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Related Archival Materials: The KGA paleontological collection record plots (on file, available for viewing upon request)

# CHAPTER 5

## Fossil Cercopithecidae of the Konso Formation

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**Abstract**

The cercopithecid sample from the Konso Formation is represented by a minimum of four species including *Theropithecus oswaldi*, a papionin comparable in size to some of the smaller populations of extant *Papio*, a smaller cercopithecine, and a large colobine. Of these, *T. oswaldi* forms the majority of the sample. Within the *T. oswaldi* material two chronosubspecies are present: *T. o. oswaldi* and *T. o. leakeyi*. The cercopithecid sample comes from three time horizons: the oldest derives from the Sorobo Member and lower part of the Turoha Member and is ~1.9 Ma; there is a small sample from deposits that are ~1.6 Ma in the middle part of the Kayle Member, and the majority of the sample derives from the ~1.45 Ma to ~1.25 Ma deposits of the upper part of the Kayle Member and Karat Member. The taxonomic and biogeographic implications of the cercopithecid assemblage from Konso are discussed, along with the relative abundances of the different taxa. The functional morphology of the postcrania allocated to *Theropithecus* is also described.

## 5.1 INTRODUCTION

One hundred forty eight cercopithecid fossils representing a minimum of four species have been recovered from the Konso Formation. This material was collected from three stratigraphic intervals. Thirty-six specimens derive from the oldest level, the Sorobo Member and the lower part of the Turoha Member (~1.9 Ma), four postcranial specimens and one molar come from the ~1.6 Ma middle part of the Kayle Member; and the remaining material is from the upper part of the Kayle Member and Karat Member, ranging from ~1.45 Ma to ~1.25 Ma in age (Katoh et al., 2000; Suwa et al., 2003; Nagaoka et al., 2005; Beyene et al., 2013; Chapter 3 of this volume). These levels correspond to intervals 1, 3, and 4/5, respectively, of Suwa et al. (2003).

The cercopithecid material from Konso was included in the faunal list of Asfaw et al. (1992), who mentioned *Theropithecus oswaldi* and *Papio* sp. Suwa et al. (2003) included the same two species, along with a colobine. These identifications are consistent with those presented here. While the sample is fairly diverse, with both subfamilies represented, the vast majority of identifiable specimens are of *T. oswaldi*, which includes two chronosubspecies: *T. o. oswaldi* and *T. o. leakeyi*. The remaining taxa are represented by fragmentary dental material and cannot be confidently assigned to genera. They include papionin fossils similar in size to smaller subspecies of extant *P. hamadryas*, a smaller cercopithecine that cannot be allocated to tribe, and a large colobine.

## 5.2 MEASUREMENTS

Several standard cranial and mandibular dimensions were recorded where sufficiently preserved, and reported in Table 5.1. Most of the cranial dimensions are between standard landmark pairs, following those used by Freedman (1957) and Jolly (1972) and need no further description here. The minimum interfrontal breadth is the minimum mediolateral dimension across the frontal bone posterior to the orbital rim (see Freedman, 1957) and is equivalent to the postorbital breadth of Delson (1973). The interorbital breadth is the minimum mediolateral breadth across the interorbital pillar. The dimension from the inferior limit of the premaxillary-maxillary suture (i.e., on the alveolar process) to the alveolar process at the position of the distal $M_3$ essentially measures the length of the maxillary portion of the alveolar process. The dimension from the inferior limit of the zygomatic-maxillary suture (i.e., the intersection of the inferior border of the zygoma and the suture) to the alveolar process at the position of the distal $M^3$ measures the position of the zygoma relative to the dentition, including anteroposterior, mediolateral, and superoinferior aspects.

Standard caliper measurements were recorded on all dental material that adequately preserved the relevant morphology, following Freedman (1957) and Delson (1973). For incisors and canines these measurements are the maximum labiolingual crown breadth ("W" in Tables 5.2–5.5); maximum mesiodistal length ("L" in Tables 5.2–5.5) and crown height as measured labially from the cervix to the occlusal tip ("O" in Tables 5.2–5.5). For all premolars except the $P_3$, only buccolingual breadth ("W") and mesiodistal length ("L") are reported. For the $P_3$, in addition to these two dimensions, the length of the mesiobuccal honing flange was also taken ("O" in Tables 5.2–5.5). It is measured from the tip of the protoconid to the inferior, mesiobuccal extreme of the flange. For molars, three dimensions are reported: the buccolingual crown breadth taken across the mesial loph(id) ("W" in Tables 5.2–5.5); the buccolingual crown breadth taken across the distal loph(id) ("O" in Tables 5.2–5.5); and mesiodistal crown length ("L" in Tables 5.2–5.5).

Dimensions of some postcranial elements are reported in Table 5.6. For humeri, maximum mediolateral and anteroposterior diameters are given for the proximal end. Distally, the biepicondylar breadth is reported, and is equivalent to the maximum mediolateral dimension of the distal humerus (see Fig. 5.7 dimension B). A second mediolateral dimension records the total width of the distal humerus from the lateral extreme of the lateral epicondyle to the medial limit of the trochlea (see Fig. 5.7 dimension A, following Harrison, 1989). This dimension effectively records the total humeral width without the medial epicondyle. Distal articular breadth is the mediolateral dimension across both the capitulum and trochlea, and is taken anteriorly (see Fig. 5.9 dimension B). The length of the medial trochlear flange is taken from the most proximal point on the trochlea to the distal tip of the flange (see Fig. 5.9 dimension A, following Delson, 1973).

On the ulna, the height of the olecranon process is measured from the proximal tip of the trochlear notch to the proximal tip of the olecranon process (see Krentz, 1993). Also recorded are the proximodistal length of the trochlear notch, and the total ulnar breadth measured across the radial and trochlear articular facets.

On the radius, the maximum diameter of the head and its diameter perpendicular to the maximum are recorded. The neck length is measured in two ways: first from the distal limit of the radial head to the proximal limit of the radial tuberosity (see Harrison, 1989); second is the mechanical length from the capitular articular facet to the midpoint of the radial tuberosity (see Jolly, 1972).

Femoral measurements reported are the anteroposterior diameter of the femoral head (Fig. 5.13 dimension B), the maximum mediolateral breadth of the femur from the trochanteric tuberosity to the medial end of the head, and finally the projection of the greater trochanter proximal to the femoral neck (Fig. 5.13 dimension A, following Ting, 2001). On the distal end, both the condylar anteroposterior depth and maximum mediolateral breadth are given.

On the proximal end of the tibia, the anteroposterior depth of the tibial condyles and the mediolateral breadth across both condyles are recorded. Distally, the mediolateral and anteroposterior diameters are also reported.

On the calcaneus four measures are reported, the maximum proximodistal length, the length of the segment proximal to talar facet (essentially the tuberosity length), the length of the talar facet, and the length of the body distal to the talar facet.

As no complete metapodials are preserved, only the maximum dorsoplantar depth and mediolateral breadth of the proximal end are reported. For phalanges, the maximum mediolateral diameter of the proximal end, and the total length are reported (see Jolly, 1972).

## 5.3 SYSTEMATIC PALEONTOLOGY

The fossils described in this chapter represent all of the cercopithecids collected from the Konso Formation that were available for study as of 2004. All of these specimens are housed in the laboratory facilities of the A.R.C.C.H. (formerly at the National Museum of Ethiopia). In the present paper, acronyms (such as KNM or NME) indicating housing institutions are shown for the comparative materials, but not for the Konso specimens. In the by-taxon lists of "Referred Konso materials", question marks indicate tentative taxonomic allocations due to an absence of definitive diagnostic morphology, e.g., for isolated teeth. While the craniodental material is allocated with some reliability, none of the postcrania are directly associated and are therefore discussed separately after the craniodental material.

Family Cercopithecidae Gray 1821
Subfamily Cercopithecinae Gray 1821
Tribe Papionini Burnett 1828
Genus *Theropithecus* Geoffroy 1843
(see Frost and Delson, 2002 for synonymy)

Generic diagnosis: see Frost and Delson (2002).

*Theropithecus oswaldi* (Andrews 1916)
(see Frost and Delson, 2002 for synonymy)

Type specimen: BM(NH)-M11539 (lectotype) from Kanjera, Kenya
Specific diagnosis: see Frost and Delson (2002).
Subspecies included:
*T. o. oswaldi* (Andrews 1916)
*T. o. leakeyi* (Hopwood 1934)
*T. o. darti* (Broom and Jensen 1946).

