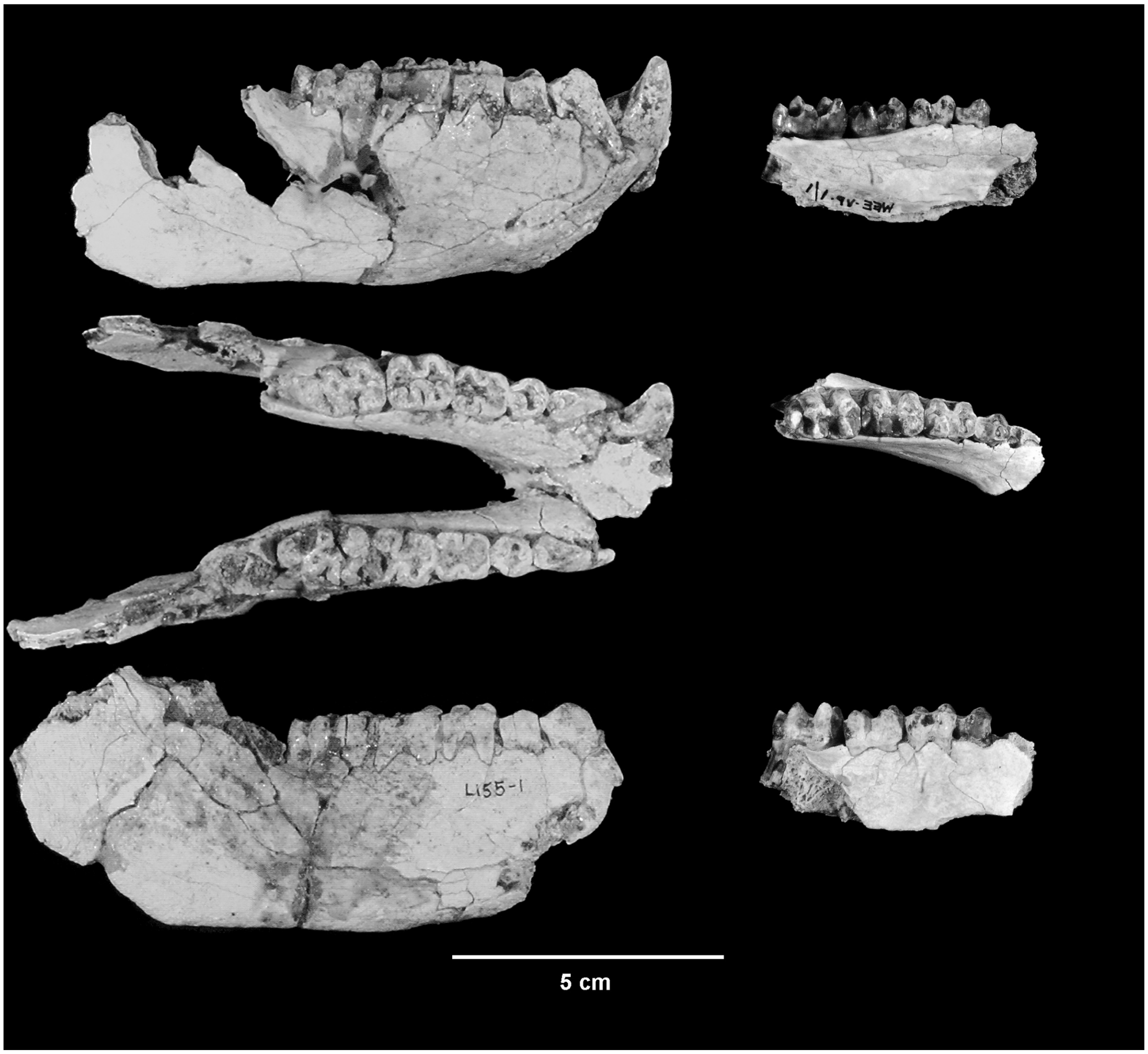


Plate 25. Mandibles of ?Theropithecus from Wee-ee. Anticlockwise from top left: KL155-1 left lateral view (reversed); KL155-1 dorsal view; KL155-1 right lateral view; WEE-VP-1/1 lingual view; WEE-VP-1/1 occlussal view; WEE-VP-1/1 lateral view.

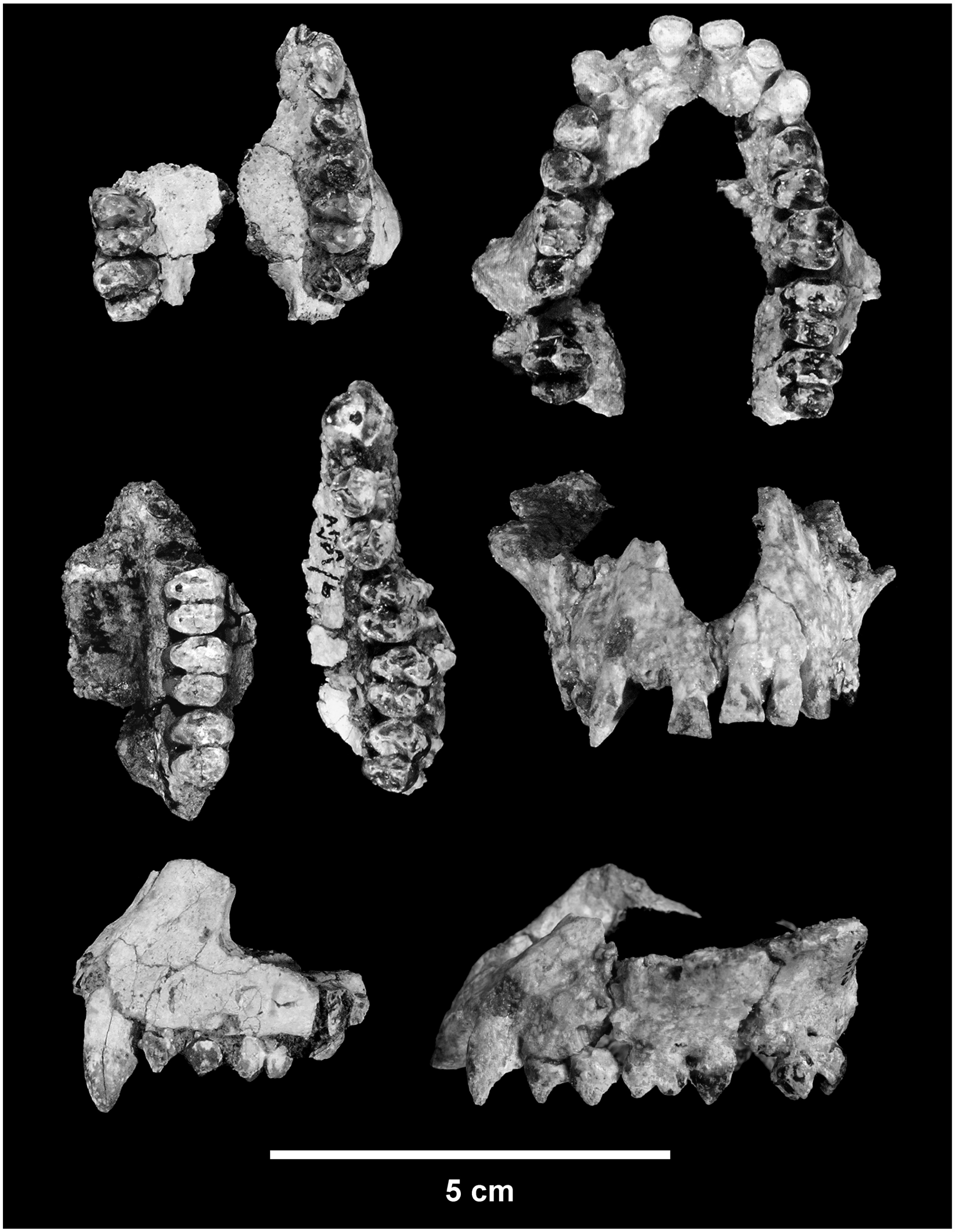


Plate 26. Maxillae of Kuseracolobus aramisi. Top row: KUS-VP-2/70, ARA-VP-6/1686. Middle row: ARA-VP-1/87, ARA-VP-1/6, ARA-VP-1/1686. Bottom row: KUS-VP-2/70, ARA-VP-1/1686 (reversed).

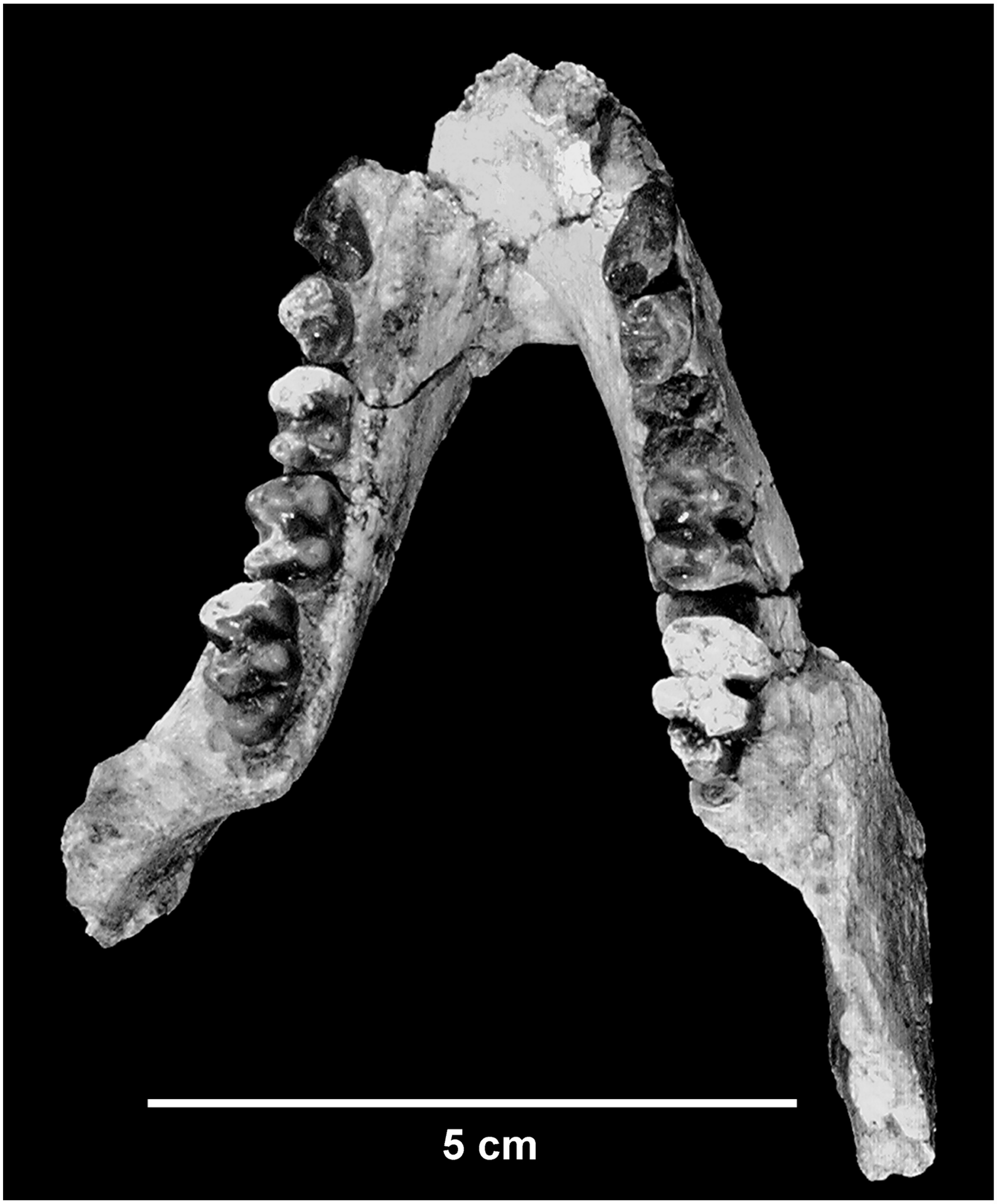


Plate 27. Holotype of Kuseracolobus aramisi ARA-VP-1/87. Occlussal view.

Plate 28. Holotype of Kuseracolobus aramisi ARA-VP-1/87. Lateral views, left side above, right (reversed) below.

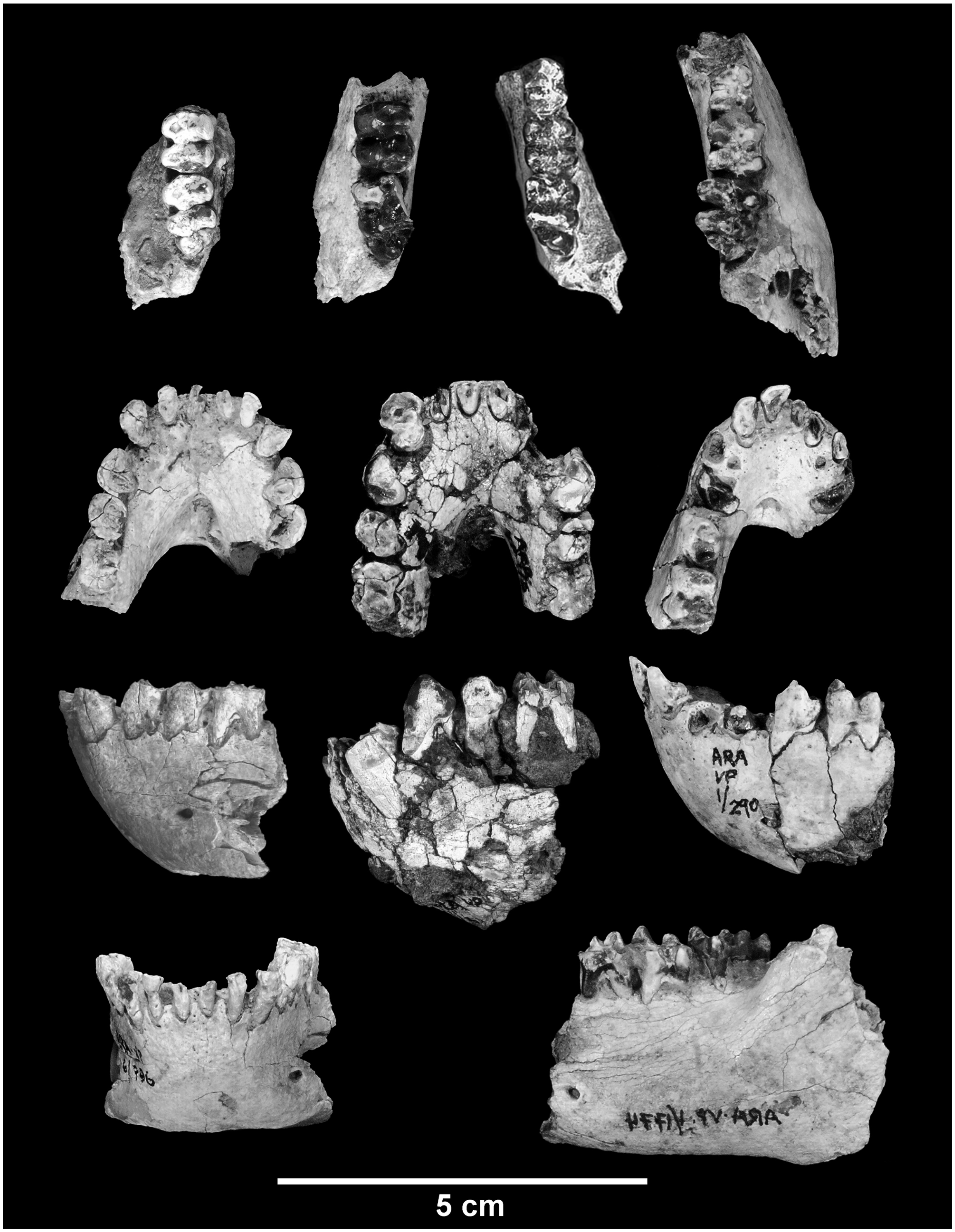


Plate 29. Mandibles of Kuseracolobus aramisi. Top row: ARA-VP-1/7, ARA-VP-1/70, ARA-VP-1/564, ARA-VP-1/1774, 2nd row: ARA-VP-6/796, ARA-VP-1/5, ARA-VP-1/290. 3rd row: ARA-VP-6/796, ARA-VP-1/5, ARA-VP-1/290. Bottom row: ARA-VP-6/796, ARA-VP-1/1774 (reversed).