***Theropithecus oswaldi oswaldi* (ANDREWS 1916)**
(see Frost and Delson, 2002 for synonymy)

Holotype: BM(NH) M11539 (lectotype) from Kanjera, Kenya
Subspecific diagnosis: see Frost and Delson (2002).

**Referred Konso materials**

Sorobo Member and lower part of Turoha Member (~1.9 Ma): 14 specimens (see Appendix Table A2.1).

**Description**

This subspecies is similar to or exceeds the largest individuals of extant *Papio* and *Mandrillus* in overall cranial size and is distinctly larger in molar and premolar size, but not the other teeth. Cranial and dental dimensions for the Konso material are provided in Tables 5.1 and 5.2, respectively. Using the equations and methods described by Delson et al. (2000) and the means of the dental dimensions from Table 5.2, population mean body masses are estimated. Sex is not known for any of the elements useable. Therefore, the equations for combined sex population means were used. Results for the population mean mass ranged from 25 kg to 30 kg with an average of 28 kg. This is equivalent to the male means for the larger subspecies of extant *Papio*, such that males of *Theropithecus oswaldi oswaldi* from Konso would have been larger than this, and females smaller.


**Fig. 5.1.** *Theropithecus oswaldi oswaldi* female left maxillary fragment KGA4-19. Lateral (top) and inferior views (bottom).

***Maxilla.*** KGA4-19 is a left maxilla from a subadult individual with the roots of the canine through second molar, and the unworn crown of $M^3$ erupting (Fig. 5.1). The specimen is female based on the small size of the canine alveolus and the morphology of the rostrum superior to it. This specimen preserves the root of the zygomatic process, the proximal part of the zygomatic bone, the lateral surface of the rostrum superior to the dentition, and a small portion of the palatal process. The lateral surface of the rostrum has a slight maxillary fossa above the molar roots. The preserved morphology indicates that the sides of the rostrum were sloped strongly towards the midline, so that the muzzle cross-section was likely rounded. These features clearly align this specimen with *Theropithecus oswaldi* and distinguish it from *T. brumpti* (Eck and Jablonski, 1987). The region of the maxillary ridges is not preserved. The inferior margin of the zygomatic process is positioned superior to the mesial half of the $M^2$. Given that the zygoma becomes more posteriorly placed with age, it is likely that it would have been above the $M^3$ if this individual had lived to adulthood. The anterior surface of the zygoma is anteroinferiorly sloping so that its inferior edge is anterior to the inferior orbital rim. Its anterior surface is smooth and unmarked by suborbital fossae, again different from *T. brumpti* as well as from *Papio* (*Papio*) (Eck and Jablonski, 1987; Delson and Dean, 1993). The dental arcade is gently curving, as is typical of female specimens of *T. o. oswaldi*: e.g., BM(NH) M14936 from Kanjera, TMP-SK 561 from Swartkrans, and KNM-ER 971 from Koobi Fora (figured in Jolly, 1972; Delson, 1993; and Jablonski et al., 2008).

***Mandible.*** The most complete mandibular specimen for this taxon is KGA4-2319, a left corpus fragment with $M_{1\text{-}3}$ (Fig. 5.2). Other mandibular fragments include: KGA4-1499 a small fragment of the left corpus and inferior ramus with the $M_3$ (Fig. 5.2); KGA4-1170 and KG4-1617 left and right corpus fragments respectively, both preserving $M_{2\text{-}3}$, but little corpus morphology.

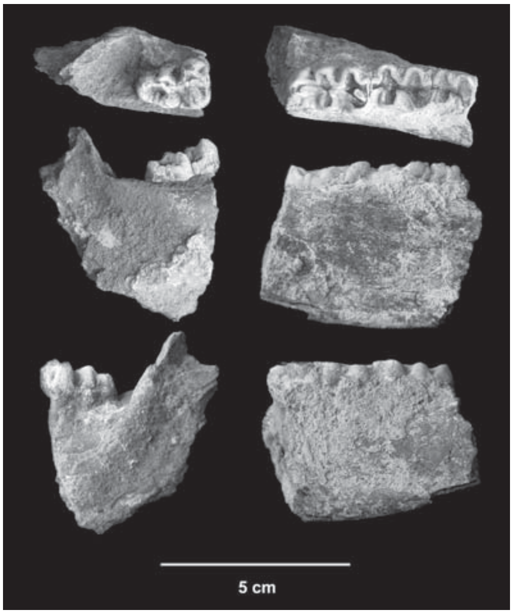


**Fig. 5.2.** Mandibles of *Theropithecus oswaldi oswaldi*. KGA4-1499 (left) and KGA4-2319 (right). Occlusal (top), medial (middle), and lateral views (bottom).

**Table 5.1.** Cranial and mandibular dimensions for *Theropithecus oswaldi oswaldi and T. o. leakeyi* (mm)

| Maxilla | KGA4-19 | KGA7-350 | KGA10-2776 |
|---|---|---|---|
| *nasion–inion* | | 146 | |
| *nasion–basion* | | 107 | |
| *glabella–inion* | | 149 | |
| *bregma–basion* | | 86 | |
| Postorbital breadth | | 58 | |
| Biporionic breadth | | 117 | |
| *basion–opisthion* | | 24 | |
| Interorbital breadth | | 17 | 14 |
| Inferior premaxillaary–maxillaary suture to alveolar process at distal limit of $M^3$ | 72 | | |
| Inferior maxillozygomatic suture to alveolar process at distal limit of $M^3$ | 32 | | |
| **Mandible** | **KGA4-2319** | **KGA10-559/1676** | **KGA12-640** |
| Width across canines | | | (37) |
| Corpus depth at $M_2/M_3$ contact | 34 | 34 | |
| Corpus breadth at $M_2/M_3$ contact | 19 | 21 | |

**Table 5.2.** Dental dimensions for *Theropithecus oswaldi oswaldi*

| Specimen no. | Sex | Tooth | WS | W | O | L |
|---|---|---|---|---|---|---|
| KGA4-647 | M | $C^1$ | | 12.6 | | 15.8 |
| KGA4-1003 | ? | $dp^4$ | 10 | 12.7 | | 13.6 |
| KGA4-2319 | ? | $M_1$ | 16 | 9.4 | 9.7 | 10.8 |
| KGA4-1170 | ? | $M_2$ | 16 | 10.9 | 11.0 | 13.1 |
| KGA4-1617 | ? | $M_2$ | | | | 15.1 |
| KGA4-2319 | ? | $M_2$ | 16 | 12.5 | 12.9 | 15.8 |
| KGA4-1170 | ? | $M_3$ | 16 | 12.2 | 11.7 | 18.9 |
| KGA4-1499 | ? | $M_3$ | 7 | 13.2 | 11.1 | 19.6 |
| KGA4-1500 | ? | $M_3$ | | | 12.3 | |
| KGA4-1616 | ? | $M_3$ | 11 | 13.6 | 12.9 | 20.6 |
| KGA4-1617 | ? | $M_3$ | | | | 20.4 |
| KGA4-2319 | ? | $M_3$ | 15 | 13.3 | 12.5 | 21.2 |
| KGA4-1996 | ? | $M_X$ | 7 | 9.8 | | |
| KGA4-2476 | ? | $M_X$ | 11 | | 9.6 | |

WS is wear stage; molars are on a scale from 0–16 and premolars from 0–8 (see Delson, 1973). W is buccolingual dimension (mm) of the crown. In the case of molars it is measured across the mesial moiety. L is mesiodistal dimension (mm) of the crown. O is other dimensions (mm): for incisors and canines it is crown height; for lower third premolars it represents the length of the mesiobuccal honing flange from protoconid to mesiobuccal tip; for molars O is the buccolingual crown dimension of the distal moiety.

Overall the corpus is thick and robust. The preserved corpus of KGA4-2319 deepens anteriorly, which is different from *Theropithecus oswaldi leakeyi*, but common among males of *T. o. darti* and *T. o. oswaldi* (Jolly, 1972; Eck, 1987, 1993; Delson and Hoffstetter, 1993; Frost and Alemseged, 2007). On the lateral corpus surface, a slight fossa is present anteriorly, inferior to the $M_1$. In general, shallow corpus fossae are variably present in *T. o. darti* and *T. o. oswaldi* but absent in *T. o. leakeyi* (Jolly, 1972; Eck, 1987, 1993; Delson and Hoffstetter, 1993; Frost and Alemseged, 2007). Inferior to $M_3$, the corpus is thick and laterally a wide extramolar sulcus is present. The small portion of the ramus of KGA4-1499 appears to be more retroflexed than it would have been in life due to damage along its anterior edge. As a result it is difficult to estimate the original angle of the ramus. In lateral view, there is a small retromolar gap of approximately 3–4 mm. The total ramal height cannot be accurately estimated from what is preserved. Its lateral surface has a deep triangular fossa, but its edges are not sharply marked.

***Dentition.*** KGA4-647 is an upper canine tentatively assigned to this taxon. In diameter it is similar to the largest individuals of extant *Papio*, but differs in shape. It is relatively short in the mesiodistal diameter due to the poorly sharpened distal border. Furthermore, the crown is relatively stout for its diameter, another feature typical of *Theropithecus*, but different from *Papio*. Other than this specimen, only the molar and deciduous premolar teeth of *T. oswaldi oswaldi* are represented at Konso with certainty. They are classic for the genus (see Szalay and Delson, 1979 for a thorough description). The crowns are tall relative to those of most primates, with columnar cusps and a low amount of basal flare. The cusps are separated by deeply excavated notches and foveae, with "flattened" floors, yielding a distinctive "double cross" pattern when they are worn. The teeth are large relative to the cranium overall, and the distal teeth are relatively large in comparison to the mesial ones. The Konso material is typical of the genus in this regard, and has more fully developed *Theropithecus* molar morphology with a more complex enamel folding pattern than do earlier samples, such as Makapansgat (Freedman, 1957; Maier, 1970) and Hadar (Eck, 1993; Frost and Delson, 2002), but less complex than younger ones, such as Olorgesailie (Jolly, 1972), Olduvai Upper Bed II and younger (Jolly, 1972; Leakey and Leakey, 1973), Ternifine (Delson and Hoffstetter, 1993), Hopefield (Singer, 1962; Dechow and Singer, 1984), Daka (Gilbert and Frost, 2008), Dawaitoli Fm. (Frost, 2007a), Asbole (Frost and Alemseged, 2007) and the Karat Member of Konso (see below). Additionally, a chronological pattern of increasing molar size has been documented in *T. oswaldi*, and the populations from Konso are of the size expected for their geologic age (e.g., Jolly, 1972; Delson, 1983; Eck, 1987; Leakey, 1993; Frost and Delson, 2002).

### ***Theropithecus oswaldi leakeyi*** **(Hopwood 1934)**

(see Frost, 2007a for synonymy)

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

Subspecific diagnosis: see Frost (2007a).

**Referred Konso materials**

Upper part of Kayle Member (~1.4 Ma to ~1.45 Ma): 33 specimens;

Karat Member (~1.25 Ma to ~1.4 Ma): 36 specimens (see Appendix Table A2.2).

**Description**

This subspecies is the largest known cercopithecid taxon. In addition, the premolars and molars are relatively even larger than those of *Theropithecus oswaldi oswaldi*. Cranial and dental dimensions are presented in Tables 5.1 and 5.3, respectively. On average, it is larger in its cranial and dental dimensions than the *T. o. oswaldi* material from the Sorobo/Turoha Members, but smaller than later populations such as Olorgesailie, Asbole, Dawaitoli Formation, Daka, Hopefield, and Ternifine (Jolly, 1972; Dechow and Singer, 1984; Delson and Hoffstetter, 1993; Frost, 2007a; Frost and Alemseged, 2007; Gilbert and Frost, 2008). Using the equations and methods from Delson et al. (2000) as described for *T. o. oswaldi* above, estimates for population mean masses were also made for *T. o. leakeyi* using means of the dimensions in Table 5.3. Estimates for combined sex population mean masses ranged from 34 kg to 57 kg, with an average of 43 kg; again males would be on average larger than this and females smaller.

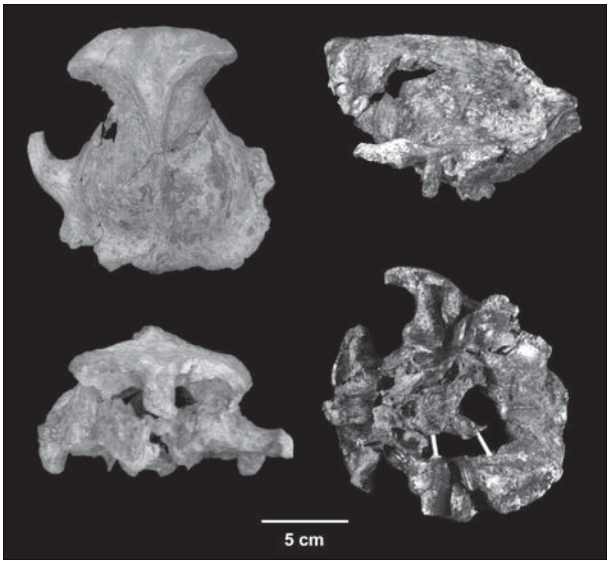


**Fig. 5.3.** Probable male calvaria of *Theropithecus oswaldi leakeyi* KGA7-350. Superior (top left), anterior (bottom left), left lateral (top right) and basal views (bottom right).

***Calvariae.*** While facial material is absent, the calvaria is well preserved in KGA7-350 (Fig. 5.3). The specimen is essentially complete including the vault and basicranium, with the only missing areas being those around the basioccipital and sphenoid. The face is absent except for the supraorbital torus and interorbital region. It is presumably from a male individual based on the large compound sagittal and nuchal crests. The Konso specimen is smaller in overall size than NME KL337-1, NME HAR-VP-1/1, and NME ASB-202 (male crania from the Dawaitoli Formation in the Middle Awash and Asbole, figured in Frost, 2001, 2007a; and Frost and Alemseged, 2007) and slightly larger than the calvaria from Upper Bed II, Olduvai (Jolly, 1972; Leakey and Leakey, 1973; Eck and Jablonski, 1987). This is reasonable as the Konso specimen is of similar age to that from Olduvai, both representing two of the earliest populations of the subspecies. KGA7-350 is also larger than the female calvaria NME BOU-VP-1/132 from the Daka Member of the Bouri Formation (Gilbert and Frost, 2008). The only other cranial specimen, KGA10-2776, is a frontal fragment preserving a small portion of the left supraorbital rim. It is slightly smaller in size than KGA7-350, but is also probably male based on the mediolateral orientation of the small preserved portion of the temporal line.

Overall, the calvaria is marked by the need to accommodate large temporal musculature, including pronounced postorbital constriction and large compound sagittal-nuchal crests. The superior surface of the frontal is flat except for thickenings of the torus superior to the middle of the orbits and a slight depression in the midline. The supraorbital rim is thick, being 9.5 mm in KGA7-350 and 8.5 mm in KGA10-2776. The supraorbital notch is large and well defined in the former specimen, but is damaged in the latter. A small portion of the temporal margin of the orbit is present, extending inferiorly to the frontozygomatic suture. The lateral margin of the orbit is broad and appears to become broader inferiorly. The interorbital area is broad in both specimens (16.5 mm and 14 mm, respectively), even relative to the large size of this subspecies.

The cranial vault is well preserved. The temporal lines are prominent and meet approximately at bregma to form a sagittal crest. In fact, the temporal lines reach a height of nearly 1 cm anterior to their junction. The sagittal crest attains its maximum height posteriorly, where it approaches 2 cm. The nuchal crests are semicircular in superior view, with a slight prominence at inion, but are large immediately posterior to the auditory meatus. The nuchal crest in combination with the zygomatic arch forms a continuous shelf lateral to the neurocranium that is approximately 1.5 cm to 2 cm wide, which along with the sagittal crest provides a very large area of attachment for the *m. temporalis*. In all of these features the Konso specimen is similar to male individuals from Hopefield, Dawaitoli Formation and Asbole, but somewhat smaller (Dechow and Singer, 1984; Frost, 2007a; Frost and Alemseged, 2007).

In overall shape the neurocranium is ovoid due to the strong postorbital constriction. In superior view, the maximum breadth of the neurocranium is across the auditory meatus. In posterior view, the widest point of the neurocranium, ignoring the prominent superstructures is positioned inferiorly at the level of the auditory meatus.

Basicranial morphology is well preserved except for the area around the foramen magnum. 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 weren't for the presence of the digastric groove, it might appear as if there were no mastoid processes. The tympanic bone is angled slightly posterolaterally. The postglenoid process is tall and thin and pressed directly against the tympanic, and is separated from the glenoid fossa by a wide sulcus. The glenoid fossa is distinctly sellar in morphology. It is concave-down in the mediolateral plane and convex-down in the anteroposterior plane. The rate of curvature of both is tighter than in *Theropithecus oswaldi darti*, and the articular surface is more prominent above the surrounding bone. In these features, the glenoid is similar to those of other *T. o. leakeyi* populations as well as some *T. o. oswaldi* (Jolly, 1972; Eck, 1987; Frost, 2007a; Frost and Alemseged, 2007; Gilbert and Frost, 2008).