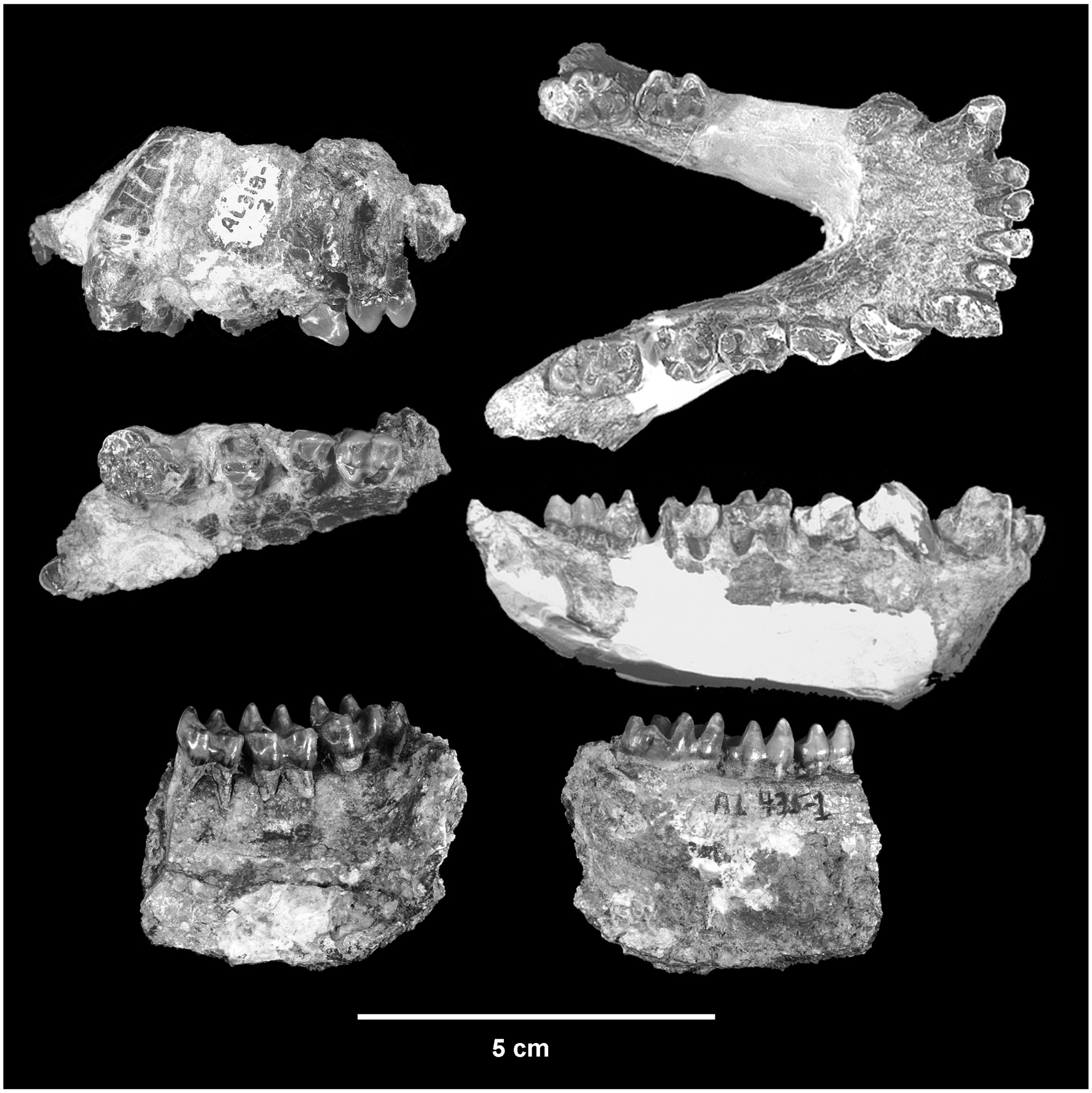


Plate 30. Specimens of cf. Rhinocolobus turkanaensis. Anticlockwise from top left: AL318-2 lateral view; AL318-2 ventral view; AL435-1 lateral view; AL435-1 lingual view; AL256-1 right lateral view; AL256-1 dorsal view.

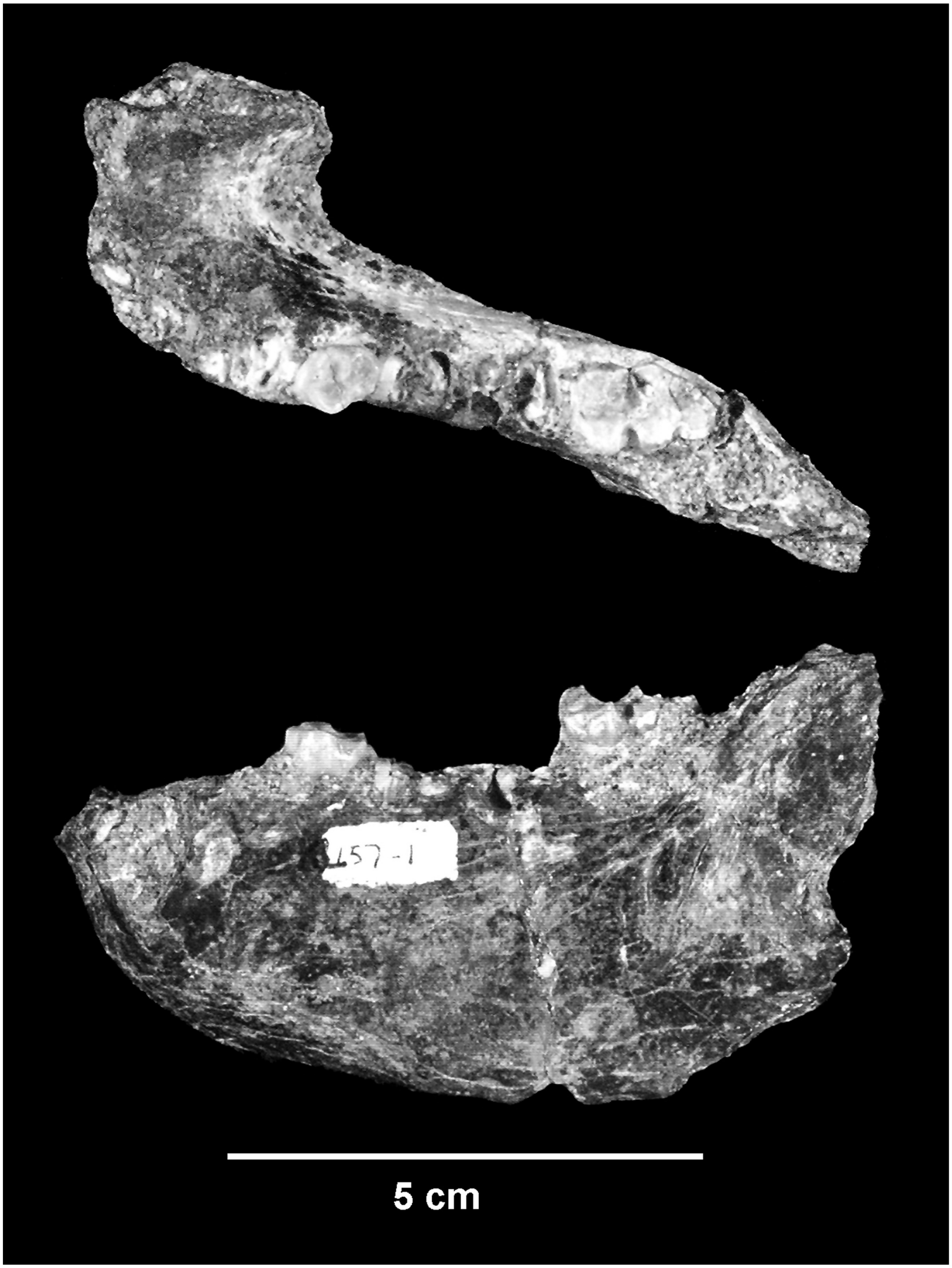


Plate 31. Male Paracolobus cf. chemeroni KL57-1. Top: Dorsal view. Bottom: lateral view.

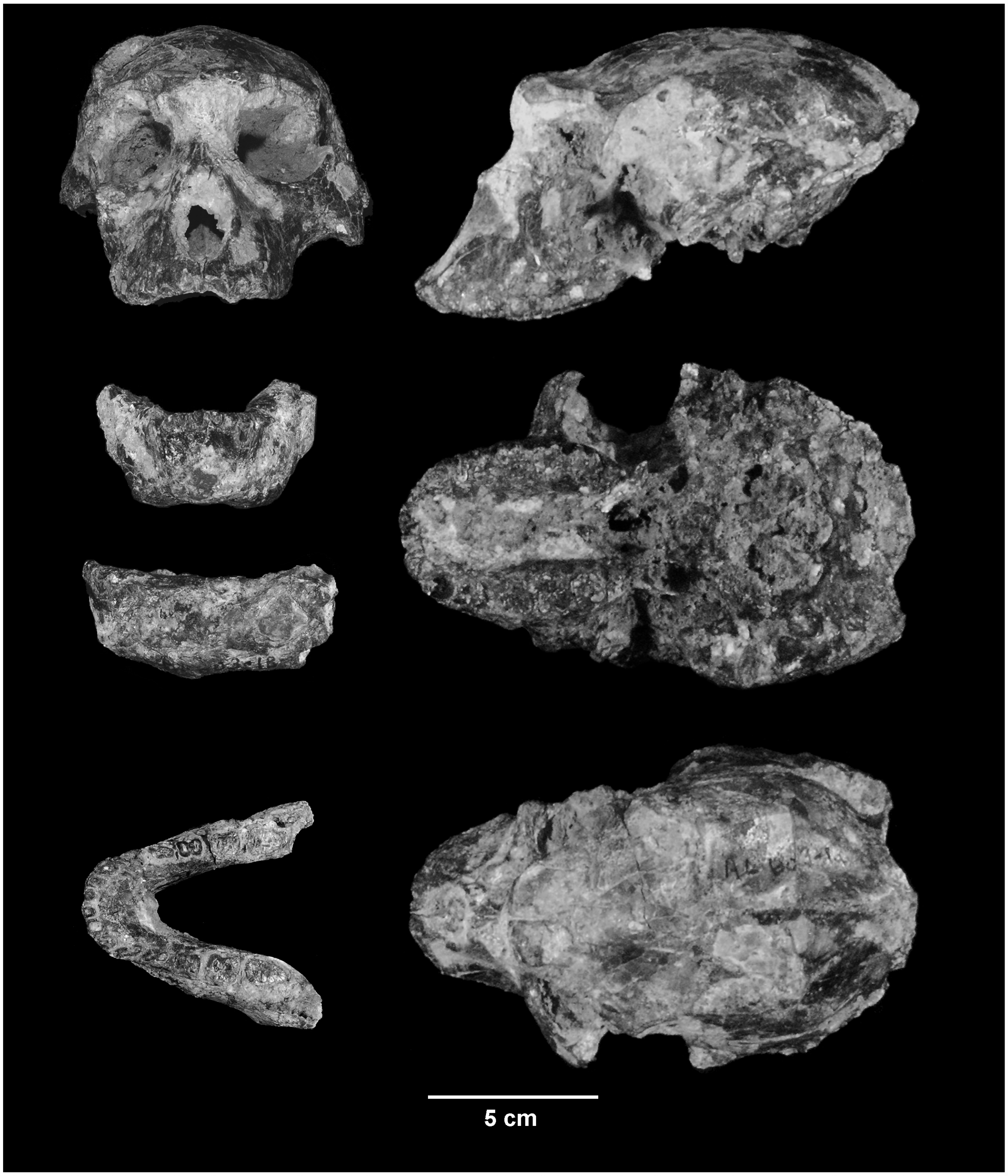


Plate 32. Female Cercopithecoides kimeui AL603-1. Clockwise from top left: AL603-1a cranium frontal, left lateral, ventral and dorsal views; AL603-1b mandible dorsal, lateral, and frontal views.

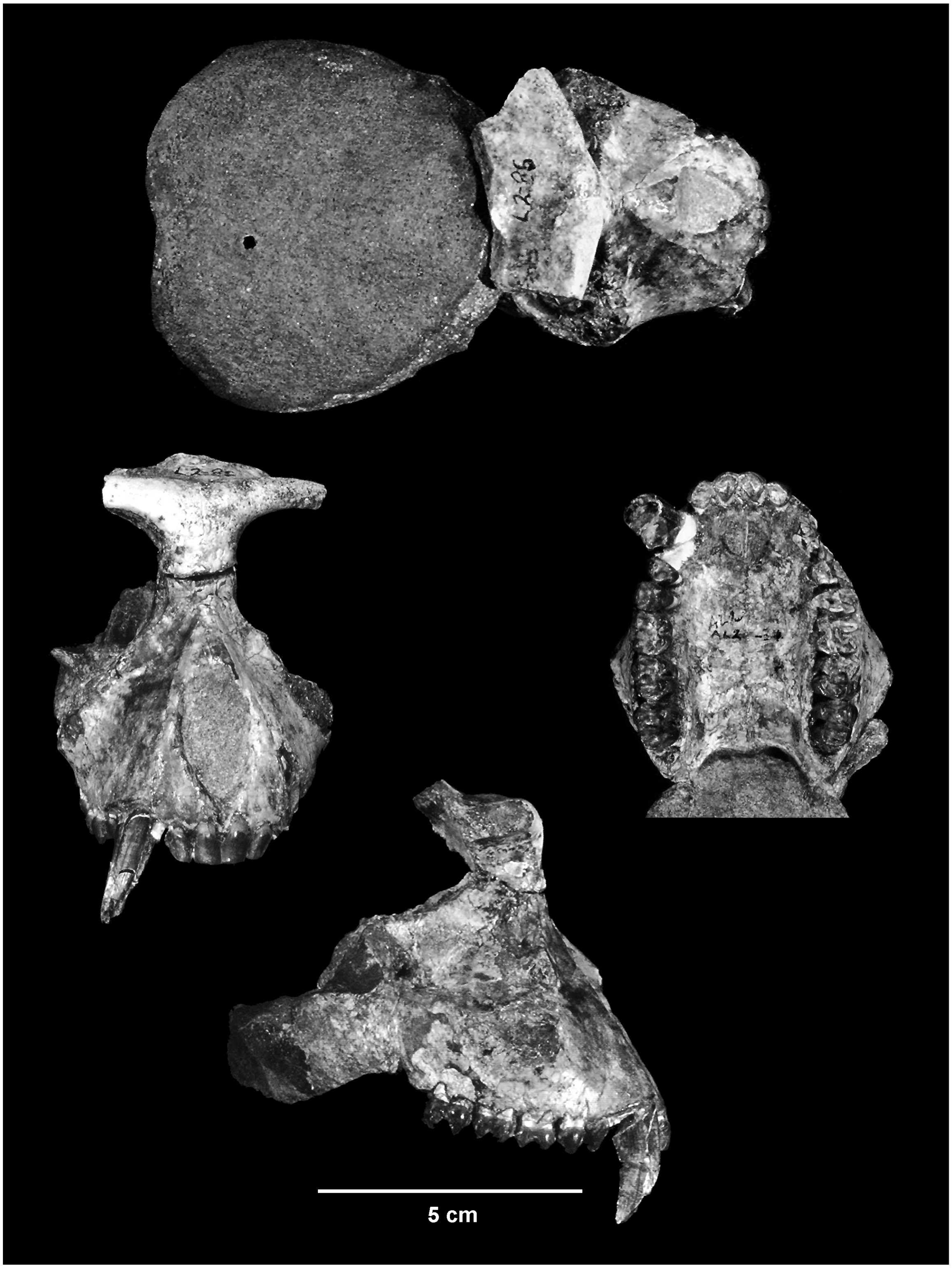


Plate 33. Male cf. Cercopithecoides sp. nov. AL2-34. Clockwise from top: dorsal (with endocast), ventral, lateral, and frontal views.