***Mandible.*** The symphysis is only represented by KGA12-640 (Fig. 5.4). Nearly all of the bone on the anterior surface is absent, so details of the mental region are not well preserved. However, it is clear that the symphysis was sloping in lateral view, essentially following the curve of large canine roots in this male specimen. Due to strong incisor reduction, the roots of the canines project anterior to those of the incisors resulting in a fossa between the canine roots. The overall depth of the corpus cannot be accurately determined, but it was at least 3.5 cm. The *planum alveolare* was long and sloping. The anterior portion of the corpus is only preserved in KGA12-650, where about 2 cm inferior to the $P_{3\text{-}4}$ is present. On the lateral aspect there is a slight depression below the $P_3$ indicating the presence of a slight corpus fossa. At the $P_3$–$P_4$ contact the corpus is approximately 15 mm in breadth. The corpus inferior to $M_{2\text{-}3}$ is reasonably well preserved in KGA10-559/1676 (Fig. 5.4), where it is thick but comparatively shallow. At the $M_2$–$M_3$ contact the depth is 34 mm and the breadth 19 mm. The mandible reaches its maximum breadth of 23 mm at approximately the midpoint of $M_3$. In all of these features, the mandibular material from Konso is similar to other mandibles of *Theropithecus oswaldi leakeyi* (e.g., KNM-OG 4; NMT-067/5603; KNM-BK 22638; MNHN-TER 1402; NME-ASB-201; figured in Jolly, 1972; Leakey and Leakey, 1973; Leakey, 1993; Delson and Hoffstetter, 1993; Frost and Alemseged, 2007, respectively).


**Fig. 5.4.** Mandibles of *Theropithecus oswaldi leakeyi*. KGA10-1676 corpus fragment (left) and KGA12-640 male symphyseal fragment (right). Occlusal (top), medial and anterior views (middle), and lateral views (bottom).

***Dentition.*** Nearly all of the adult dentition is represented in the sample, with the exception of male $C^1$, $P^3$, $M^3$, and female $P_3$. The incisors are generally similar in morphology to those of other papionins, except that they are smaller relative to the cheek-teeth and overall body size, and are stouter in morphology than those of other papionins. The $I^1$ crown is flaring in anterior view, and spatulate, the $I^2$ is narrower and more mesially inclined. The lower incisors are smaller and more peg-like than those of most papionins. While those of most papionins lack lingual enamel (Szalay and Delson, 1979; Gantt et al., 1999), it is present in KGA11-274. The crowns of the incisors on KGA12-640 are damaged making this feature difficult to assess. The presence of lingual enamel on the lower incisors of *Theropithecus oswaldi leakeyi* appears to also occur at Olorgesailie (personal observations). The canines are sexually dimorphic and typical of cercopithecoids in their morphology. The males in particular are, however, larger in caliber relative to their height than in most cercopithecids. The premolars are similar to those of other cercopithecids, except that they are generally more molariform. Related to the reduction in relative size of the canines, particularly in crown height, the $P_3$ mesiobuccal flange is also relatively short. The molars show the classic features of the genus discussed above, but to a greater degree. The enamel is more elaborately folded and complex as is typical of *T. o. leakeyi*.

***Theropithecus oswaldi* ssp. indet.**

**Referred Konso materials**

Middle part of Kayle Member: KGA21-84 (right $M_{1or2}$) (~1.6 Ma).

**Description**

The single dental specimen from stratigraphic interval 3 is an isolated lower right first or

**Table 5.3.** Dental dimensions for *Theropithecus oswaldi leakeyi*

| Specimen no. | Sex | Tooth | WS | W | O | L |
|---|---|---|---|---|---|---|
| KGA7-383 | ? | $I^1$ | | 7.1 | 12.1 | 7.5 |
| KGA8-300 | ? | $I^2$ | | 5.7 | 10.5 | 4.1 |
| KGA10-554 | F | $C^1$ | | 8.7 | 16.0 | 11.4 |
| KGA12-552 | F | $C^1$ | | 7.3 | 15.0 | 9.2 |
| KGA7-321 | ? | $P^4$ | 0 | 10.1 | | 8.8 |
| KGA10-2150 | ? | $P^4$ | | | | 9.6 |
| KGA12-685 | ? | $P^4$ | 4 | 12.2 | | 10.4 |
| KGA12-590 | ? | $M^1$ | 16 | 13.0 | 12.9 | 16.4 |
| KGA16-10 | ? | $M^1$ | 9 | 13.2 | 11.5 | 14.5 |
| KGA12-590 | ? | $M^2$ | 15 | 16.3 | 16.4 | 20.9 |
| KGA8-299 | ? | $M^X$ | | 17.3 | | |
| KGA7-310 | ? | $M^X$ | 11 | 14.6 | 14.6 | 18.3 |
| KAG10-242 | ? | $M^X$ | 9 | 12.2 | 11.5 | 14.4 |
| KAG10-688 | ? | $M^X$ | 9 | 13.7 | | 15.0 |
| KGA10-1579 | ? | $M^X$ | 5 | 12.9 | 12.5 | 15.6 |
| KGA10-1635 | ? | $M^X$ | 3 | 14.2 | 12.7 | 17.7 |
| KGA12-184 | ? | $M^X$ | 10 | | 12.5 | (14.4) |
| KGA16-1 | ? | $M^X$ | 8 | 15.8 | 14.9 | 19.6 |
| KGA16-2 | ? | $M^X$ | 8 | 13.0 | 12.4 | 14.2 |
| KGA11-274 | ? | $I_1$ | | 6.0 | 7.9 | 4.2 |
| KGA12-640 | M | $I_1$ | | 6.7 | 6.1 | 5.0 |
| KGA12-640 | M | $I_2$ | | 6.3 | 6.4 | 4.5 |
| KGA7-373 | F | $C_1$ | | 8.9 | 11.4 | 5.8 |
| KGA7-429 | M | $C_1$ | | 15.2 | | 10.2 |
| KGA8-539 | M | $C_1$ | | 17.2 | 11.6 | 21.8 |
| KGA12-640 | M | $C_1$ | | 16.6 | 23.6 | 11.9 |
| KGA14-4 | M | $C_1$ | | 18.4 | 24.7 | 13.7 |
| KGA10-1712 | F | $P_3$ | | 6.7 | 12.5 | 9.2 |
| KGA10-1862 | M | $P_3$ | | 8.4 | (15.8) | 12.4 |
| KGA12-650 | M | $P_3$ | | 8.0 | 17.2 | 10.9 |
| KGA7-392 | ? | $P_4$ | 4 | 8.8 | | 10.5 |
| KGA10-1732 | ? | $P_4$ | 2 | 8.7 | | 7.1 |
| KGA12-840 | ? | $P_4$ | 5 | 9.3 | | 10.3 |
| KGA12-1193 | ? | $P_4$ | 5 | 9.0 | | 10.8 |
| KGA12-664 | ? | $M_1$ | 16 | 10.4 | 11.2 | 11.9 |
| KGA12-664 | ? | $M_2$ | 16 | 11.8 | 12.4 | 15.6 |
| KGA7-465 | ? | $M_3$ | 6 | 15.3 | 13.5 | 25.2 |
| KGA8-361 | ? | $M_3$ | 6 | 15.6 | 13.8 | 26.5 |
| KGA10-590 | ? | $M_3$ | 9 | 14.0 | 11.8 | 21.1 |
| KGA10-559/1676 | ? | left $M_3$ | 12 | 13.5 | 12.5 | 21.0 |
| KGA10-559/1676 | ? | right $M_3$ | 8 | (14.1) | 13.7 | 21.0 |
| KGA10-1559 | ? | $M_3$ | 10 | 14.8 | 12.8 | 24.8 |
| KGA12-1146 | ? | $M_3$ | 9 | 15.7 | 14.9 | 25.5 |
| KGA12-1198 | ? | $M_3$ | 10 | | 11.8 | 23.3 |
| KGA4-1295 | ? | $M_X$ | 10 | (15.3) | | |
| KGA4-2610 | ? | $M_X$ | 1 | 10.2 | 9.6 | 14.5 |
| KGA7-260 | ? | $M_X$ | 9 | | 11.2 | 16.0 |
| KGA7-466 | ? | $M_X$ | | | 13.8 | |
| KGA10-1643 | ? | $M_X$ | 7 | 9.6 | 10.1 | 14.3 |
| KGA10-2478 | ? | $M_X$ | 6 | 11.2 | 11.2 | 14.7 |
| KGA10-2756 | ? | $M_X$ | 3 | | 13.4 | 19.7 |
| KGA12-411 | ? | $M_X$ | | | 11.8 | |
| KGA16-3 | ? | $M_X$ | 3 | 13.4 | 13.3 | 20.4 |
| *KGA21-84 | ? | $M_X$ | 12 | 13.1 | 12.5 | 16.0 |

Abbreviations as for Table 5.2.
*KGA21-84 is considered subspecies indet.

second molar that is clearly *Theropithecus* based on its morphology. In shape it is more likely to represent a second molar rather than a first. In size it overlaps the known ranges for both *T. oswaldi oswaldi* and *T. o. leakeyi*. Given this, and that its age is intermediate between the larger samples from intervals 1 and 4/5, and that it is similar in age to *T. o. oswaldi* from the Okote Member at Koobi Fora, and *T. o. leakeyi* from upper Bed II at Olduvai it is left here without assigning it to subspecies.

**Papionini gen. et sp. indet.**

**Referred Konso materials**

Sorobo Member: 3 specimens (>~1.9 Ma);
upper part of Kayle Member: 4 specimens (~1.44 Ma);
Karat Member: 2 specimens (~1.25 Ma to ~1.4 Ma) (see Appendix Table A2.3).

**Description** (Fig. 5.5)

This is a collection of nine isolated teeth, all of which are in the size range for extant *Papio hamadryas*, but larger than *P. h. kindae* (Table 5.4). During the Late Pliocene and Early Pleistocene there are several papionin taxa known that are similar in size to this material (Jablonski and Frost, 2010). These include *Papio*, *Parapapio*, and *Procercocebus* from South Africa (Freedman, 1957; Szalay and Delson, 1979; Gilbert, 2007), *Lophocebus* sp. nov. from Koobi Fora, Omo Shungura, and Olduvai (Eck, 1976; Leakey and Leakey, 1976; Frost, 2001; Jablonski et al.,

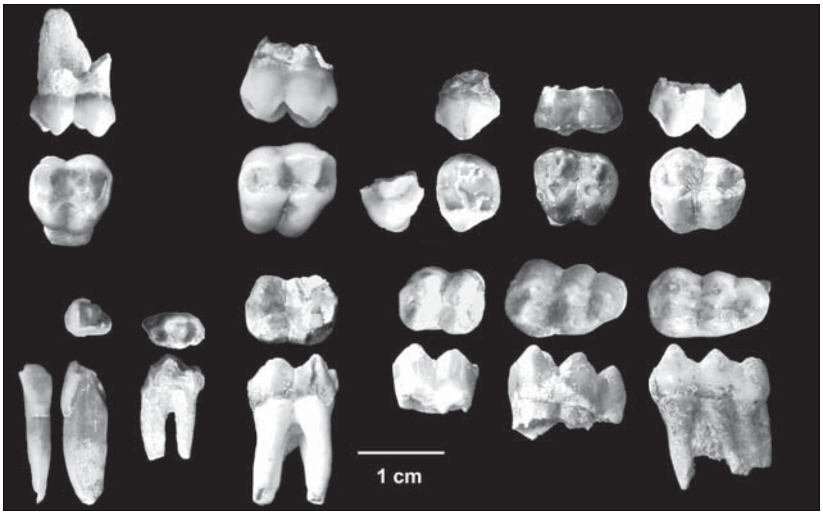


**Fig. 5.5.** Konso dental material not allocated to *Theropithecus*. Upper rows, buccal and occlusal views, left to right: KGA12-1042 (Colobinae gen. et sp. indet. right $M^X$); KGA4-1995 (Papionini gen. et sp. indet. right $M^X$); KGA4-1005 (Papionini gen. et sp. indet. left $P^3$); KGA4-1004 (Papionini gen. et sp. indet. left $P^4$); KGA12-914 (Papionini gen. et sp. indet. left $dp^4$); KGA10-1456 (Papionini gen. et sp. indet. left $M^X$). Lower rows, occlusal and lingual views (except the labial and distal views are shown for the incisor), left to right: KGA10-1525 (Colobinae gen. et sp. indet. left $I_1$); KGA10-1619 (Cercopithecinae tribe indet. right $P_4$); KGA10-10 (Papionini gen. et sp. indet. left $M_X$); KGA10-2790 (Papionini gen. et sp. indet. right $M_X$); KGA8-305 (Papionini gen. et sp. indet. right $M_3$); KGA16-24 (Papionini gen. et sp. indet. right $M_3$).

2008) as well as an unnamed species of papionin from Olduvai (Leakey and Leakey, 1976). This material also overlaps the size range of Papionini B in the Omo Shungura formation and some of the smaller and medium-sized papionins from Koobi Fora (Eck, 1976, 1977; Leakey and Leakey, 1976; Frost, 2001; Jablonski et al., 2008). As papionin teeth, other than those of *Theropithecus*, are generally not diagnostic to genus or species based on their morphology alone, and given that there are several taxa of the appropriate size, they are not classified below tribe.

KGA8-305 is a right $M_3$. KGA4-1995 is an unworn right upper molar, probably an $M^{2.}$ KGA10-1456 is a left upper molar crown germ, likely an $M^3$, that is not completely formed. KGA10-10 is a left $M_1$ or $M_2$, most likely an $M_2$. There is damage to the mesial lophid on both buccal and lingual sides. KGA12-914 is a moderately worn left $dp^4$. The crown is flat with a large amount of lingual flare. The protoloph is relatively long in the mesiodistal direction in comparison to the hypoloph, as are the mesial and distal foveae. KGA4-1004 is a moderately worn left $P^4$. KGA4-1005 is a left $P^3$ missing the buccal half of the paracone. KGA10-2790 is a right $M_1$ or $M_2$ that is slightly smaller than one would expect from the other teeth, but is conservatively grouped here.

In general, the molars show a level of basal flare comparable to most papionins, which is greater than that of colobines, cercopithecins, and *Theropithecus*, but less than that of *Cercocebus* or to a lesser degree extant *Lophocebus*. The lingual notches of the lowers, and buccal notches of the uppers are relatively tall and the cusps relatively short so that most of the crown height is cervical to the level of the notch. In general they are free of accessory cuspules, except for the $dp^4$ (KGA12-914) where there is a small cuspule in the buccal cleft.

Finally there is an additional ninth specimen, KGA16-24, which is similar in size to the remaining teeth from this category but is fairly different in its morphology. It is grouped with the above because it is not certain that it represents a distinct taxon. It is a right $M_3$, and is cercopithecine in morphology with a lingual notch that is relatively tall and low, bunodont cusps. In length, it is slightly longer than KGA8-305 but substantially narrower and less flaring. If fact, while the other teeth from this series fall within the extant *Papio* range in both the level of flare and in crown shape (as measured by length to width ratio) this specimen is at the very lower limit for flare and just outside the known range in crown shape. Additionally, the distal lophid is broad relative to the mesial, as is the hypoconulid and the *tuberculum sextum*, giving the tooth a relatively rectangular outline as opposed to the more normal trapezoidal outline of KGA8-305.

**Table 5.4.** Dental dimensions for cercopithecines other than *Theropithecus*

| Specimen no. | Sex | Tooth | WS | W | O | L |
|---|---|---|---|---|---|---|
| KGA12-1148 | M | $C^1$ | | 7.2 | | 9.6 |
| KGA4-1005 | ? | $P^3$ | 0 | | | 7.0 |
| KGA4-1004 | ? | $P^4$ | 5 | 9.0 | | 7.2 |
| KGA10-1456 | ? | $M^3$ | 0 | 9.7 | 8.2 | 11.0 |
| KGA4-1995 | ? | $M^X$ | 0 | 10.4 | 10.0 | 11.5 |
| KGA12-914 | ? | $dp^4$ | 7 | 8.4 | 8.1 | 9.7 |
| KGA10-1619 | ? | $P_4$ | 4 | 3.8 | | 6.2 |
| KGA8-305 | ? | $M_3$ | 0 | 9.3 | 8.0 | 13.5 |
| KGA16-24 | ? | $M_3$ | 5 | 8.3 | 7.8 | 13.8 |
| KGA10-10 | ? | $M_X$ | 5 | | 8.0 | 10.6 |
| KGA10-2790 | ? | $M_X$ | 6 | 6.8 | 6.8 | 9.4 |

Abbreviations as for Table 5.2.