Plate 34. Mandibles of cf. Cercopithecoides sp. nov. Top row left to right: AL231-1a, AL2-34 dorsal view. Middle row: AL231-1a, AL2-34 left lateral view. Bottom row: AL231-1a (right half) lingual view; AL2-34 frontal view.

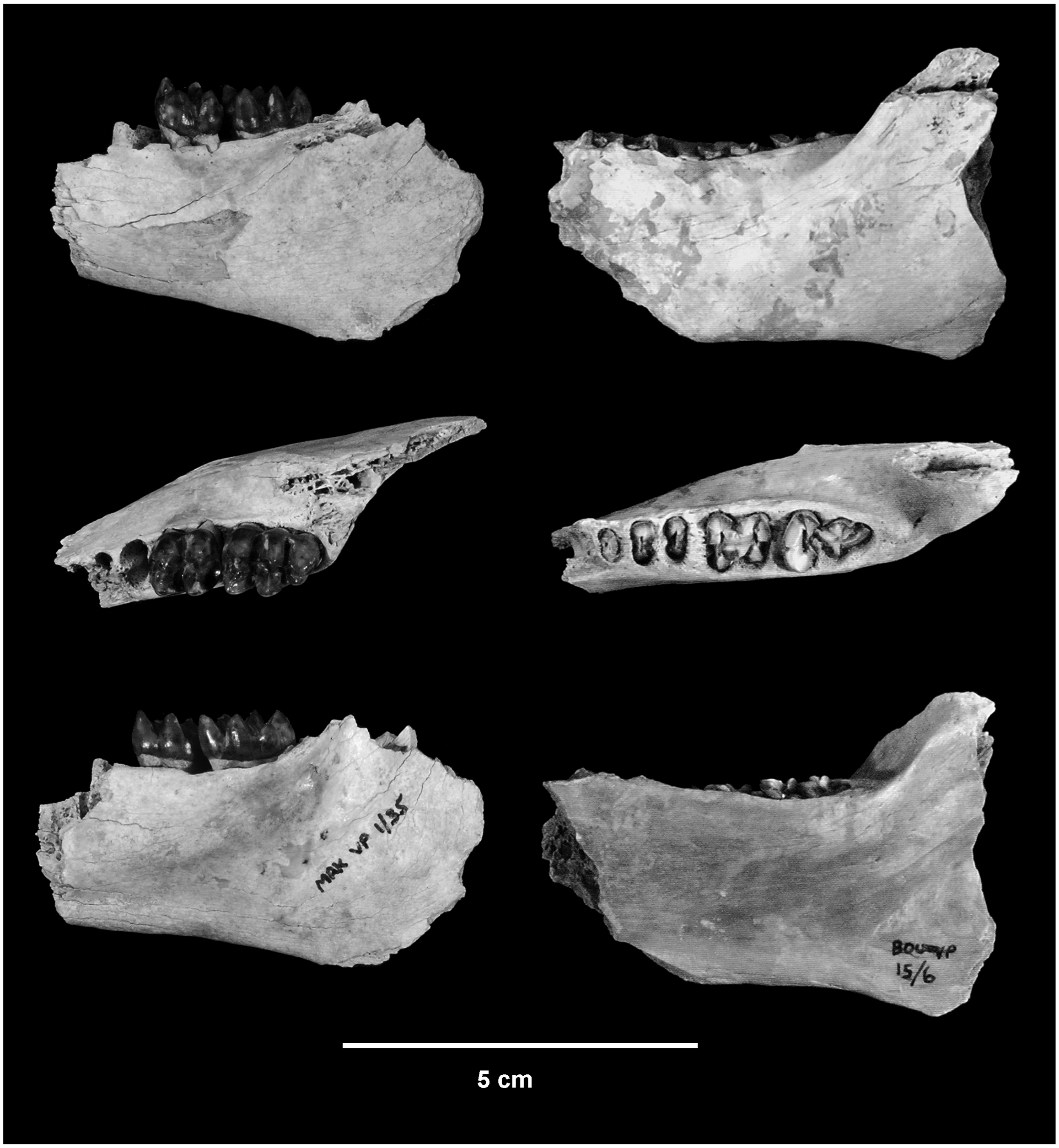


Plate 35. Mandibles of cf. Cercopithecoides sp. Top row left to right: MAK-VP-1/35, BOU-VP-15/6 lateral view. Middle row: MAK-VP-1/35, BOU-VP-15/6 ventral view. Bottom row: MAK-VP-1/35, BOU-VP-15/6 lingual view.

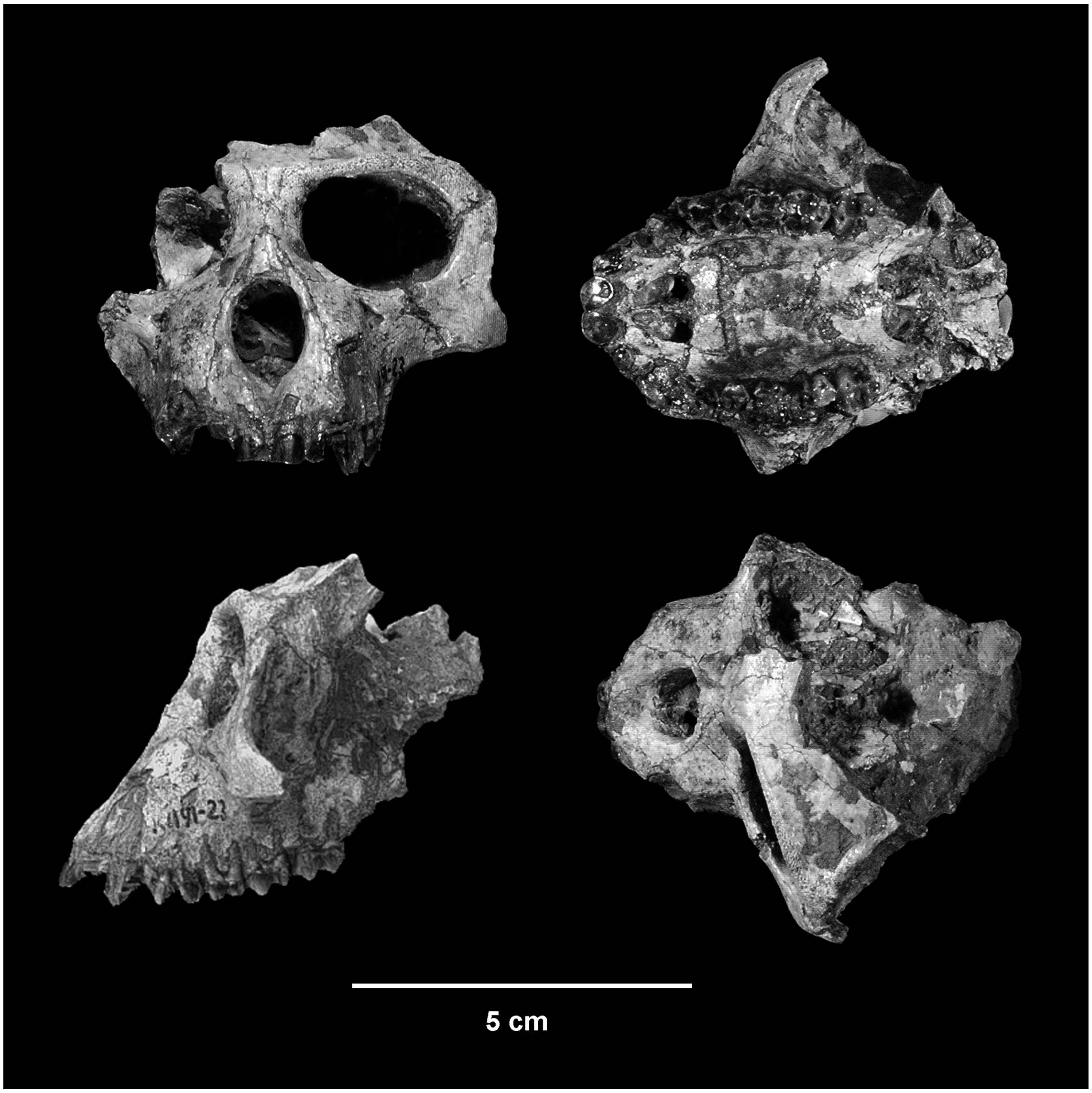


Plate 36. Male Colobus sp. KL191-23. Clockwise from top left: frontal, ventral, dorsal and lateral views.

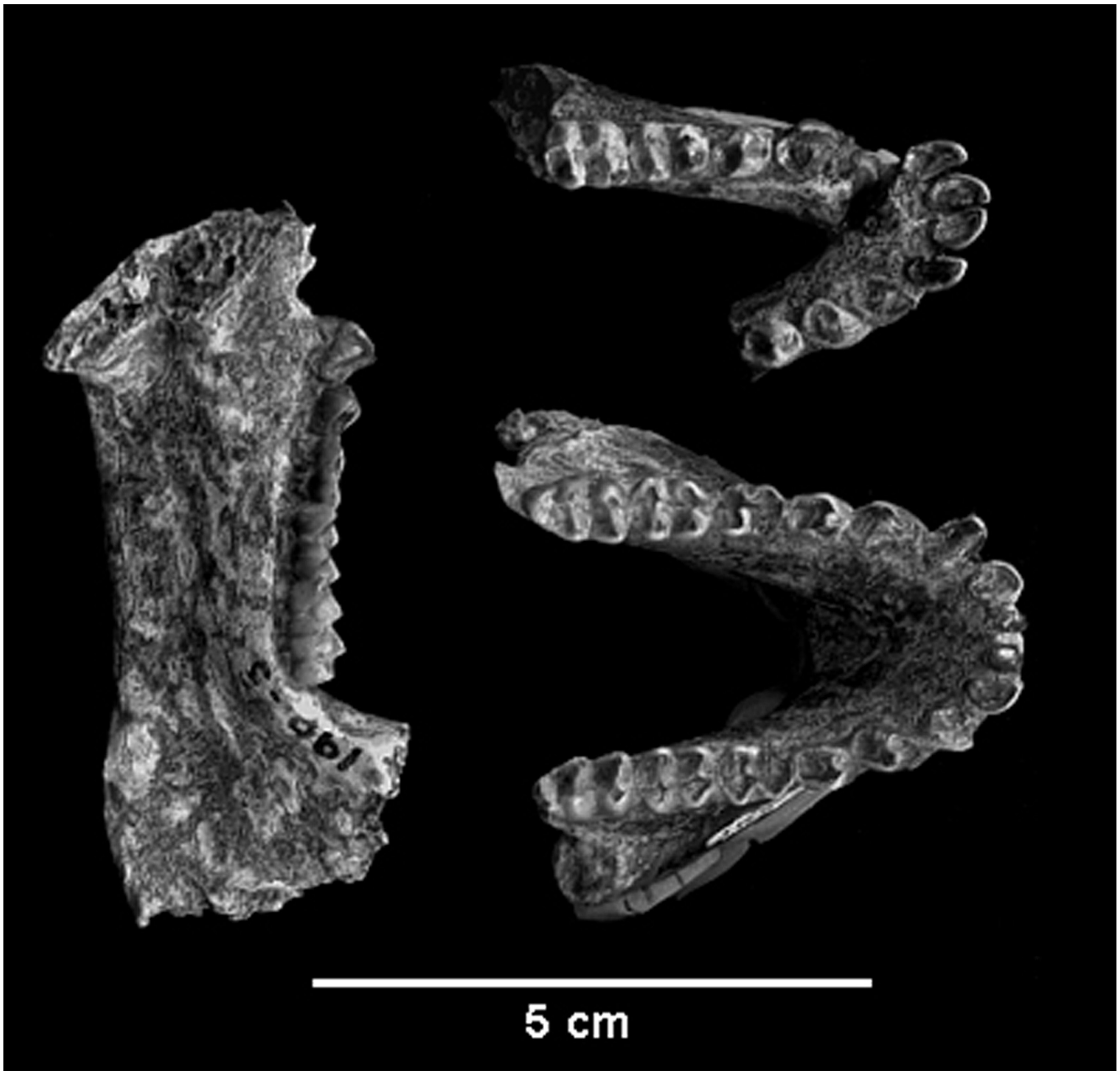


Plate 37. Mandibles of Colobus sp. Clockwise from top right: KL188-3 dorsal view; KL188-2 dorsal view; KL190-3 lingual view.

Appendix 1: specimens allocated to *Cercopithecus* sp.

Catalog Number	Sex	Side	Element	Comments
KL183 - 4		Right	Mandible	(P4-M3)
KL183 - 5		Right	Mandible	(M1-3)
KL183 - 6	Female	Right	Mandible	(M2-3)
KL183 - 7	Male	Right	Mandible	(P4-M2)
KL183 - 8		Right	Mandible	(M2-3)
KL183 - 9	Male	Left	Maxilla	(P3-M1)
KL183 - 15		Left	LM1 or 2	
KL183 - 26			Ulna	trochlear notch
KL187 - 2		Right	Mandible	(P4-M3)
KL188 - 4	Female	Left	Mandible	(P3-M1)
KL188 - 5	Female	Left	Mandible	(I2-M1)
KL188 - 7	Male	Right	Mandible	(P3-M2)
KL188 - 9		Right	Maxilla	(P4-M3)
KL188 - 11		Left	Mandible	(M1-3)
KL188 - 15	Female		Mandible	symphysis, (L.I1-C)
KL188 - 19		Right	Mandible	(M3)
KL188 - 21		Right	Mandible	symphysis, (I1-2)
KL188 - 28		Right	LM3	
KL188 - 30		Right	LM	
KL188 - 33		Right	LP4	
KL188 - 45		Left	Femur	proximal fragment
KL189 - 3	Female		Mandible	symphysis, (L.I1-C;R.I1-C)
KL189 - 4		Left	Maxilla	(M2-3)
KL191 - 25	Male	Right	Maxilla	edentulous
KL191 - 26	Female		Mandible	symphysis, (L.I1-C;R.I1-2)
KL191 - 27		Left	Maxilla	juvenile (dP3-M1, erupting M2)
KL191 - 58			Mandible	(L.C-M3; R.C-P3,M2-3)
KL191 - 62		Right	UM	
KL191 - 67		Left	Maxilla	(P4-M2)
KL191 - 71		Left	UI1	
KL191 - 83		Right	Humerus	distal fragment
KL191 - 87	Female	Left	Maxilla	(I1-M3)
KL191 - 93		Left	UI1	
KL191 - 97		Left	Maxilla	(M3)
KL191 - 100		Right	Mandible	(M2-3)
KL191 - 101		Right	Maxilla	(dP3-M1)
KL191 - 104	Male		Mandible	(L.P3-M3;R.P3)
KL191 - 105	Female	Right	Mandible	(P3-M3)
KL191 - 106	Male		Mandible	(L.P4-M3;R.I1-P3)
KL191 - 108		Right	Mandible	(P4,M2)
KL191 - 162		Right	Mandible	(M2-3)
KL191 - 163		Right	Maxilla	(M1-2)
KL191 - 174		Right	Maxilla	(P4-M2)
KL191 - 283	Male	Left	Mandible	symphysis, edentulous
KL191 - 316		Right	Femur	distal fragment
KL191 - 469		Right	Humerus	trochlea