### Cercopithecinae Tribe indet.

**Referred Konso materials**

Upper part of Kayle Member: KGA10-1619 (right $P_4$) (~1.44 Ma).

**Description** (Fig. 5.5)

KGA10-1619 is a right $P_4$, too small to represent the same taxon as Papionini gen. et sp. indet. It is slightly larger than the range for $P_4$s of extant *Chlorocebus aethiops*, but is longer and narrower in shape (Table 5.4). It is missing the enamel on the lingual surface of the posterior 2/3 of the crown. In spite of the lack of lingual enamel it can be seen that the lingual notch was relatively tall and the cusps low, clearly marking it as cercopithecine.

Subfamily Colobinae JERDON 1867

### Colobinae gen. et sp. indet.

**Referred Konso materials**

Upper part of Kayle Member: KGA10-1525 (left $I_1$) (~1.45 Ma);

Karat Member: KGA12-1042 (right $M^X$) (~1.25 Ma).

**Description** (Fig. 5.5)

There are two specimens that can be diagnosed as colobine. The first, KGA12-1042 is the crown of a right $M^1$ or $M^2$ of a large colobine (Table 5.5). As is typical of colobine molars, the lophs are well-formed and the cusps are widely spaced, the crown has a low level of basal flare, and the notch is relatively deep. However, it is relatively low-crowned for a colobine upper molar, being reminiscent of some *Cercopithecoides* specimens, particularly *C. kimeui* in this feature. In its overall dimensions it overlaps upper molars of *Rhinocolobus turkanaensis*, *C. williamsi*, and the small end of *Kuseracolobus hafu*. The second colobine specimen, KGA10-1525 is a left $I_1$. The crown is small and peg-like in comparison to most cercopithecine incisors. The clear presence of lingual enamel is also indicative of the subfamily. In size it is within the range of modern *Colobus* and *Procolobus* (*Piliocolobus*).

**Table 5.5.** Dental dimensions for Colobinae gen. et. sp. indet.

| Specimen no. | Sex | Tooth | WS | W | O | L |
|---|---|---|---|---|---|---|
| KGA12-1042 | ? | $M^X$ | 8 | 9.0 | 8.4 | 9.3 |
| KGA10-1525 | ? | $I_1$ | | 4.9 | 6.2 | 3.2 |

Abbreviations as for Table 5.2

### Cercopithecidae Subfamily indet.

**Referred Konso materials**

Upper part of Kayle Member: KGA10-641 ($M_X$ fragment), KGA10-2287 (M or dp fragment) (~1.44 Ma);

Karat Member: KGA12-1148 (male left $C^1$) (~1.25 Ma).

**Description**

KGA12-1148 is a left upper canine of a male individual, but is too small to be *Theropithecus oswaldi* (Table 5.4). It cannot be determined which of the other taxa present it is most likely to represent. It is also probably too large to be the same taxon as Cercopithecinae tribe indet. or postcranial size A.

KGA10-641 is a very heavily worn fragment of a lower molar. KGA10-2287 is distal fragment of either an M1 or a dp4, and could be either an upper or a lower. If it is from *Theropithecus oswaldi leakeyi*, then it is almost certainly a dp4, if not then an M1. Although the condition of the specimen precludes making a final determination, it is more likely *Theropithecus* than not. Additionally, while preservation prevents measurement, it is approximately 10 mm in breadth.

## Postcranial Descriptions

While none of the postcranial material is directly associated with the craniodental, some are tentatively allocated to *Theropithecus oswaldi*. Given the overwhelming preponderance of this species in the craniodental sample, most of the postcrania are likely to represent this taxon. Furthermore, the large size of *T. oswaldi* is also used, although the lower part of its estimated size range overlaps that of the largest extant *Papio* and *Mandrillus* individuals. It is also probable that some individuals of the large colobine may have been comparable to smaller individuals of *T. oswaldi*. Finally, based on what is known from other sites, *T. oswaldi* postcrania show adaptations to terrestriality and a few unique features that appear to be diagnostic for the genus (e.g., Jolly, 1972; Krentz, 1993; Elton, 2002; Gilbert et al., 2011; Guthrie, 2011). Therefore, most of the large, terrestrially adapted postcranial elements are probably of *T. oswaldi* and are here allocated on this basis. Elements assigned to *T. oswaldi* are then divided by stratigraphy into *T. o. oswaldi* (for the Sorobo/Turoha Member materials), *T. o. leakeyi* (for the upper part of the Kayle Member and Karat Member materials), and *T. oswaldi* ssp. indet. (for the middle part of the Kayle Member materials). These are listed in Appendix Table A2.4. The remaining postcrania are grouped into size categories: A, approximately equivalent to *Chlorocebus aethiops*; B, to *Colobus guereza*, and C to *Papio* and slightly larger, and listed in Appendix Table A2.5 Some standard dimensions are provided in Table 5.6 for the postcranial material from Konso.

### *?Theropithecus oswaldi oswaldi*

All of the following specimens are from the Sorobo Member and lower part of the Turoha Member (~1.9 Ma) and tentatively allocated to *Theropithecus oswaldi oswaldi* based on a combination of size and morphology. Many of the elements are comparable in size to the largest individuals of extant *Papio* and *Mandrillus*. Females of *T. o. oswaldi* are estimated to be approximately the same size as males of these extant taxa (Delson et al., 2000). Therefore, it is possible some of this material may represent large males of Papionini gen. et sp. indet. or some other similarly sized taxon not identified in the craniodental sample of the Sorobo/Turoha Members, such as *Cercopithecoides*—a terrestrial colobine similar in size to the colobine from the Karat Member and known from deposits of similar age in the Turkana and Afar Basins (Leakey, 1982; Frost, 2001; Frost and Delson, 2002; Jablonski et al., 2008).

***Scapula.*** KGA4-549 and KGA4-1615 are left and right partial scapulae each preserving the glenoid and a small portion of the blade, spine, and coracoid, though the latter specimen is more complete. Both are large and most likely *Theropithecus*, but overlap the largest individuals of *Papio* and *Mandrillus* in size. Morphologically they are similar to each other. The articular surface of the glenoid fossa is relatively deep and concave in lateral view. The glenoid fossa is also relatively broad (breadth of the articular surface for both specimens is 23 mm, length is 31 mm and 29 mm for KGA4-549 and KGA4-1615, respectively). The lateral margin of the fossa flares laterally so that the anterior portion is a narrow wedge, and the posterior portion more broad and rounded.


**Fig. 5.6.** Konso distal humeri, anterior (above) and distal (below) views. Upper rows left to right: KGA10-2013 (Cercopithecidae indet. postcranial size A); KGA4-389 (?*Theropithecus oswaldi oswaldi*); KGA4-550 (?*T. o. oswaldi*). Lower rows left to right: KGA8-540, KGA8-433, KGA12-311, and KGA17-39 (all ?*T. o. leakeyi*).

***Humerus.*** KGA4-389 and KGA4-550 are both distal fragments of left humeri (Figs. 5.6–5.9). KGA4-389 preserves the distal articular surface, epicondyles, and approximately 4 cm of shaft. KGA4-550 preserves the entire articular area and epicondyles, but is broken approximately 1 cm proximal to the articular surface across the proximal limit of the olecranon fossa. In size both humeri are relatively small for *Theropithecus oswaldi oswaldi* and perhaps represent females (Table 5.6). They are morphologically similar, being from relatively large terrestrial cercopithecids. The majority of the *m. brachioradialis* flange is preserved on KGA4-389. Unlike the case in *Mandrillus* and *Cercocebus*, it is not prominent or strongly marked. Anteriorly, the supra-articular fossae appear to be equal in height and depth on KGA4-389, and similar in depth on KGA4-550. Height cannot be judged for certain on the latter specimen as the proximal ends of the fossae are broken. The medial epicondyles of both are large and retroflexed. The distal articular surface makes up a relatively large portion of the total distal width. The medial trochlear keel is long and sharp. The lateral edge of the trochlea is only weakly marked, and separated from the zona conoidea by a low crest. The capitulum is low and cylindrical. Posteriorly, the olecranon fossa is relatively broad and short.

***Ulna.*** KGA4-391, KGA4-1352, and KGA4-1668 are proximal ulnar fragments (Fig. 5.10). The first is a left and the latter two are rights, all are similar in their morphology. KGA4-391 is larger than the others, and too large to articulate with the distal humeri KGA4-389 and

KGA4-550, whereas KGA4-1352 and KGA4-1668 are approximately the right size (Table 5.6). Presumably the former is a male and the latter two are females. The olecranon of KGA4-391 is short and strongly retroflexed (Fig. 5.11). That of KGA4-1668 is somewhat longer, but also strongly retroflexed. KGA4-1352 has extensive damage to the olecranon, making its height and inclination impossible to judge. The proximal border of the trochlear articular surface is highly asymmetrical, with the medial aspect extending more proximally than the lateral. The radial notch is well preserved only on KGA4-1352, where it is deep and appears that the articular surface may have been doubled. None of these specimens preserve enough of the shaft to accurately judge its curvature. The interosseous border is not prominent on any of these specimens.

***Femur.*** Two specimens preserve the proximal end of the femur, KGA4-1981 and KGA4-765 (Fig. 5.12). Both preserve the head, neck and both trochanters, but relatively little of the shaft. The surface of the latter specimen is extensively cracked causing mild distortion. They are at the largest extreme of the modern *Papio hamadryas* size range (Table 5.6). The heads of both specimens have relatively elongate *foveae capitis*, and the articular surface extends onto the posterior surface of the neck, particularly that of KGA4-765. Both specimens have a low neck-shaft angle and the head is not cranially oriented (Fig. 5.13). The neck of KGA4-765 is longer relative to head diameter than that of KGA4-1981. Both specimens have greater trochanters which extend proximal to the head, and with tips that are medially curved, especially that of KGA4-765 (Fig. 5.14). Both specimens have prominent lesser trochanters, but that of KGA4-1981 is fairly cracked and damaged. Neither specimen is complete enough to determine if the carrying angle was reversed or not, a feature present only in *Theropithecus* (Jolly, 1972; Gilbert et al., 2011; Guthrie, 2011).

There are two right distal femoral fragments, KGA4-281 and KGA4-1669. The first specimen preserves little of the shaft, the second is missing the medial condyle, but preserves between 1/3 and 1/2 of the shaft. Both are large, being at the upper extreme of extant *Papio* variation. In addition to their large size, both specimens appear to have a reverse carrying angle and therefore are likely to represent *Theropithecus* (Jolly, 1972; Gilbert et al., 2011; Guthrie, 2011). In anterior view, therefore, the lateral condyle of KGA4-281 extends further distally than does the medial, also typical of *Theropithecus* (Gilbert et al., 2011; Guthrie, 2011). The patellar groove is broad and shallow, with margins that are not tall or sharp. The medial margin is more prominent than the lateral. This morphology is typical of *Theropithecus*, but opposite of most cercopithecoids where the lateral tends to be more prominent, and perhaps related to the reverse carrying angle (personal observation). The condyles are relatively deep and symmetrical on KGA4-281.

***Tarsus.*** KGA4-1618 and KGA4-2271 are both left astragali, the former is essentially complete, whereas the latter specimen lacks the head (Fig. 5.15). They show the cercopithecine morphology described by Strasser (1988). The trochlea is asymmetrical with a high and sharp lateral border. The articular surface of the medial maleolar cup reaches the calcaneal articular surface. In anterior view, the head is medially rotated. The distal margin does not show a groove for the *m. flexor fibularis*.

KGA4-285, KGA4-388 and KGA4-913 are right and two left calcanei, respectively (Fig. 5.16). They all show morphology typical for the family. The first two are larger than the last specimen. There is also some damage to the proximal end of KGA4-913. The proximal astragalar facet is relatively short, and is not tightly curved in lateral view, and lacks the posterior extension of its surface typical of colobines (Strasser, 1988).

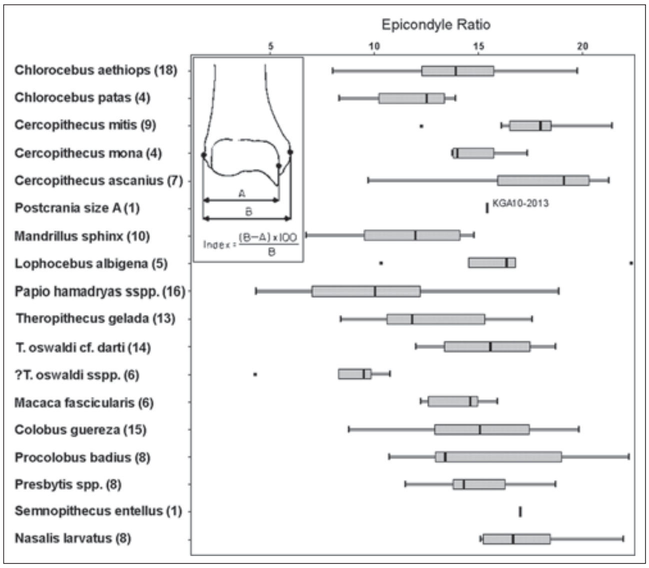


**Fig. 5.7.** Box and whisker plot of medial epicondyle projection: the ratio of B (biepicondylar breadth) minus A (medial distal articular limit to lateral epicondyle) ×100 divided by biepicondylar breadth. The central bar of each box represents the median (50th percentile). The left and right of each box represent the value of the 25th and 75th percentiles, respectively. 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. Some data from T. Harrison.

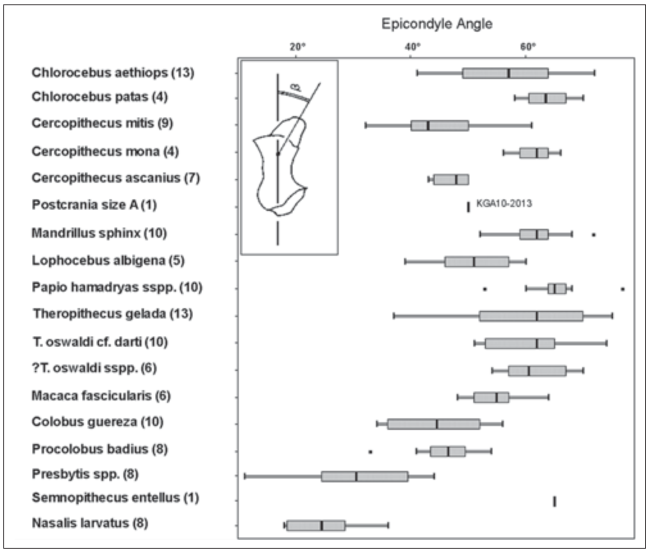


**Fig. 5.8.** Box and whisker plot of angle of medial epicondyle relative to axis of distal articular surface. Some data from T. Harrison.

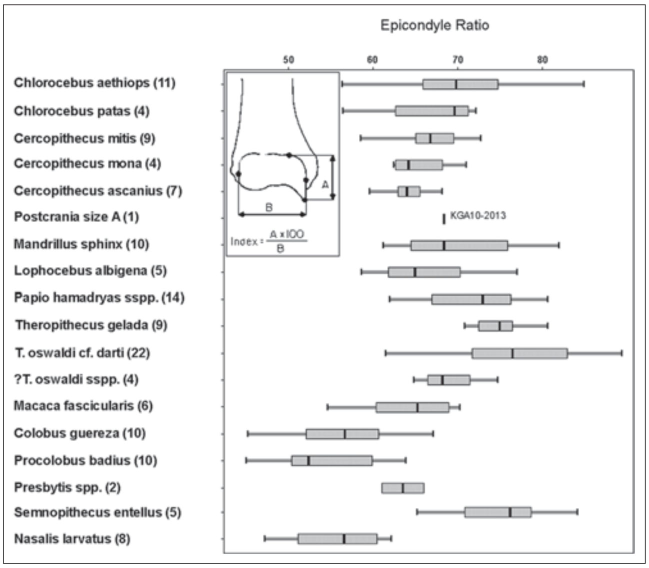


**Fig. 5.9.** Box and whisker plot of medial trochlear flange length (A) divided by distal humeral articular breadth (B). Some data from T. Harrison.


**Fig. 5.10.** Konso proximal ulnae, lateral view. Upper row left to right: KGA4-1668, KGA4-1352, KGA4-391 (all ?*Theropithecus oswaldi oswaldi*). Lower row left to right: KGA12-1147, KGA4-1303 (both Cercopithecidae indet. postcranial size C).