Appendix 2: Specimens assignable to *Pl. alemui*

Catalog Number	Sex	Side	Element	Comments
ARA-VP-1/8		Left	Mandible	(M3)
ARA-VP-1/9		Left	LM3	
ARA-VP-1/12		Left	LM3	
ARA-VP-1/19		Right	UM1 or 2	
ARA-VP-1/20		Right	UM1 or 2	
ARA-VP-1/23		Left	UM1 or 2	
ARA-VP-1/24		Left	LM3	
ARA-VP-1/45		Right	Mandible	(M3)
ARA-VP-1/73	Male		Mandible	(R. I2-M3; L. P3-M3)
ARA-VP-1/132		Left	UM1 or 2	
ARA-VP-1/133	Female?		Mandible	(L.+R.P4-M3)
ARA-VP-1/135		Right	LM1 or 2	
ARA-VP-1/139	Male	Right	Maxilla	(M1)
ARA-VP-1/185		Right	LM3	
ARA-VP-1/190		Right	LM3	
ARA-VP-1/191		Left	LI1	
ARA-VP-1/239		Right	LM3	fragment
ARA-VP-1/289		Left	LM3	
ARA-VP-1/309		Left	LI1	
ARA-VP-1/330		Right	UM1 or 2	
ARA-VP-1/333		Left	UM1 or 2	
ARA-VP-1/339		Left	UM1 or 2	
ARA-VP-1/359		Left	UM	
ARA-VP-1/362		Left	LM2	
ARA-VP-1/390		Left	LM3	
ARA-VP-1/403		Right	UM	
ARA-VP-1/404		Right	LM1 or 2	
ARA-VP-1/405			UM	fragment
ARA-VP-1/406		Left	UI1	
ARA-VP-1/427	Male		Dentition	(UP,C,M,LM,R.LM3)
ARA-VP-1/485		Left	UI1	
ARA-VP-1/486		Right	LI1	
ARA-VP-1/487		Left	LI1	
ARA-VP-1/489		Right	Mandible	(dp4 - erupt. M1)
ARA-VP-1/491		Right	LM1 or 2	
ARA-VP-1/492		Left	LM3	
ARA-VP-1/494		Right	Udp4	
ARA-VP-1/496		Right	LM1 or 2	
ARA-VP-1/499		Left	UM3	
ARA-VP-1/505		Right	UM1 or 2	
ARA-VP-1/545		Left	LM1 or 2	
ARA-VP-1/548		Right	Mandible	(dp4 - M1)
ARA-VP-1/563	Female		Mandible	(RI1-LM2, RP3)
ARA-VP-1/695		Right	UI1	
ARA-VP-1/740			Mandible	(L.dc-M1;R.dp3-M1;L.I1-2 roots.)
ARA-VP-1/743		Right	Mandible	(I2?,dc-M1)
ARA-VP-1/744	Male		Cranial	fragments, (L. LI1-C;R. LI2,M3)
ARA-VP-1/791		Right	UM	fragment
ARA-VP-1/820		Right	UI1	

Catalog Number	Sex	Side	Element	Comments
ARA-VP-1/831		Left	LM3	fragment
ARA-VP-1/852		Right	UM3	
ARA-VP-1/884		Right	UM	
ARA-VP-1/885		Right	Udp4	
ARA-VP-1/890		Left	UI1	
ARA-VP-1/893		Right	LP4	
ARA-VP-1/936		Left	Maxilla	(M1)
ARA-VP-1/938		Left	Maxilla	(I2)
ARA-VP-1/944		Left	UM1 or 2	
ARA-VP-1/948		Left	LM1 or 2	
ARA-VP-1/949		Left	UI2	
ARA-VP-1/953	Female	Left	LP3	
ARA-VP-1/953	Female	Left	LM1	
ARA-VP-1/953	Female	Left	LM2	
ARA-VP-1/953	Female	Left	LM3	
ARA-VP-1/1006	Female		Mandible	(L.I2-M3;R.P3-M3)
ARA-VP-1/1007	Female	Left	Maxilla	(I2-M1)
ARA-VP-1/1008		Right	LI1	
ARA-VP-1/1008			Indet.	fragment
ARA-VP-1/1097		Right	LM1 or 2	
ARA-VP-1/1132		Left	UI1	
ARA-VP-1/1236		Right	UI2	
ARA-VP-1/1237		Left	UI1	
ARA-VP-1/1262		Right	LI1	
ARA-VP-1/1266		Left	LM1 or 2	
ARA-VP-1/1347		Right	UM	
ARA-VP-1/1377		Left	LM3	
ARA-VP-1/1408		Right	LP4	
ARA-VP-1/1483		Left	UI	fragment
ARA-VP-1/1539		Right	UI2	
ARA-VP-1/1542		Right	UI2	
ARA-VP-1/1553		Right	LM1 or 2	
ARA-VP-1/1554		Right	LM2	
ARA-VP-1/1555		Left	LM2	
ARA-VP-1/1556		Right	LM1 or 2	
ARA-VP-1/1558		Right	LM1	
ARA-VP-1/1559		Right	LM1 or 2	
ARA-VP-1/1560		Right	LM1 or 2	
ARA-VP-1/1568			M	fragment
ARA-VP-1/1569		Right	LM3	
ARA-VP-1/1571		Right	LM3	
ARA-VP-1/1573		Left	LM3	
ARA-VP-1/1574		Left	LM3	
ARA-VP-1/1575		Left	LM3	
ARA-VP-1/1596		Right	UI1	
ARA-VP-1/1615		Left	LM3	
ARA-VP-1/1639		Right	LI1	
ARA-VP-1/1662		Left	Ldp4	
ARA-VP-1/1675			M	
ARA-VP-1/1723	Female	Right	Maxilla	(C-M3)
ARA-VP-1/1917		Left	LM1 or 2	

Catalog Number	Sex	Side	Element	Comments
ARA-VP-1/1922		Left	UI1	
ARA-VP-1/1948		Left	LM3	
ARA-VP-1/1951		Right	LM1 or 2	
ARA-VP-1/1954		Left	UI2	
ARA-VP-1/1983		Left	Udp4	
ARA-VP-1/2045		Right	UM	
ARA-VP-1/2057		Left	UM	
ARA-VP-1/2059		Left	LM1 or 2	fragment
ARA-VP-1/2061	Male	Left	LP3	
ARA-VP-1/2075		Right	UI1	
ARA-VP-1/2076		Right	UI1	
ARA-VP-1/2078		Right	UM	
ARA-VP-1/2079		Left	UM3	
ARA-VP-1/2080		Left	LP4	
ARA-VP-1/2082		Left	LM1	fragment
ARA-VP-1/2085		Left	LM3	
ARA-VP-1/2086		Left	LM1 or 2	
ARA-VP-1/2090		Left	LM1 or 2	
ARA-VP-1/2098	Male	Left	LI2	
ARA-VP-1/2098	Male	Left	LC	
ARA-VP-1/2098	Male	Left	LP3	
ARA-VP-1/2098	Male	Left	LP4	
ARA-VP-1/2099		Left	UM	fragment
ARA-VP-1/2168		Right	LI2	
ARA-VP-1/2353	Female	Right	LI1	
ARA-VP-1/2353	Female	Right	LI2	
ARA-VP-1/2353	Female	Right	LC	
ARA-VP-1/2353	Female	Right	LP3	
ARA-VP-1/2353	Female	Right	LP4	
ARA-VP-1/2353	Female	Right	LM1	
ARA-VP-1/2354	Female	Left	UI2	
ARA-VP-1/2354	Female	Left	UC	
ARA-VP-1/2354	Female	Left	UP3	
ARA-VP-1/2354	Female	Left	UM3	
ARA-VP-1/2354	Female	Right	UI1	
ARA-VP-1/2354	Female	Right	UM1 or 2	
ARA-VP-1/2431		Left	LP4	
ARA-VP-1/2441		Right	UM	M2 or 3
ARA-VP-1/2470	Male?	Left	UI1	crown, root forming
ARA-VP-1/2470	Male?	Left	Udi2	
ARA-VP-1/2470	Male?	Left	Udc	
ARA-VP-1/2470	Male?	Left	Udp3	
ARA-VP-1/2470	Male?	Left	Udp4	
ARA-VP-1/2470	Male?	Left	UC	tip, crown still forming
ARA-VP-1/2470	Male?	Left	UP4	crown still forming
ARA-VP-1/2470	Male?	Right	UI1	crown
ARA-VP-1/2470	Male?	Right	Udc	
ARA-VP-1/2470	Male?	Right	UM1	
ARA-VP-1/2494		Right	LM1 or 2	
ARA-VP-6/8		Right	Mandible	(M2-3)
ARA-VP-6/9		Right	UM3	

Catalog Number	Sex	Side	Element	Comments
ARA-VP-6/52		Right	UI1	
ARA-VP-6/52		Left	UI1	
ARA-VP-6/57		Left	UM1 or 2	
ARA-VP-6/61		Right	LM	
ARA-VP-6/62		Left	LM1 or 2	
ARA-VP-6/63		Right	UM	
ARA-VP-6/83		Left	UM	
ARA-VP-6/95		Right	LM3	fragment
ARA-VP-6/96		Right	UI1	
ARA-VP-6/437	Male	Right	Maxilla	(C-P4 roots, I1,P3)
ARA-VP-6/576		Left	LM1 or 2	in tiny MAN frag.
ARA-VP-6/577		Left	UM	
ARA-VP-6/586		Right	LM3	
ARA-VP-6/597		Left	LI1	
ARA-VP-6/599		Left	LM3	
ARA-VP-6/600		Right	LM3	
ARA-VP-6/602		Right	LM1 or 2	
ARA-VP-6/623		Left	LP4	
ARA-VP-6/625		Left	LP4	
ARA-VP-6/627		Left	LP4	
ARA-VP-6/628		Left	UM2	
ARA-VP-6/629		Right	UM2	
ARA-VP-6/632		Right	UM1	
ARA-VP-6/643		Left	Udp4	
ARA-VP-6/647		Left	Ldp4	
ARA-VP-6/656		Right	UI2	
ARA-VP-6/659		Right	LM3	
ARA-VP-6/771		Right	LM	
ARA-VP-6/797			Mandible	(M1 erupting), juvenile
ARA-VP-6/799		Right	LM3	
ARA-VP-6/809		Left	LI1	
ARA-VP-6/810		Left	LI2	
ARA-VP-6/933			Skull	
ARA-VP-6/1277		Right	UI2	
ARA-VP-6/1281		Right	LM1 or 2	
ARA-VP-6/1283		Right	Ldp4 or M1	
ARA-VP-6/1284			M	fragment
ARA-VP-6/1289		Right	UM1 or 2	
ARA-VP-6/1292		Right	UI1	
ARA-VP-6/1296		Right	UM1 or 2	
ARA-VP-6/1307		Left	LI2	
ARA-VP-6/1562		Right	UM1 or 2	
ARA-VP-17/004	Female		Mandible	(roots L.P3-R.P3)
KUS-VP-2/085		Right	UM1 or 2	
KUS-VP-2/092		Left	LI1	
KUS-VP-2/098		Right	LM3	
KUS-VP-2/104		Right	UI2	
KUS-VP-2/115		Right	LI1	
KUS-VP-2/118		Left	UI1	
KUS-VP-2/118		Left	LI	fragment
KUS-VP-2/139		Left	UM	M2 or 3

Catalog Number	Sex	Side	Element	Comments
KUS-VP-2/142		Right	LM1 or 2	
SAG-VP-7/103		Left	LM3	
SAG-VP-7/106		Left	LM3	
SAG-VP-7/133		Right	UM	M2 or 3
SAG-VP-7/155		Left	UM1 or 2	

Appendix 3: cranial specimens allocated to *T. o. darti*.

Catalog Number	Sex	Side	Element	Comments
AL2 - 10b		Right	LM1or2	
AL100 - 290		Left	LM3	
AL100 - 291		Right	LM3	
AL100 - 292		Right	UM3	
AL100 - 293		Right	Mandible	(P4)
AL100 - 294		Left	Mandible	(P4)
AL100 - 320	Female	Left	LP3	
AL100 - 321	Female	Left	LP3	
AL100 - 322		Left	LP4	
AL100 - 323		Left	LP4	
AL100 - 324	Male	Right	LP4	
AL100 - 325		Left	UP	
AL100 - 326		Right	UP4	
AL100 - 327		Right	LP4	
AL100 - 328		Left	UP4	
AL100 - 330		Right	UP4	
AL100 - 331		Right	UP	
AL100 - 332		Left	UI1	
AL100 - 333		Right	LI1	
AL100 - 334		Right	LI	
AL100 - 337		Left	LI2	
AL100 - 338		Left	LdC	
AL100 - 339		Right	UI2	
AL100 - 340		Right	UI1	
AL100 - 345		Left	LM1or2	
AL100 - 346		Right	LM3	
AL100 - 349		Right	LM3	
AL100 - 350		Right	LM1or2	
AL100 - 351		Left	LM1or2	
AL100 - 352		Left	LM3	
AL100 - 353		Right	LM1or2	
AL100 - 358		Left	LM1or2	
AL100 - 359		Right	LM2	
AL100 - 360		Right	LM1or2	
AL100 - 361		Right	UM	
AL100 - 362		Left	UM3	
AL100 - 363		Right	LM1or2	
AL100 - 364		Left	UM	
AL100 - 366	Male	Right	UC	
AL100 - 367	Male	Right	LC	
AL100 - 368	Female	Left	UC	
AL100 - 369	Female	Left	UC	
AL100 - 370		Left	UdC	
AL100 - 371		Left	dC	
AL100 - 372		Left	LdC	
AL100 - 373		Right	LdC	
AL100 - 374	Male	Left	UC	
AL100 - 376	Male	Left	LC	
AL100 - 377		Right	LdP	
AL100 - 378		Right	UM	

Catalog Number	Sex	Side	Element	Comments
AL100 - 379		Right	UM	
AL100 - 382		Left	LM3	
AL100 - 383		Right	UM	
AL100 - 385			UM	
AL100 - 386		Right	LM1or2	
AL100 - 387		Left	UM	
AL100 - 388		Left	LM3	
AL100 - 392		Right	LM	
AL100 - 394		Left	UM	
AL100 - 396		Right	LM	
AL100 - 402		Right	Frontal	
AL108 - 12		Left	Mandible	juvenile, (dC-dP4,M1)
AL108w - 107	Male	Right	Mandible	(P3,M1)
AL113 - 5a	Female	Right	Mandible	(M3)
AL113 - 5b	Female		Mandible	edentulous
AL113 - 5c	Female	Left	Mandible	edentulous
AL113 - 5d	Female	Right	Mandible	edentulous
AL116 - 10			LM	
AL116 - 23		Right	Maxilla	juvenile, (M1-2)
AL126 - 30	Female	Right	Mandible	(C-M3)
AL126 - 78		Left	LM3	
AL127 - 54		Left	Mandible	(P4)
AL128 - ?		Left	UM	
AL129 - 8	Female		Mandible	(L.C-P3,R.C-M3)
AL132 - 26b		Right	Maxilla	juvenile, (dP4)
AL132 - 26c		Left	Maxilla	juvenile, (dP3-4)
AL132 - 26e		Right	UdP3	
AL132 - 26f		Right	UdC	
AL132 - 26g		Left	UdI1	
AL133 - 4			M	
AL133 - 54			LM2	
AL134 - 5a			Face	(L.P3-M2,R.M2)
AL137 - 11		Right	Mandible	(M2-3)
AL137 - 12		Left	LM1	
AL142 - 19	Male	Left	Mandible	(C-M2)
AL144 - 1		Left	Mandible	(M2-3)
AL148 - 105	Male	Left	UC	
AL148 - 107	Male		Mandible	(L.C-M1,R.C)
AL148 - 119		Right	Mandible	(M1-3)
AL148 - 120		Left	Mandible	(M2-3)
AL153 - 14a	Male	Right	Mandible	(P3-M3)
AL153 - 14b	Male	Left	Mandible	(P4-M2)
AL153 - 18		Right	Mandible	juvenile, (dP3-M1)
AL154 - 95	Female	Right	Maxilla	subadult, (P4-M2)
AL156 - 28		Right	UM	
AL158 - 91		Right	Mandible	(M2)
AL158 - 92		Left	LI2	
AL161 - 23		Left	Mandible	(M2-3)
AL163 - 11	Male	Right	Mandible	(P3-M3)
AL165 - 8	Female	Right	LC	
AL173 - 26	Female	Left	Mandible	(P3-M3)

Catalog Number	Sex	Side	Element	Comments
AL174 - 10	Male	Right	Mandible	(M2-3)
AL178 - 12a		Left	Mandible	(P4-M3)
AL178 - 12b		Left	Mandible	(M1-2)
AL183 - 45		Right	Mandible	(M3)
AL185 - 16		Right	UM3	
AL185 - 22h		Left	Mandible	juvenile, (M2)
AL185 - 5a	Female		Calvaria	subadult
AL185 - 5b	Female	Left	Maxilla	subadult, (I2,P4-M2)
AL185 - 5c	Female	Left	Mandible	subadult, (P3-M3)
AL186 - 16a		Left	Maxilla	juvenile, (dP3-M1)
AL186 - 16b			UM1	juvenile
AL186 - 16c		Right	UI2	juvenile
AL186 - 17	Female		Mandible	(L.M1-3,R.M2-3)
AL187 - 10	Male		Calvaria	
AL187 - 17	Female	Right	Mandible	(P4-M2)
AL188 - 19		Left	UI2	
AL193 - 1		Right	Mandible	juvenile, (M1)
AL196 - 3a	Female	Right	Mandible	(P4-M3)
AL199 - 4		Right	Mandible	(M3)
AL199 - 8		Left	Mandible	(M1 or 2)
AL200 - 12		Right	UM	
AL200 - 14		Left	Mandible	(M2)
AL200 - 16		Right	UC	not full formed at edj
AL200 - 17		Left	UP3	
AL200 - 18		Right	UI2	
AL200 - 19		Left	UI2	
AL200 - 20	Female	Right	Mandible	(P3-M3)
AL200 - 21		Right	Mandible	(P3-M3)
AL200 - 22		Right	Maxilla	(M1;M2 roots)
AL200 - 23		Right	Maxilla	(M)
AL200 - 24		Left	Mandible	(P4-M3)
AL202 - 3	Female	Right	Mandible	subadult, (P3,dP4-M1,M3)
AL204 - 4	Female	Left	Mandible	juvenile, (P3-M1)
AL205 - 1a/b	Male		Cranium	(L.P3-M2,R.P4-M2)
AL205 - 1c	Male	Left	Mandible	(P3-M1)
AL208 - 10a	Male		Mandible	(L.P3-M3,R.P3-M3)
AL208 - 10b	Male	Left	Maxilla	(P4-M3)
AL208 - 6		Right	LM3	
AL211 - 4			Occipital	
AL217 - 1	Female	Right	Mandible	(P4-M3)
AL217 - 7		Left	Mandible	(M1-2)
AL221 - 4		Left	LM3	
AL223 - 28		Right	Mandible	(M3)
AL223 - 29	Male	Left	Mandible	(I2-P4)
AL225 - 5		Right	UM	
AL225 - 9		Left	Mandible	(P4-M3)
AL231 - 9		Left	Maxilla	(M1-3)
AL236 - 28a		Right	Mandible	(M2-3)
AL236 - 28b	Male	Left	Mandible	(I1-C)
AL237 - 7	Male	Left	LC	
AL238 - 5			Frontal	

Catalog Number	Sex	Side	Element	Comments
AL238 - 6		Left	Maxilla	(M2-3)
AL249 - 24		Left	UP3	
AL249 - 25		Right	LM3	
AL252 - 6		Right	Mandible	(M1-2)
AL253 - 2	Male	Left	LC	
AL258 - 2		Left	Mandible	(M2-3)
AL269 - 1		Left	Maxilla	juvenile, (dP3-4)
AL269 - 3	Female		Mandible	(L.M2-3,R.P4-M3)
AL270 - 1	Female	Right	Mandible	(P4-M3)
AL284 - 2		Left	Mandible	(I1,dC-dP4,M1)
AL288 - 14		Left	Mandible	(M1 roots)
AL288 - 45		Left	LdP4	
AL288 - 46			M	
AL289 - 5		Left	Mandible	(M3)
AL300 - 6		Right	UM1or2	
AL304 - 1		Left	LM3	
AL310 - 15	Female	Left	Mandible	(P4-M3)
AL310 - 19	Male		Face	
AL316 - 8		Left	Mandible	(P3-M2)
AL316 - 9		Right	Mandible	(dI2-dP4)
AL317 - 2		Right	Mandible	(M3)
AL319 - 10			Calvaria	
AL321 - 12	Female		Cranium	(L.P3-M3,R.P4-M3)
AL327 - 2		Right	Mandible	juvenile, (L.I2-R.C,dP3)
AL329 - 1	Male	Left	Mandible	juvenile, (L.I1-M3,R.I1-P4)
AL345 - 1	Female	Left	Mandible	juvenile, (M1)
AL362 - 15	Female	Right	Maxilla	(P3-M2), could also be Papio?
AL363 - 8	Female	Left	Mandible	(P3-M2)
AL366 - 1		Left	UM	not in catalog
AL383 - 1a		Left	Maxilla	
AL383 - 1b		Left	Mandible	
AL390 - 10		Left	Mandible	(P4-M2)
AL391 - 1		Left	Mandible	(M2-3 roots)
AL391 - 2		Left	UM	
AL391 - 3		Right	UM	
AL400 - 11			UM1or2	
AL400 - 8		Right	LM1	
AL401 - 8		Left	LM1or2	M2?
AL403 - 43		Left	LM3	
AL412 - 1	Male		Cranium	
AL414 - 1a		Left	Mandible	edentulous
AL414 - 1b		Left	Mandible	(P3-M3 roots)
AL415 - 1a		Left	Mandible	(dP3-4,M1-2)
AL415 - 1b		Right	UP4	crown only
AL415 - 1c			UM	
AL415 - 1d		Left	LdI2	
AL415 - 1e		Right	UI1	
AL415 - 1f		Left	UI1	
AL415 - 1g		Right	UI2	
AL415 - 1h		Left	UI2	
AL415 - 1i		Right	LI1	

Catalog Number	Sex	Side	Element	Comments
AL415 - 1j		Right	LI2	
AL415 - 1k	Male	Right	UC	tip, still forming
AL415 - 1l	Male	Left	LC	tip, still forming
AL415 - 1m			Calvaria	(6 fragments)
AL415 - 1n			Cranial	
AL415 - 1o		Right	Occipital	
AL415 - 1p			Cranial	
AL415 - 1q			Cranial	
AL426 - 1	Female	Left	Mandible	(P3-M2)
AL430 - 1a		Right	Temporal	exploded
AL430 - 1b		Right	Maxilla	(M3), exploded
AL430 - 1c		Left	Maxilla	(M2-3), exploded
AL430 - 1d		Left	Mandible	(M3 roots), exploded
AL430 - 1e			Cranial	exploded
AL430 - 1f			Cranial	exploded
AL430 - 1g			Cranial	exploded
AL433 - 2	Male	Left	Mandible	edentulous
AL433 - 6h			Bone	
AL486 - 2	Male	Left	Mandible	(P3-M3)
AL487 - 2		Right	Mandible	(P4-M2)
AL52 - 1		Right	Maxilla	(P3-M1)
AL55 - 43		Left	Mandible	juvenile, (dP4-M1)
AL56 - 17		Left	LM2	
AL58 - 23	Male	Left	Mandible	(P4-M3)
AL700 - 2		Left	Mandible	(P3-4 roots;M1-3 worn flat
AL700 - 3	Male		Maxilla	(I1-2 roots;C)
AL700 - 4a		Left	Zygomatic (jugal)	
BUN-VP-2/23	Male	Left	LC	
BUN-VP-2/24	Male	Right	LP3	
BUN-VP-2/27	Male?	Right	UP3	
BUN-VP-2/28		Right	UP4	
BUN-VP-2/29		Left	LM1or2	
BUN-VP-2/30		Right	LM1or2	
BUN-VP-2/31		Left	LM1or2	
BUN-VP-2/32		Right	UM1or2	
BUN-VP-2/33		Right	UM	
BUN-VP-2/34			M	
BUN-VP-2/35		Left	UP4	
BUN-VP-2/36		Right	UM	
BUN-VP-2/37		Right	UM	
MAK-VP-1/015		Left	LM3	
MAK-VP-1/017		Right	Mandible	(M3)
MAK-VP-1/043		Left	Mandible	(M1-3)
MAK-VP-1/056		Left	UM	
MAK-VP-1/066		Right	Maxilla	(M1-3)
MAK-VP-1/067		Right	UM3	
MAK-VP-1/092			Cranial	(Including: L. temp., R.meatus, occiput, 5 misc.frags.)
MAK-VP-1/094	Male	Left	LC	
MAK-VP-1/100	Male		Cranium	

Catalog Number	Sex	Side	Element	Comments
MAK-VP-1/109		Left	Mandible	(M2-3)
MAK-VP-1/117		Left	LI1	
MAK-VP-1/130		Right	Mandible	(M3)
MAT-VP-7/02		Left	LM3	
MAT-VP-7/03		Left	LM1or2	
MAT-VP-7/04		Right	UM	
WEE-VP-5/06		Right	LM3	
WEE-VP-5/08		Left	Temporal	
WEE-VP-5/08		Left	UM2	
WEE-VP-5/08		Left	UM3	
WEE-VP-5/08		Left	UP3	
WEE-VP-5/08		Left	UP4	
WEE-VP-5/08		Right	Temporal	
WEE-VP-5/08		Right	UdP	
WEE-VP-5/08		Right	UM1	
WEE-VP-5/08		Right	UM2	
WEE-VP-5/08		Right	UM3	
WEE-VP-5/08		Right	UP3	
WEE-VP-5/08		Right	UP4	

Appendix 4: cranial specimens allocated to *T. o. oswaldi*.

Catalog Number	Sex	Side	Element	Comments
AL18 - 17	Female		Mandible	all Teeth Damaged
AL416 - 2	Male		Maxilla	(R+L.C-M3)
AL532 - 1a		Right	Mandible	(M3)
AL532 - 1b		Left	Mandible	(P4-M2)
AL532 - 1c		Left	UI2	
AL532 - 1d		Right	UI2	
AL532 - 1e		Left	LM1or2	
AL532 - 1f			M	
AL532 - 1g			M	
AL535 - 5		Right	Mandible	(M1)
AL537 - 4		Right	Mandible	(M1-3), very broken
AL537 - 5		Right	Mandible	(dp3-4;I1-2 erupting)
AL537 - 9		Right	UI2	
AL539 - 6	Male	Left	UC	
AL552 - 2a			Mandible	
AL558 - 1		Right	LM1or2	
AL571 - 1a			Calvaria	
AL571 - 1b		Left	Face	(P4-M3)
AL571 - 1c		Right	Face	(M2-3 roots)
AL593 - 1		Right	Mandible	(dp3-4)
AL596 - 1			Mandible	(L.I1-M2;RI1-P3)
AL606 - 1		Left	Mandible	(M1-2), juvenile
AL607 - 1a/b		Right	Mandible	(P4-M3)
AL607 - 1c/d		Left	Mandible	(P4-M3)
AL623 - 6		Left	UI1	
AL653 - 3		Right	UM	
AL666 - 10		Right	LI	
AL666 - 15		Left	LI2	
AL666 - 5		Right	UM	probably M3
AL666 - 7		Right	UI2	
AL666 - 9	Male	Right	UC	
AL74 - 3		Left	Mandible	(M3)
GAM-VP-1/08		Left	Mandible	(dP3-M1)
KL5 - 5	Female	Left	LC	
KL11 - 4			UM	
KL13 - 12		Right	LM3	
KL13 - 3		Right	UM	
KL16 - 5		Right	Mandible	(M2-3)
KL18 - 1		Right	Maxilla	(P3 - M1)
KL19 - 1		Right	UM1or2	
KL22 - 1		Right	Mandible	(P4-M2)
KL29 - 1		Right	Maxilla	(M1)
KL37 - 1		Right	Calvaria	
KL38 - 1	Male		Cranium	juvenile
KL39 - 1	Male		Cranium	
KL40 - 1			Bone	L.UC-M3;R.UC,M2-3)
KL43 - 1			UM	
KL44 - 1		Left	LM1	
KL44 - 3a		Left	Mandible	(M1-3)
KL44 - 4a		Right	LM1or2	

Catalog Number	Sex	Side	Element	Comments
KL45 - 1		Right	UM	
KL46 - 1	Female	Right	Mandible	(C-M3)
KL64 - 3d		Right	Mandible	(P4-M2 roots)
KL65 - 1		Left	Mandible	(M2-3)
KL74 - 2a	Male		Mandible	(L.P3-M1,M3;R.P3-M2)
KL74 - 2b			Mandible	(L.M3)
KL74 - 2b			Mandible	(R.P4-M1)
KL74 - 2c	Male	Left	Maxilla	(M2-3)
KL74 - 2c	Male	Right	Maxilla	(I2-P4,M2-3)
KL74 - 2c	Male	Right	Temporal	
KL74 - 2c	Male	Left	Occipital	
KL74 - 2c	Male		Cranial	
KL74 - 2c	Male	Right	Frontal	
KL74 - 2c	Male	Left	Mandible	
KL74 - 2c	Male	Left	Temporal	
KL157 - 1	Male		Cranium	
KL235 - 1	Female	Left	Maxilla	(I2-M3)
MAT-VP-2/12		Left	Mandible	(M3)
MAT-VP-3/03	Female		Mandible	edentulous
MAT-VP-4/14	Male?	Right	Mandible	(I1,dC,P3-M2, M3 in crypt.)
MAT-VP-5/21	Female	Right	Mandible	(M3)
MAT-VP-5/30a		Left	Mandible	(M2-3)
MAT-VP-5/30b		Right	Mandible	(M3)
MAT-VP-6/11	Female	Left	Mandible	(C)
MAT-VP-6/15		Left	LM3	
MAT-VP-6/16		Right	LM1or2	
MAT-VP-6/17	Female	Right	LC	
WIL-VP-2/14		Left	UM1or2	
WIL-VP-2/15		Left	Maxilla	(P4-M3)
WIL-VP-3/1		Right	Mandible	(M3)

Appendix 5: specimens allocated to *K. aramisi*

Catalog Number	Sex	Side	Element	Comments
ARA-VP 1/5	Male		Mandible	symphysis, (L.I1-M1;R.I1,P3-M1)
ARA-VP 1/6	Male	Left	Maxilla	(C-M3)
ARA-VP 1/7		Left	Mandible	(M2-3)
ARA-VP 1/10		Left	LM3	
ARA-VP 1/11		Left	LM3	
ARA-VP 1/13			Frontal	glabella with small bit of nasals
ARA-VP 1/14		Left	LM1 or 2	
ARA-VP 1/15		Left	LM1 or 2	
ARA-VP 1/16		Left	Ldp4	
ARA-VP 1/17			M	fragment
ARA-VP 1/18		Right	UM3	
ARA-VP 1/21		Right	UM	
ARA-VP 1/22		Right	UM	
ARA-VP 1/46		Right	LM1 or 2	fragment
ARA-VP 1/48		Left	Ldp4	
ARA-VP 1/49		Left	UM1 or 2	
ARA-VP 1/50		Right	UM1 or 2	
ARA-VP 1/70		Left	Mandible	(M2-3)
ARA-VP 1/87	Male		Mandible	(L.P3-4,M2-3;R.P3-M3)
ARA-VP 1/87	Male		Maxilla	(M1-3)
ARA-VP 1/87	Male	Left	LC	
ARA-VP 1/87	Male	Right	UC	
ARA-VP 1/87	Male	Left	UC	
ARA-VP 1/116		Right	LM3	
ARA-VP 1/121		Left	UM	
ARA-VP 1/130		Right	LM3	
ARA-VP 1/134		Left	UM3	
ARA-VP 1/169		Left	LP4	
ARA-VP 1/170		Right	LM3	
ARA-VP 1/177		Left	Maxilla	(dp4-M1)
ARA-VP 1/178		Right	Maxilla	(dp4-M1)
ARA-VP 1/179		Right	UM	
ARA-VP 1/180		Left	LP4	
ARA-VP 1/186		Right	UM3	
ARA-VP 1/189		Left	LM	fragment
ARA-VP 1/192		Right	Udp or M	fragment
ARA-VP 1/196		Right	LI2	
ARA-VP 1/197		Left	Maxilla	damaged, (L.P3,M1-3)
ARA-VP 1/197		Right	Cranial	fragment, (R.UP4)
ARA-VP 1/197			Temporal	ectotympanic and mastoid
ARA-VP 1/198		Left	Mandible	(M1-3)
ARA-VP 1/205		Right	UM	
ARA-VP 1/238		Left	LM3	
ARA-VP 1/286		Right	LM1 or 2	
ARA-VP 1/290			Mandible	(L.I1-2,P4-M1, L.+R.P3 erupting)
ARA-VP 1/306	Male	Left	LP3	
ARA-VP 1/306	Male	Left	LM1	
ARA-VP 1/306	Male	Left	LM3	
ARA-VP 1/306	Male	Right	LC	

Catalog Number	Sex	Side	Element	Comments
ARA-VP 1/306	Male	Right	LP3	
ARA-VP 1/306	Male	Right	LM2	
ARA-VP 1/306	Male	Right	LM3	
ARA-VP 1/308		Right	LM3	
ARA-VP 1/324		Right	LM1 or 2	
ARA-VP 1/329		Left	LM3	
ARA-VP 1/331		Left	LM3	
ARA-VP 1/336		Left	LP4	
ARA-VP 1/337		Left	LM3	
ARA-VP 1/338		Right	LM1 or 2	
ARA-VP 1/351		Right	LM3	
ARA-VP 1/379		Left	UM1 or 2	
ARA-VP 1/383	Male	Right	Mandible	(P3-M1)
ARA-VP 1/389		Right	Maxilla	(P3-4)
ARA-VP 1/483		Right	UI1	
ARA-VP 1/484		Left	UI1	
ARA-VP 1/490		Right	UI1	
ARA-VP 1/497		Right	UM1 or 2	
ARA-VP 1/549		Left	LM1 or 2	
ARA-VP 1/550		Right	LM3	
ARA-VP 1/551		Right	UM	
ARA-VP 1/559		Right	Mandible	(M3)
ARA-VP 1/564		Right	Mandible	(M1-3)
ARA-VP 1/566		Left	Mandible	(P4-M2)
ARA-VP 1/694		Left	UM1 or 2	
ARA-VP 1/742		Right	UM	
ARA-VP 1/747		Right	LM	fragment
ARA-VP 1/748		Right	LM1 or 2	fragment
ARA-VP 1/785		Right	Mandible	(M1-3)
ARA-VP 1/788		Right	Maxilla	fragment, (M3)
ARA-VP 1/790		Right	LM1 or 2	fragment
ARA-VP 1/793		Left	UM3	
ARA-VP 1/794		Left	UM	
ARA-VP 1/795		Left	UI1	
ARA-VP 1/795		Left	UI2	
ARA-VP 1/850		Right	UM1 or 2	
ARA-VP 1/853		Left	LI2	
ARA-VP 1/872		Right	UI1	
ARA-VP 1/879		Left	LM1 or 2	
ARA-VP 1/887		Left	LM1 or 2	
ARA-VP 1/889		Left	UM	
ARA-VP 1/892		Right	UM	
ARA-VP 1/894		Right	LP4	
ARA-VP 1/896		Right	UM	
ARA-VP 1/900		Right	Maxilla	(M1-2)
ARA-VP 1/939		Left	LM1 or 2	fragment
ARA-VP 1/943		Right	UM3	
ARA-VP 1/950		Right	LM1 or 2	
ARA-VP 1/1168		Right	UI1	fragment
ARA-VP 1/1168		Right	LI2	fragment
ARA-VP 1/1238		Left	UM	

Catalog Number	Sex	Side	Element	Comments
ARA-VP 1/1241		Left	Ldp4	
ARA-VP 1/1255		Right	UM	
ARA-VP 1/1256		Left	UM	
ARA-VP 1/1258		Right	UM	
ARA-VP 1/1259		Right	LI1	
ARA-VP 1/1267		Right	LM1 or 2	
ARA-VP 1/1268		Right	Ldp4	fragment
ARA-VP 1/1271		Right	Ldp4	
ARA-VP 1/1483		Left	UI2	fragment
ARA-VP 1/1483		Left	LI2	fragment
ARA-VP 1/1537		Right	UI1	
ARA-VP 1/1540		Left	LI2	
ARA-VP 1/1546		Right	LP4	
ARA-VP 1/1548		Right	UM	
ARA-VP 1/1549		Right	LM1 or 2	
ARA-VP 1/1550		Left	LM1 or 2	
ARA-VP 1/1551		Left	LM1 or 2	
ARA-VP 1/1557		Right	LM1 or 2	
ARA-VP 1/1561			M	fragment
ARA-VP 1/1562		Left	UM	
ARA-VP 1/1563		Right	UM	
ARA-VP 1/1565		Right	UM1 or 2	
ARA-VP 1/1566		Left	UM	
ARA-VP 1/1570		Right	LM3	fragment
ARA-VP 1/1572		Left	LM3	
ARA-VP 1/1592		Left	UI1	
ARA-VP 1/1593		Left	UP3	
ARA-VP 1/1601		Left	LM1 or 2	
ARA-VP 1/1661		Right	UI1	
ARA-VP 1/1713		Right	LM1 or 2	fragment
ARA-VP 1/1715		Left	LM3	
ARA-VP 1/1720		Left	LM1 or 2	
ARA-VP 1/1721		Left	LP4	
ARA-VP 1/1774		Right	Mandible	(M1-3)
ARA-VP 1/1781		Left	UM	fragment
ARA-VP 1/1783		Left	UM	
ARA-VP 1/1807		Left	LM2	
ARA-VP 1/1808	Male	Left	LP4	
ARA-VP 1/1809		Right	LM1 or 2	
ARA-VP 1/1840	Female	Right	Mandible	(I2-P4)
ARA-VP 1/1841		Right	UI1	
ARA-VP 1/1863		Right	UI1	
ARA-VP 1/1867		Left	UM1 or 2	
ARA-VP 1/1869		Right	LM3	
ARA-VP 1/1888		Left	UM3	
ARA-VP 1/1891		Left	UI2	
ARA-VP 1/1918		Right	UM	M2 or 3
ARA-VP 1/1919		Left	UM	
ARA-VP 1/1924		Left	LI1	
ARA-VP 1/1950		Left	UI2	
ARA-VP 1/1984		Left	UM	

Catalog Number	Sex	Side	Element	Comments
ARA-VP 1/1986		Right	UM1 or 2	
ARA-VP 1/2046		Right	LM1 or 2	
ARA-VP 1/2047		Right	UI2	
ARA-VP 1/2060		Left	UP3	
ARA-VP 1/2064		Left	LM1 or 2	
ARA-VP 1/2065		Right	UI2	
ARA-VP 1/2068		Left	UM	
ARA-VP 1/2069		Right	LM1 or 2	
ARA-VP 1/2070		Left	Udp4	
ARA-VP 1/2072		Left	UM3	
ARA-VP 1/2073		Right	LM1 or 2	
ARA-VP 1/2074		Left	LM1 or 2	
ARA-VP 1/2083		Right	UM	
ARA-VP 1/2087		Left	LM1	
ARA-VP 1/2091		Right	LM3	
ARA-VP 1/2095		Left	UP3	
ARA-VP 1/2159		Left	LM3	
ARA-VP 1/2164		Right	UM3	fragment
ARA-VP 1/2167		Right	UI1	
ARA-VP 1/2175		Right	Maxilla	(dp4-M1)
ARA-VP 1/2440		Left	UI1	
ARA-VP 1/2451		Right	UP4	
ARA-VP 1/2451		Right	UM1	
ARA-VP 1/2451		Right	UM2	
ARA-VP 1/2451		Right	UM3	
ARA-VP 1/2473		Left	LP4	
ARA-VP 6/25		Right	UI1	
ARA-VP 6/56		Right	LM1 or 2	
ARA-VP 6/60		Left	LM1 or 2	
ARA-VP 6/87		Right	LM3	
ARA-VP 6/88		Left	UI1	
ARA-VP 6/97		Left	LI2	
ARA-VP 6/286		Right	LM1 or 2	
ARA-VP 6/570		Right	Mandible	(M3)
ARA-VP 6/575		Left	UM1 or 2	in tiny MAX frag.
ARA-VP 6/578		Right	LM1 or 2	
ARA-VP 6/579		Left	UM1 or 2	in tiny MAX frag.
ARA-VP 6/580		Right	UM1 or 2	
ARA-VP 6/583		Right	LM3	
ARA-VP 6/584		Left	LM3	
ARA-VP 6/585		Right	LM3	
ARA-VP 6/593		Right	LM	fragment
ARA-VP 6/595		Left	UI1	
ARA-VP 6/598		Right	UI1	
ARA-VP 6/605		Right	LM1 or 2	
ARA-VP 6/606		Right	LM	
ARA-VP 6/607		Left	LM	
ARA-VP 6/608		Left	LM1 or 2	
ARA-VP 6/610		Left	LM3	fragment
ARA-VP 6/626		Left	LP4	
ARA-VP 6/630		Left	UM1 or 2	

Catalog Number	Sex	Side	Element	Comments
ARA-VP 6/635		Left	Udp4	
ARA-VP 6/637		Right	UM1 or 2	
ARA-VP 6/639		Right	UM	fragment
ARA-VP 6/640		Left	Ldp4	
ARA-VP 6/641		Left	LM1 or 2	
ARA-VP 6/644		Left	Ldp or M	
ARA-VP 6/650			Ldp	fragment
ARA-VP 6/654	Female	Left	Mandible	(P3-4)
ARA-VP 6/796	Female		Mandible	symphysis, (L.I1-M1, R.I1-P2)
ARA-VP 6/798		Left	LM1 or 2	
ARA-VP 6/800		Left	UI2	
ARA-VP 6/931		Right	UM1 or 2	
ARA-VP 6/1282		Right	Ldp	fragment
ARA-VP 6/1285		Right	LI2	
ARA-VP 6/1287		Left	LI1	
ARA-VP 6/1294		Right	LM3	
ARA-VP 6/1295		Right	LM1 or 2	
ARA-VP 6/1619		Left	LM1 or 2	
ARA-VP 6/1620		Right	LM1 or 2	
ARA-VP 6/1686			Face	inferior part, (L.I1-M3,R.I1,C-M3)
ARA-VP 17/3		Right	Mandible	(M1)
ARA-VP 17/5		Left	LI2	
KUS-VP 2/2	Male	Right	LC	
KUS-VP 2/2	Male	Right	LP3	
KUS-VP 2/2	Male	Right	LP4	
KUS-VP 2/2	Male	Right	LM1	
KUS-VP 2/2	Male	Left	LC	
KUS-VP 2/2	Male	Left	LP3	
KUS-VP 2/5		Right	LP4	
KUS-VP 2/5		Right	LM1	
KUS-VP 2/5		Right	LM2	
KUS-VP 2/5		Left	LM2	
KUS-VP 2/20		Right	LM3	
KUS-VP 2/70	Female	Left	Maxilla	(L.C-M1)
KUS-VP 2/70	Female	Right	Maxilla	(M1-2)
KUS-VP 2/70	Female	Left	UI1	
KUS-VP 2/70	Female		Frontal	glabella
KUS-VP 2/89		Left	LM1 or 2	
KUS-VP 2/90		Left	UI2	
KUS-VP 2/91		Right	Ldp4	
KUS-VP 2/93		Left	UM	
KUS-VP 2/94		Left	UM3	
KUS-VP 2/96		Right	UM1 or 2	
KUS-VP 2/97		Right	LM1 or 2	
KUS-VP 2/116		Left	LI2	
KUS-VP 2/118		Left	LP4	fragment
KUS-VP 2/118		Left	LM1 or 2	fragment
KUS-VP 2/140		Left	LI2	
KUS-VP 2/145		Right	UI2	LdP3 no longer present.
KUS-VP 2/146		Right	UP3	
SAG-VP 7/1	Male	Left	UI2	

Catalog Number	Sex	Side	Element	Comments
SAG-VP 7/1	Male	Left	UC	
SAG-VP 7/1	Male	Right	UI2	
SAG-VP 7/1	Male	Right	UC	
SAG-VP 7/1	Male		UM	
SAG-VP 7/57		Left	UI2	
SAG-VP 7/101		Right	LM1 or 2	
SAG-VP 7/107		Left	UM	

Appendix 6: cranial specimens allocated to *Colobus* sp.

Catalog Number	Sex	Side	Element	Comments
KL183 - 10		Left	Mandible	(M1-3), no M3 hypoconulid
KL183 - 11		Left	Mandible	(M2)
KL183 - 16		Right	UP4	
KL183 - 3	Male	Right	Mandible	(P3-M1)
KL188 - 1	Female		Face	complete dentition, except LC.
KL188 - 16		Right	Mandible	juvenile (dP4-M1)
KL188 - 17	Female	Right	Mandible	(I2-P3)
KL188 - 18		Left	Mandible	(M2-3)
KL188 - 2	Female		Mandible	(L.+R.I1-M3)
KL188 - 23		Left	LP4	
KL188 - 24		Left	LM	
KL188 - 27		Right	LM	
KL188 - 3	Male		Mandible	(L.I1-M2;R.I1-P4; C's erupting)
KL188 - 6			Mandible	juvenile (L.dp3-M1;R.dC-dP3)
KL188 - 8	Male		Mandible	(L.I1-C;R.I1-M2)
KL189 - 6		Right	LM	
KL189 - 8		Right	Maxilla	(M2-3)
KL189 - 9		Right	Mandible	(M1-2)
KL190 - 1		Left	Mandible	(dp4-M1, M2 erupting)
KL190 - 2		Right	Mandible	(M1,M2 erupting)
KL190 - 3	Female	Right	Mandible	(P3-M3)
KL190 - 6	Male	Left	Mandible	(P3-M2)
KL191 - 23	Male		Cranium	most of face, complete dentition, L. orbit
KL191 - 24		Left	Cranium	juvenile (L.I1,dp3-M1)
KL191 - 28		Left	Mandible	(M2-3)
KL191 - 291	Male	Left	Mandible	edentulous
KL191 - 33		Right	UM	
KL191 - 59a			Mandible	juvenile (M2)
KL191 - 59b		Right	Mandible	juvenile (M2)
KL191 - 59c		Right	Mandible	juvenile (dP3-M1)
KL191 - 60		Right	Mandible	(M3)
KL191 - 62	Female	Right	Premaxilla	(I1-C)
KL191 - 66		Right	Mandible	(M3)
KL191 - 68		Right	Mandible	(M1)
KL191 - 80	Male	Left	Mandible	edentulous
KL191 - 88		Right	Mandible	(M2)
KL191 - 91		Right	LM1or2	
KL191 - 96	Male		Face	(R.M1-3;L.P3-M1)
KL191 - 98	Female	Right	Maxilla	(I1-M3)
KL191 - 99		Left	Maxilla	(P4-M3)
KL191 - 102	Male		Mandible	(L.P3-4;R.M2-3)
KL191 - 110		Right	Mandible	juvenile (dP3-4)
KL191 - 116		Left	UI1	
KL191 - 116		Right	UdI1	
KL191 - 141		Left	Maxilla	(P4-M2)
KL191 - 153		Right	LM1or2	
KL191 - 161		Right	Mandible	(M3)

Adamson D.A., Williams, M.A.J. 1987. Geological setting of Pliocene rifting and deposition in the Afar Depression of Ethiopia. *Journal of Human Evolution*, 16:597-610.

Alemseged Z., Geraads D. 2001. A new Middle Pleistocene fauna from the Busidima-Telalak region of the Afar, Ethiopia. *C. R. Acad. Sci. Paris, Sciences de la Terre et des planetes*, 331:549-556.

Alemseged Z., Geraads D., Bellon, H. 2000. The Late Miocene mammalian fauna of Chorora, Awash Basin, Ethiopia: systematics, biochronology and Ar40-Ar39 ages of associated volcanics. *Tertiary Research*, 21:

Andrews, P., Harrison, T., Delson, E., Martin, L.B., and Bernor, R.L. 1996. Systematics and biochronology of European and Southwest Asian Miocene catarrhines. In: (R.L. Bernor, V. Fahlbusch, and H.W. Mittmann, eds.) *Evolution of Western Eurasian Late Neogene Mammal Faunas*. Columbia University Press, New York. Pp. 168-207.

Aronson, J.A., Taieb, M. 1981. Geology and paleogeography of the Hadar hominid site, Ethiopia. In: (Rapp, G., and Vondra, C.F. Eds.) Hominid sites: Their geological settings. Westview Press, Boulder, Colorado. p. 165-195.

Asfaw, B., Ebinger, C., Harding, D., White, T.D., WoldeGabriel, G. 1990. Space-based imagery in paleoanthropological research: an Ethiopian Example. *National Geographic Research*, 6:418-434.

Asfaw, B., Beyene, Y., Suwa, G., Walter, R.C., White, T.D., WoldeGabriel, G., Yemane, T. 1991. The earliest Acheulean from Konso-Gardula. *Nature*, 360:732-735.

Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., Suwa, S. 1999. *Australopithecus ghari*: a new species of early hominid from Ethiopia. *Science*, 284:629-635.

Behrensmeyer, A.K., Todd N.E., Potts, R., McBrinn, G.E. 1997. Late Pliocene Faunal Turnover in the Turkana Basin, Kenya and Ethiopia. *Science*, 278:1589-1594.

Benefit, B.R. 1999. Biogeography, dietary specialization, and the diversification of African Plio-Pleistocene monkeys. In: (T.G. Bromage and F. Schrenk, eds.) *African Biogeography, Climate Change, and Early Hominid Evolution*. pp. 172-188. Oxford University Press, Oxford.

Benefit, B.R. 2000. Old World monkey origins and diversification: an evolutionary study of diet and dentition. In: (P. F. Whitehead, C. J. Jolly Eds.) *Old World Monkeys*. Pp. 133-179. Cambridge University Press.

Benefit, B.R., McCrossin, M.L. 1990. Diet, species diversity and distribution of African fossil baboons. *Kroeber Anthropological Society Papers*, Nos. 71-72.

Benefit, B.R., McCrossin, M.L. 1997. Earliest known Old World monkey skull. *Nature*, 388:368-371.

Benefit, B.R., Pickford, M. 1986. Miocene fossil cercopithecoids from Kenya. *American Journal of Physical Anthropology*, 69:441-464.

Bernor, R., Armour-Chelu, M. 1999. Toward an Evolutionary History of African Hipparionine Horses. In: (T.G. Bromage and F. Schrenk, eds.) *African Biogeography, Climate Change, and Early Hominid Evolution*. pp. 189-215. Oxford University Press, Oxford.

Birchette, M. 1981. Postcranial remains of *Cercopithecoides. American Journal of Physical Anthropology*, 54:201.

Birchette, M. 1982. The postcranial skeleton of *Paracolobus chemeroni*. Ph.D. dissertation, Harvard University.

Bishop, L.C. 1999. Reconstructing omnivore paleoecology and habitat preference in the Pliocene and Pleistocene of Africa. In: (T.G. Bromage and F. Schrenk, eds.) *African Biogeography, Climate Change, and Early Hominid Evolution*. Oxford University Press, Oxford.

Bobé, R. 1997. *Hominid Environments in the Pliocene: An Analysis of Fossil mammals from the Omo Valley, Ethiopia*. Ph.D. dissertation, University of Washington.

Brain, C.K. 1981. *The hunters or the hunted? An introduction to African cave taphonomy*. University of Chicago Press, Chicago.

Brown, F.H. 1992. Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar. *Nature*, 300:631-635.

Brown, F.H. 1994. Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites. In: (R.S. Corrucini and R.L. Ciochon, eds.*)* *Integrative paths to the past*, pp. 285-312. Prentice-Hall, Englewood Cliffs, N.J.

Brown, F.H. 1995. The potential of the Turkana Basin for paleoclimatic reconstruction in East Africa. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins*, pp. 319-330. Yale University Press, New Haven, London.

Brown, F.H. 2000. Turkana Basin. In: (E. Delson, I. Tattersall, J. A. Van Couvering, and A. S. Brooks, Eds) *Encyclopedia of Human Evolution and Prehistory*, 2nd ed. Pp. 711-714. New York: Garland.

Brown, F.H. and Feibel, C.S. 1986. Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of Geological Society*, 43:297-310.

Brown, F.H., Feibel, C.S. 1991. Stratigraphy, Depositional Environments and Palaeogeography of the Koobi Fora Formation. In: (J.M. Harris, ed.) *Koobi ForaResearch Project*. Vol. 3, *Stratigraphy, artiodactyls and paleoenvironments*, pp. 321-346. Clarendon Press, Oxford.

Ciochon, R.L. 1993. Evolution of the cercopithecoid forelimb, phylogenetic and functional implications from morphometric analyses. *University of California Publications in Geological Sciences*, 138:1-251.

Clark, J.D., Asfaw, B., Assefa, G., Harris, J.W.K., Kurashina, H., Walter, R.C., White, T.D., Williams, M.A.J. 1984. Palaeoanthropological discoveries in the Middle Awash Valley, Ethiopia. *Nature*, 307:423-428.

Clark, J.D., De Heinzelin, J., Schick, K.D., Hart, W.K., White, T.D., WoldeGabriel, G., Walter, R.S., Walter, R.C., Suwa, G., Asfaw, B., Vrba, E., Heile-Selassie, Y. 1994. African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. *Science*, 264:1907-1910.

Coffing, K., Feibel, C.S., Leakey, M.G., Walker, A. 1994. Four-million-year-old hominids from East Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 93:55-65.

Conroy, G.C., Jolly, C.J., Cramer, D., and Kalb, J.E. 1978. Newly discovered fossil hominid skull from the Afar Depression, Ethiopia. *Nature*, 276:67-70.

Cooke, H.B.S. 1978. Suid evolution and correlation of African hominid localities: An alternative taxonomy. *Science*, 201:460-463.

de Heinzelin, J. 1983. *The Omo Group*. Musee Royale de l’Afrique Central, Tervuren, Belgique. Annales-Serie in 8. Sci. Geol., no. 85.

de Heinzelin, J., Clark, J.D., White, T.D., Hart, W., Renne, P., WoldeGabrial, G., Beyene, Y., Vrba, E. 1999. Environment and Behavior of 2.5-Million-Year-Old Bouri Hominids. *Science*, 284:625-629.

Delson, E. 1973. *Fossil colobine monkeys of the circum-Mediterranean region and the evolutionary history of the Cercopithecidae (Primates, Mammalia)*. Ph.D. dissertation, Columbia University.

Delson, E. 1975. Evolutionary history of the Cercopithecidae. In: (F.S. Szalay ed.) *Approaches to Primate Paleobiology*. Contrib. Primat., vol 5, pp. 167-217. S. Karger, Basel.

Delson, E. 1980. Fossil macaques, phyletic relationships and a scenario of deployment. In: (D.G. Lindburg, ed.) *The Macaques: Studies in Ecology, Behavior and Evolution*. New York: von Nostrand Reinhold Co.

Delson, E. 1983. Evolutionary tempos in catarrhine primates. In: (J. Chaline ed.) Modalités, Rhythmes et Mécanismes de l'Evolution Biologique. CNRS, Paris. Pp. 101-106.

Delson, E. 1984. Cercopithecid biochronology of the African Plio-Pleistocene: Correlation among eastern and southern hominid-bearing localities. *Courier Forschungsinstitut Senckenberg*, 69:199-218.

Delson, E. 1988. Chronology of South African australopith site units. In: (F.E. Grine ed.) *Evolutionary history of the "robust" australopithecines,* pp. 317-324. Aldine, New York.

Delson, E. 1993. Theropithecus fossils from Africa and India and the taxonomy of the genus. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 157-189. Cambridge University Press.

Delson, E. 1994. Evolutionary history of the colobine monkeys in paleoenvironmental perspective. In: (A.G. Davies, J.F. Oates, Eds.) *Colobine Monkeys: their ecology, behaviour and evolution*. Cambridge University Press.

Delson, E. 2000a. Cercopithecidae. In: (E. Delson, I. Tattersall, J. A. Van Couvering, and A. S. Brooks, Eds) *Encyclopedia of Human Evolution and Prehistory*, 2nd ed. Pp.. New York: Garland.

Delson, E., Dean, D. 1993. Are *Papio baringensis* R. Leakey, 1969, and *P. quadratirostris* Iwamoto, 1982, species of Papio or Theropithecus? In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 125-156. Cambridge University Press.

Delson, E, Eck, G.G., Leakey, M.G., Jablonski, N.G. 1993. A partial catalogue of fossil remains of *Theropithecus*. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 499-525. Cambridge University Press.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G, Dechow, P.C. 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. *American Museum of Natural History, Anthropological Papers,* 83:1-159.

deMenocal, P.B. 1995. Plio-Pleistocene African Climate. *Science,* 270:53-59.

Denton, G. H. 1999. Cenozoic climate change. In: (T.G. Bromage and F. Schrenk, eds.) *African Biogeography, Climate Change, and Early Hominid Evolution*. pp. 94-114. Oxford University Press, Oxford.

Disotell, T.R. 1994. Generic level relationships of the Papionini (Cercopithecoidea). *American Journal of Physical Anthropology*, 94:47-57.

Disotell, T.R. 1996. The phylogeny of Old World monkeys. Evolutionary Anthropology, 5:18-24.

Disotell, T.R. 2000. Molecular systematics of the Cercopithecidae. In: (P. F. Whitehead, C. J. Jolly Eds.) *Old World Monkeys*. Pp. 29-56. Cambridge University Press.

Ditchfield, P., Hicks, J., Plummer, T., Bishop, L.C., Potts, R. 1999. Current research on the Late Pliocene and Pleistocene deposits north of Homa Mountain, southwestern Kenya. *Journal of Human Evolution*, 36:123-150.

Drake R., Curtis, G.H. 1987. K-Ar Geochronology of the Laetoli fossil localities. In: (M.D. Leakey and J.M. Harris eds.) *The Pliocene site of Laetoli, northern Tanzania*, pp. 48-52. Oxford University Press, Oxford and New York.

Dryden I.L. and Mardia, K.V. 1998. *Statistical shape analysis*. Wiley, New York.

Dutrillaux, B., Muleris, M., Couturier, J. 1988. Chromosomal evolution of Cercopithecinae. In: (A. Gautier-Hion, F. Bourliere, J-P. Gautier, and J. Kingdon, Eds.) *A primate radiation-evolution of the African guenons*. Pp. 150-159. Cambridge University Press, Cambridge.

Eck, G.G. 1976. Cercopithecoidea from Omo group deposits. In: (Y. Coppens, F.C. Howell, G. Ll. Isaac, R.E.F. Leakey, Eds.) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 332-344. University of Chicago Press, Chicago.

Eck, G.G. 1977. Diversity and frequency distribution of Omo group Cercopithecoidea. *Journal of Human Evolution* 6, 55-63.

Eck, G.G. 1987a. *Theropithecus oswaldi* from the Shungura Formation, Lower Omo Basin, Southwestern Ethiopia. In: *Les faunas Plio-Pleistocenes de la Basse Vallee de l'Omo (Ethiopie).* Tome 3, *Cercopithecidae de la Formation de Shungura*, pp. 123-139. Cahiers de Paleontologie, Travaux de Paleontologie Est-Africaine. Paris: Editions du CNRS.

Eck, G.G. 1987b. Plio-Pleistocene specimens of Cercopithecus from the Shungura Formation, Southwestern Ethiopia. In: *Les faunas Plio-Pleistocenes de la Basse Vallee de l'Omo (Ethiopie).* Tome 3, *Cercopithecidae de la Formation de Shungura*, pp. 143-146. Cahiers de Paleontologie, Travaux de Paleontologie Est-Africaine. Paris: Editions du CNRS.

Eck, G.G.1993. Theropithecus darti from the Hadar Formation, Ethiopia. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 15-76. Cambridge University Press.

Eck, G.G., Howell, F.C. 1972. New fossil Cercopithecus material from the lower Omo Basin, Ethiopia. *Folia Primatologica*, 18:325-355.

Eck, G.G., Jablonski, N.G. 1984. A reassessment of the taxonomic status and phyletic relationships of *Papio baringensis* and *Papio quadratirostris* (Primates: Cercopithecidae). *American Journal of Physical Anthropology*, 65:109-134.

Eck, G.G., Jablonski, N.G. 1987. The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. In: *Les faunas Plio-Pleistocenes de la Basse Vallee de l'Omo (Ethiopie).* Tome 3, *Cercopithecidae de la Formation de Shungura*, pp. 11-122. Cahiers de Paleontologie, Travaux de Paleontologie Est-Africaine. Paris: Editions du CNRS.

Eisenhart, W.L. 1974. The fossil cercopithecoids of Makapansgat and Sterkfontein. B.A. Thesis. Harvard College.

Feibel, C.S., Brown, F.H., McDougall, I. 1989. Stratigraphic context of fossil hominids from the Omo Group deposits, northern Turkana Basin, Kenya and Ethiopia. American Journal of Physical Anthropology, 78:595-622.

Feibel, C.S., Harris, J.M., Brown, F.H. 1991. Neogene paleoenvironments of the Turkana Basin. In: (J.M. Harris, ed.) *Koobi ForaResearch Project*. Vol. 3, *Stratigraphy, artiodactyls and paleoenvironments*, pp. 321-346. Clarendon Press, Oxford.

Fleagle, J.G. 1988. Primate Adaptation & Evolution. Academic Press, San Diego.

Fleagle, J.G., McGraw, S. 1999. Skeletal and dental morphology supports diphyletic origin of baboons and mandrills. *Proceedings of the National Academy of Science*, 96:1157-1161.

Freedman, L. 1957. Fossil Cercopithecoidea of South Africa. *Ann. Transvaal Museum*, 23, 121-262.

Freedman, L. 1965. Fossil and subfossil primates from the limestone deposits at Taung, Bolt's Farm, and Witkrans South Africa. *Palaeontologia Africana*, 9:19-48.

Freedman, L. 1976. South African fossil Cercopithecoidea: A reassessment including a description of new material from Makapansgat, Sterkfontein and Taung. *Journal of Human Evolution*, 5:297-315.

Frost, S.R. in press. New Early Pliocene Cercopithecidae from Aramis, Middle Awash Valley, Ethiopia. Amer. Mus. Nat. History Novitates.

Gantt, D.G., Rafter, J.A., Strickland, C.P. 1999. Enamel thickness in the lower incisors of Old World Monkeys. In: *Dental Morphology '98: Proceedings of the 11th International Symposium on Dental Morphology*. Pp. 212-221. Oulu Univeristy Press, Oulu.

Gebo, D.L., Sargis, E.J. 1994. Terrestrial adaptations in the postcranial skeletons of guenons. *American Journal of Physical Anthropology*, 93:341-371.

Greenacre, M.J. 1993. *Correspondence analysis in practice*. Academic Press, London.

Groves, C.P. 1978. Phylogenetic and population systematics of the mangabeys (Primates: Cercopithecoidea). *Primates*, 19:1-34.

Groves, C.P. 1989. *A Theory of Human and Primate Evolution*. Oxford: Clarnedon Press.

Groves, C.P. 2000. The phylogeny of the Cercopithecoidea. In: (P. F. Whitehead, C. J. Jolly Eds.) *Old World Monkeys*. Pp. 77-98. Cambridge University Press.

Gundling, T., Hill, A. H. 2000. Geological context of fossil Cercopithecoidea from eastern Africa. In: (P. F. Whitehead, C. J. Jolly Eds.) *Old World Monkeys*. Pp. 180-213. Cambridge University Press.

Haileab B., Brown, F.H. 1992. Turkana basin-Middle Awash Valley correlations and the age of the Sagantole and Hadar Formations. *Journal of Human Evolution*, 22:453-468.

Harris, E.E. 1997. Unpublished PhD. Thesis. New York University, New York.

Harris, E.E., Disotell, T.R. 1998. Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates:Papionini). *Molecular Biology and Evolution*, 5:626-644.

Harris, J.M. 1983. Background to the study of the Koobi Fora fossil faunas. In (Harris, J.M. ed.) *Koobi Fora Research Project* Vol. 2. *The fossil ungulates: Proboscidea, Perissodactyla, and Suidae*. Pp. 1-21. Clarendon Press, Oxford.

Harris, J.M., White, T.D. 1979. Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society*, 69:1-128.

Harris, J.M., Brown, F.H., Leakey, M.G. 1988. Stratigraphy and paleontology of Pliocene and Pleistocene localities West of Lake Turkana, Kenya. *Contributions in Science, Natural History Museum of Los Angeles County*, 399:1-128.

Harrison, T., Harris, E.E. 1996. Plio-Pleistocene cercopithecids from Kanam East, western Kenya. *Journal of Human Evolution*, 30:539-561.

Hay, R.L. 1987. Geology of the Laetoli area. In: (M.D. Leakey and J.M. Harris eds.) *The Pliocene site of Laetoli, northern Tanzania*, pp. 23-47. Oxford University Press, Oxford and New York.

Hill, A. 1995. Faunal and environmental change in the Neogene of East Africa: evidence from the Tugen Hills Sequence, Baringo District, Kenya. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins*, pp. 178-193. Yale University Press, New Haven, London.

Hull, D.B. 1979. A craniometric study of the black and white *Colobus* Illiger, 1811 (Primates: Cercocpithecoidea). *American Journal of Physical Anthropology*, 51:163-181.

Iwamoto, M. 1982. A Fossil Baboon Skull from the Lower Omo Basin, Southwest Ethiopia. *Primates*, 23(4): 533-541.

Jablonski, N.G. 1986. The hand of *Theropithecus brumpti*. In: (Lee, P. and Else, J. Eds.) *Primate Evolution*, Proceedings of the 10th Congress of the International Primatological Society, Vol. 1. Cambridge University Press, Cambridge.

Jablonski, N.G. 1993. Evolution of the masticatory apparatus in *Theropithecus*. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 299-329. Cambridge University Press.

Jablonski, N.G. 1994. New fossil cercopithecid remains from the Humpata Plateau, Southern Angola. *American Journal of Physical Anthropology*, 94:435-464.

Jablonski, N.G. 1998. The evolution of the doucs and snub-nosed monkeys and the question of the phyletic unity of the odd-nosed colobines. In: (N.G. Jablonski ed.) *The natural history of the doucs and snub-nosed monkeys. Recent advances in human biology, Vol 4.* Pp. 13-52. World Scientific.

Jolly, C.J. 1972. The classification and natural history of *Theropithecus (Simopithecus)* (Andrews, 1916), baboons of the African Plio-Pleistocene. *Bulletins of the Brisish Museum (Natural History), Geology*, 22:1-122.

Kalb, J.E. 1993. Refined stratigraphy of the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Newsletters Stratigraphy*, 29(1):21-62.

Kalb, J.E., Jaegar, M., Jolly, C.J., Kana, B. 1982a. Preliminary Geology, Palaeontology and Paleoecology of a Sangoan site at Andalee, Middle Awash Valley, Ethiopia. *Journal of Archaeological Science*, 9:349-363.

Kalb, J.E., Jolly, C.J., Tebedge, S., Mebrate, A., Smart, C., Oswald, E.B., Whitehead, P.F., Wood, C.B., Tsrha A., Rawn-Schatzinger, V. 1982b. Vertebrate faunas from the Awash group, Middle Awash Valley, Afar, Ethiopia. *Journal of Vertebrate Paleontology* 2(2):237-258.

Kalb, J.E., Oswald, E.B., Mebrate, A., Tebedge, S., Jolly, C.J. 1982c. Stratigraphy of the Awash Group, Middle Awash Valley, Afar, Ethiopia. *Newsletters Stratigraphy*, 11 (3):95-127.

Kalb, J.E., Wood, C.B., Smart, C., Oswald, E.B., Mebrate, A., Tebedge, S., Whitehead, P. 1980. Preliminary geology and palaeontology of the Bodo D'ar Hominid site, Afar, Ethiopia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 30:107-120.

Kalb, J.E., Jolly, C.J., Oswald, E.B., Whitehead, P.F. 1984. Early hominid habitation in Ethiopia. *American Scientist*, 72:168-178.

Katoh, S., Nagaoka, S., WoldeGabriel, G., Renne, P., Snow, M., Beyene, Y., Suwa, G. Chronostratigraphy and correlation of the Plio-Pleistocene tephra layers of the Konso Formation, southern Main Ethiopian Rift, Ethiopia. *Quaternary Science Reviews*, 19:1305-1317.

Kimbel, W.H. 1995. Hominid speciation and Pliocene Climatic Change. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins*, pp. 425-437. Yale University Press, New Haven, London.

Kimbel, W.H., Johanson, D.C., Rak, Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. Nature, 368:449-451.

Kimbel, W.H., Walter, R.C., Johanson, D.C., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C.W., Eck, G.G., Bobe, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evensen, N.M., Smith, P.E. 1996. Late Pliocene *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution*, 31:549-561.

Kingdon, J. 1971. *East African mammals: an atlas of evolution in Africa*. Vol. 1. (Primates, Hyraxes, Pangolins, Protoungulates, Sirenians). Academic Press, London.

Krentz, H.B. 1992. *The forelimb anatomy of* Theropithecus brumpti *and* Theropithecus oswaldi *from the Shungura Formation, Ethiopia*. Ph.D. Dissertation, University of Washington.

Krentz, H.B. 1993. Postcranial anatomy of extant and extinct species of *Theropithecus*. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 383-422a. Cambridge University Press.

Leakey, M.G. 1976. Cercopithecoidea of the East Rudolf succession. In: (Y. Coppens, F.C. Howell, G. Ll. Isaac, R.E.F. Leakey, Eds.) *Earliest Man and Environments in the Lake Rudolf Basin*, pp. 345-350. University of Chicago Press, Chicago.

Leakey, M.G. 1982. Extinct Large Colobines From the Plio-Pleistocene of Africa. *American Journal of Physical Anthropoplogy*, 58:153-172.

Leakey, M.G. 1987. Colobinae (Mammalia, Primates) from the Omo Valley, Ethiopia. In: *Les faunas Plio-Pleistocenes de la Basse Vallee de l'Omo (Ethiopie).* Tome 3, *Cercopithecidae de la Formation de Shungura*, pp. 148-169. Cahiers de Paleontologie, Travaux de Paleontologie Est-Africaine. Paris: Editions du CNRS.

Leakey, M.G. 1988. Fossil evidence for the evolution of the guenons. In: (A. Gautier-Hion, F. Bourliere, J-P. Gautier, and J. Kingdon, Eds.) *A primate radiation-evolution of the African guenons*. Cambridge University Press, Cambridge.

Leakey, M.G. 1993. Evolution of *Theropithecus* in the Turkana Basin. In: (N.G. Jablonski ed.) *Theropithecus: The rise and fall of a primate genus.* Pp. 15-76. Cambridge University Press.

Leakey, M.G., Delson, E. 1987. Fossil Cercopithecidae from the Laetolil Beds, Tanzania. In: (M.D. Leakey and J.M. Harris eds.) *The Pliocene site of Laetoli, northern Tanzania*, pp. 91-107. Oxford University Press, Oxford and New York.

Leakey, M.G., Feibel, C.S., McDougal, I., Walker, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376:565-571.

Leakey, M.G., Feibel, C.S., Bernor, R.L., Harris, J.M., Cerling, T.E., Stewart, K.M., Storrs, G.W., Walker, A., Werdelin, L., and Winkler, A.J. 1996. Loghagam: A record of faunal change in the Late Miocene of East Africa. *Journal of Vertebrate Paleontology*, 16:556-570.

Leakey, M.G., Leakey, R.E.F. 1973a. Further evidence of *Simopithecus* (Mammalia, Primates) from Olduvai and Olorgesailie. *Fossil Vertebrates of Africa*, 3:101-120.

Leakey, M.G., Leakey, R.E.F. 1973b. New Large Pleistocene Colobinae (Mammalia, Primates) from East Africa. *Fossil Vertebrates of Africa*, 3:121-138.

Leakey, M.G., Leakey, R.E.F. 1976. Further Cercopithecinae (Mammalia, Primates) from the Plio/Pleistocene of East Africa. *Fossil Vertebrates from Africa,* 4:121-146.

Leakey, M.G., Teaford, M., Ward, C.V. in press. Cercopithecidae from Lothagam. In: (M. G. Leakey and J. M. Harris eds). *Lothagam: Dawn of humanity in eastern Africa*. Columbia Universtiy Press, New York.

Leakey, R.E.F. 1969. New Cercopithecidae from the Chemeron Beds of Lake Baringo, Kenya. In: *Fossil Vertebrates of Africa.* Leakey, L.S.B., Ed. Vol. 1: 53-70. Academic Press, London and New York

Maier, W. 1970. New fossil Cercopithecoidea from the Lower Pleistocene cave deposits of the Makapansgat Limeworks, South Africa. *Palaeontologia Africana*, 3:69-107.

Maier, W. 1972. Anpassungstyp und systematische Stellung von *Theropithecus gelada* Rüppel, 1835. *Zeitschrift fur Morphologische Anthropologie*, 63:370-384.

McKee, J.K. 1996. Faunal turnover patterns in the Pliocene and Pleistocene of southern Africa. *South African Journal of Science*, 92:111-113.

Messier, W., Stewart, C.B. 1997. Episodic adaptive evolution of primate lysozimes. *Nature*, 385:151-154.

Morales, J.C., Melnick, D.J. 1998. Phylogenetic relationships of the macaques (Cercopithecoidea: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial rhibosomal genes. *Journal of Human Evolution*, 34:1-23.

Napier, P. H. 1981. *Catalog of Primates in the British Museum (Natural History) and elsewhere in the British Isles, Part II: Family Cercopithecinae, Subfamily Cercopithecinae*. BM(NH), London.

Napier, P. H. 1985. *Catalog of Primates in the British Museum (Natural History) and elsewhere in the British Isles, Part III: Family Cercopithecinae, Subfamily Colobinae*. BM(NH), London.

Oates, J.F. (1996) *African Primates: Status Survey and Conservation Action Plan*. Revised Edition. IUCN, Gland.

Patterson, B. 1968. The extinct baboon, *Parapapio jonesi*, in the Early Pleistocene of Northwest Kenya. *Breviora*, 282:1-4.

Patterson, B., Behrensmeyer, A.K., Sill, W.D. 1970. Geology and fauna of a new Pliocene locality in northwestern Kenya. *Nature*, 226:918-21.

Ravosa, M. J., Profant, L. P. 2000. Evolutionary morphology of the skull in Old World Monkeys. In: (P. F. Whitehead, C. J. Jolly Eds.) *Old World Monkeys*. Cambridge University Press.

Renne, P.R., WoldeGabriel, G., Hart, W.K., Heiken, G., White, T.D. 1999. Chronostratigraphy of the Mio-Pliocene Sagantole Formation, Middle Awash Valley, Afar Rift, Ethiopia. *Geological Society of America Bulletin*, 111(6):869-885.

Shackleton, N.J., Backman, J., Zimmerman, H., Kent, D.V., Hall, M.A., Roberts, D.G., Schnitker, D., Baldauf, J.G., Desprairies, A., Homrighausen, R., Huddlestun, P., Keene, J.B., Kaltenback, A.J., Krumsiek, K.A.O., Morton, A.C., Murray, J.W., Westberg-Smith, J. 1984. Oxygen isotope calibration of the onset of ice-rafting and history of glaciation in the North Atlantic region. *Nature*, 307:620-623.

Simons, E. L. 1967. A fossil *Colobus* skull from the Sudan (Primates, Cercopithecidae). *Postilla Yale Peabody Museum*, 111:1-12.

Slice, D. 1998. Morpheus et al.

Strasser, E., Delson, E. 1987. Cladistic analysis of cercopithecid relationships. *Journal of Human Evolution*, 16:81-99.

Strasser, E. 1988. Pedal evidence for the origin and diversification of cercopithecid clades. *Journal of Human Evolution*, 17:225-245.

Szalay, F.S., Delson, E. 1979. *Evolutionary history of the Primates*. Academic Press, San Diego.

Taieb, M. 1974. Évolution Quaternaire du Bassin de l'Awash. Ph.D. Thesis. University of Paris VI.

Taieb, M., Johanson, D.C., Coppens, Y., Aronson, J.L. 1976. Geological and palaeontological background of Hadar hominid site, Afar, Ethiopia. *Nature*, 260:289-293.

Teaford, M.F. (1993) Dental microwear and diet in extant and extinct *Theropithecus*: preliminary analyses. In (N.G. Jablonski, ed.) Theropithecus*: Rise and Fall of a Primate Genus*, pp. 331-349. Cambridge: Cambridge Univ. Press.

Tiercelin, J-J. 1986. The Pliocene Hadar Formation, Afar Depression, Ethiopia. In: (L.E. Frostic, R.W. Reneaut, I. Read, and J-J. Tiercelin, eds.) *Sedimentation in the African Rifts*, pp. 221-240. Blackwell Scientific Publications, Oxford.

Ting and Ward, 2001. Functional Analysis of the hip and thigh of *Paracolobus* and other large bodied fossil cercopithecids. *American Journal of Physical Anthropology*, S32:150.

Tosi, A.J., Morales, J.C., Melnick, D.J. 2000. Comparison of Y chromosome and mtDNA phylogenies leads to unique inferences of macaque evolutionary history. *Molecular Phylogenetics and Evolution*, 17(2):133-144.

Turner A., Wood, B. 1993. Taxonomic and geographic diversity in robust australopithecines and other African Plio-Pleistocene larger mammals. *Journal of Human Evolution*, 24:147-168.

Verheyen, W.N. 1962. Contribution a la craniologie comparee des primates. *Ann. Musee Royale de l'Afrique Central*, 105:1-247.

Vrba, E.S. 1975. Some evidence of chronology and paleoecology of Sterkfontein, Swartkrans and Kromdraai from the fossil Bovidae. *Nature*, 250:19-23.

Vrba, E.S. 1976. Fossil Bovidae from Sterkfontein, Swartkrans and Kromdraai. *Transvaal Mus. Mem.* 21, 1-166.

Vrba, E.S. 1980. The significance of bovid remains as indicators of environment and predation patterns. In (A. K. Behrensmeyer & A. P. Hill, Ed.) *Fossils in the Making*, pp. 247- 271. Chicago: Univ. Chicago Press.

Vrba, E.S. 1982. Biostratigraphy and chronology, based particularly on Bovidae, of southern hominid-associated assemblages: Makapansgat, Sterkfontein, Taung, Kromdraai, Swartkrans; also Elandsfontein (Saldanha), Broken Hill (now Kabwe) and Cave of Hearths. In (H. d. Lumley, Ed.) *Prétirage, Ier Cong. Internat. Paléo. Humaine (vol. II)*, pp. 707-752. Nice: Cent. Nat. Rech. Sci.

Vrba, E.S. 1985. Ecological and adaptive changes associated with early hominid evolution. In: (E. Delson, Ed.) *Ancestors: the hard evidence,* Pp. 63-71. New York:Alan R. Riss, Inc.

Vrba, E.S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy,* 73(1):1-28.

Vrba, E.S. 1995. On the connections between paleoclimate and evolution. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins,* pp. 24-45. Yale University Press, New Haven, London.

Vrba, E.S. 1997. New fossils of Alcelaphini and Caprinae (Bovidae: Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeontologia Africana*, 34:127-198.

Vrba, E.S. 1999. Some thoughts on climatic change and evolution in African Neogene biota and hominids. In: (T.G. Bromage and F. Schrenk, eds.) *African Biogeography, Climate Change, and Early Hominid Evolution*. pp. 19-34. Oxford University Press, Oxford.

Walter, R.C. 1994. Age of Lucy and the First Family: single-crystal ^{40}Ar/^{39}Ar dating of the Denen Dora and lower Kada Hadar members of the Hadar Formation, Ethiopia. *Geology*, 22:6-10.

Walter, R.C., Aronson, J.L. 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. *Journal of Human Evolution*, 25:229-240.

Wesselman, H.B. 1995. Of mice and almost-men: regional paleoecology and human evolution in the Turkana basin. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins,* pp. 356-368. Yale University Press, New Haven, London.

White, T.D. 1995. African omnivores: global climatic change and Plio-pleistocene hominids and suids. In: (E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burkle eds.) *Paleoclimate and Evolution with an emphasis on human origins,* pp. 369-384. Yale University Press, New Haven, London.

White, T.D. 2000. Middle Awash. In: (E. Delson, I. Tattersall, J. A. Van Couvering, and A. S. Brooks, Eds) Encyclopedia of Human Evolution and Prehistory, 2nd ed. New York: Garland.

White, T.D., Suwa, G., Asfaw, B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371:306-312.

White, T.D., Suwa, G., Asfaw, B. 1995. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia-Corrigendum. *Nature*, 375:88.

White, T.D., Suwa, G., Hart, W.K., Walter, R.C., WoldeGabriel, G., de Heinzelin, J., Clark, J.D., Asfaw, B., Vrba, E. 1993. New discoveries of Australopithecus at Maka in Ethiopia. *Nature*, 366:261-265.

White, T.D., Suwa, G., Simpson, S., Asfaw, B. 2000. Jaws and teeth of *Australopithecus afarensis* from Maka, Middle Awash, Ethiopia. *American Journal of Physical Anthropology*, 111:45-68.

WoldeGabriel, G., White, T.D., Suwa, G., Renne, P., de Heinzelin, J., Hart, W.K., Heiken, G. 1994. Ecological placement of early Pliocene hominids at Aramis, Ethiopia. *Nature*, 371:330-333.

Wynne, J.G. 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, Northern Kenya. *Journal of human evolution*, 39:411-432.