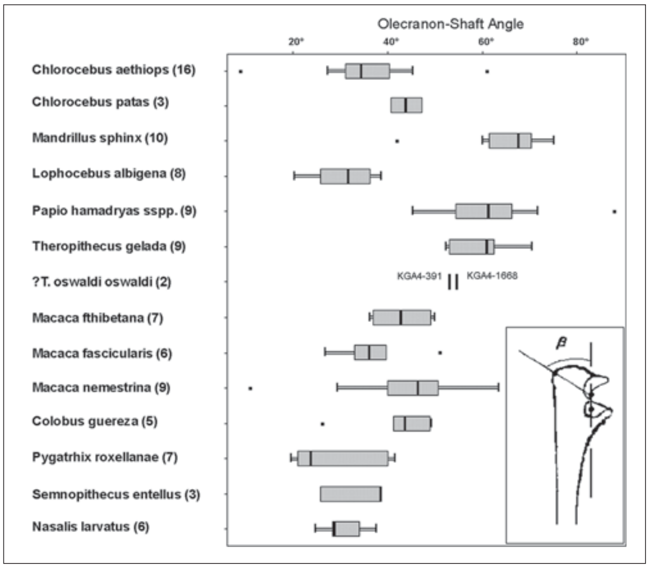


**Fig. 5.11.** Box and whisker plot of angle of retroflexion of the olecranon. Some data from N. Ting.

*?**Theropithecus oswaldi leakeyi***

The following material is tentatively allocated to *Theropithecus oswaldi leakeyi*, and all derives from the upper part of the Kayle Member and Karat Member (~1.25 Ma to ~1.45 Ma). On average, this material is slightly larger than equivalent elements from the Sorobo/Turoha Members assigned to *T. o. oswaldi*. Nonetheless, they are either slightly larger, or just within, the size ranges of extant *Papio* and *Mandrillus*. Thus, the same caveats apply to this group as to postcrania assigned to *T. o. oswaldi*, except for a few of the largest specimens. These are noted individually below.

***Humerus.*** KGA12-1195 is a right humeral shaft. It is very large and almost certainly represents *Theropithecus*. The shaft is strongly retroflexed with a well-marked deltoid tuberosity. KGA8-433, KGA8-540, KGA12-311 and KGA17-39 are a right and three left distal humeral fragments (Figs. 5.6–5.9). All are quite large and show moderately terrestrial adaptations (Table 5.6). The medial epicondyle is relatively short, except in KGA12-311 where it is somewhat longer, and ranges from moderately (KGA12-311) to strongly retroflexed (KGA8-540). The medial trochlear keel is long and sharp, but still relatively shorter than those of modern *Papio*. The zona conoidea is essentially flat and does not form a crest. The capitulum is also relatively flat and is not very spherical. Additionally, KGA12-311 has a lateral epicondyle that is more projecting and a *m. brachioradialis* flange that is less prominent than the others.

***Radius.*** KGA7-101 is the proximal end of a left radius. It is large and robust with a stout neck. In diameter, the head is at the maximum size for extant individuals of *Papio* and *Mandrillus* (Table 5.6). In proximal view, it is relatively circular in outline. The shaft is comparatively straight, and has a well-marked interosseous border and oblique line.

***Femur.*** KGA4-2229 is a proximal fragment of a large left femur, lacking both the head and proximal tip of the greater trochanter. The diameter of the shaft (Table 5.6) is larger than that for extant *Papio*, at the upper limit for *Mandrillus*, and overlaps the smallest individuals from *Theropithecus oswaldi leakeyi* from Olorgesailie (Jolly, 1972) and Daka (Gilbert and Frost, 2008).

***Tibia.*** KGA10-647 is a left distal tibial fragment. Based on the size (Table 5.6), this is almost certainly *Theropithecus* being outside the extant *Papio* and *Mandrillus* size ranges and overlapping distal tibiae from Olorgesailie (pers. observation). The medial malleolus is long with an anteriorly facing articular facet. The trochlear articular surface is strongly folded with a marked midline keel. It would have articulated with an asymmetrical trochlea. On the posterior surface, there is a broad and deep groove for the long flexor tendons.

***Tarsus.*** KGA12-405 is a left astragalus (Fig. 5.15). It is large in size, and shows a number of morphological features described by Strasser (1988) as cercopithecine. The trochlea is asymmetrical in height with the lateral margin being taller than the medial with a sharp lip. The medial malleolar cup reaches the plantar surface. The head is not rotated relative to the body. The posterior calcaneal facet is relatively flat in lateral view, and the proximal margin is in line with the trochlea.

KGA5-151 is a right calcaneus of a large cercopithecid and is beyond the extant *Papio* and *Mandrillus* size ranges (Fig. 5.16; Table 5.6). The proximal astragalar facet is comparatively flat and not tightly curved in lateral view, and is short relative to the overall length of the specimen. These are both features described by Strasser (1988) as more consistent with cercopithecines than colobines.

***Pes.*** KGA12-678 is a nearly complete right third metatarsal preserving the proximal articular region and shaft, lacking only the distal articular area. The preserved length is 58 mm, and the missing area would have added approximately 8–10 mm. KGA12-551 is a similarly preserved right fifth metatarsal, preserving the entire specimen except for the distal articular area. The preserved functional and maximum lengths of the specimen are 51 mm and 56 mm, respectively. Similar to KGA12-678, the missing area would have added approximately 8–10 mm to these figures. This specimen may have been from an immature individual as the break at the distal end may approximate the epiphyseal surface. KGA10-2365 and KGA7-388 are two additional fifth metatarsals, both lefts, preserving the proximal articular areas and three and two centimeters of the shaft respectively. All are approximately the same size, being larger in their proximal dimensions than the equivalent elements in *Papio* (Table 5.6). The shafts are stout and robust, being similar to those reported by Jolly (1972) from Olorgesailie. In stoutness they are comparable to extant *Theropithecus gelada*. KGA4-2576 is a distal fragment of a metapodial from a large cercopithecid preserving the articular area and approximately 4 cm of the shaft. Damage has obscured the articular keel. The preserved portion of the shaft is stout and robust and its morphology is consistent with the proximal metapodial fragments above.

***Phalanges.*** KGA12-794 is a nearly complete proximal phalanx, with some damage to the distal articular area. The shaft is broad and flat, similar to that of other large papionins. It is short and robust, in shape it lies within the range for *Theropithecus*, though close to that for *Papio* (Jolly, 1972: figure 15). In size, its dimensions place it in the range for both *T. oswaldi* and *T. brumpti* (Jolly, 1972; Jablonski, 1986; Jablonski et al., 2002). It is not certain whether this specimen represents a manual or pedal phalanx, though its dimensions are consistent with both.

**?*Theropithecus oswaldi* ssp. indet.**

A single postcranial specimen from the middle part of the Kayle Member (~1.6 Ma) can be tentatively allocated to *Theropithecus* for the same reasons as that assigned to subspecies above, a proximal humerus, KGA4-2294 (Fig. 5.17). Given its intermediate age, and size that overlaps other known samples of both *T. oswaldi oswaldi* and *T. o. leakeyi*, it not allocated to subspecies here. KGA4-2294 is a proximal fragment of a large left humerus (Table 5.6), outside of the extant *Papio* size range, but only slightly larger than the largest *Mandrillus*. The greater tuberosity extends considerably proximal to, and the lesser tuberosity is equal or slightly higher than the head. On the lateral surface of the greater tuberosity, the *m. infraspinatus* fossa is relatively deep. The bicipital groove is not broad, given the overall size of the specimen. It is deep and overhung by the greater tuberosity. In superior view, the head is not spherical, being relatively narrow in the mediolateral plane and rather elongate, with its posterior extreme coming to something of an apex.

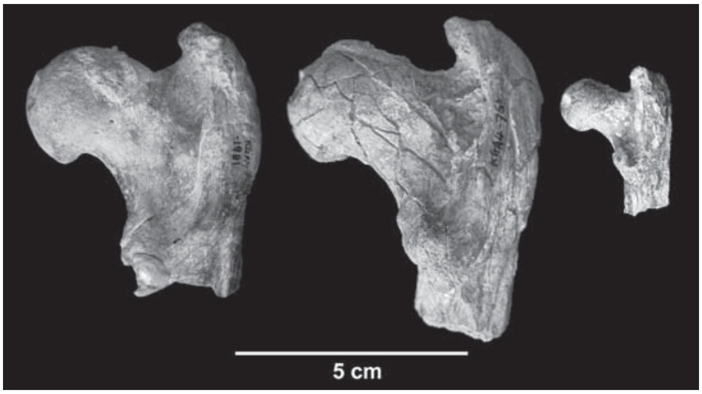


**Fig. 5.12.** Konso proximal femora, posterior view. Left to right: KGA4-1981 (?*Theropithecus oswaldi oswaldi*); KGA4-765 (?*T. o. oswaldi*); KGA4-1251 (Cercopithecidae indet. postcranial size A).

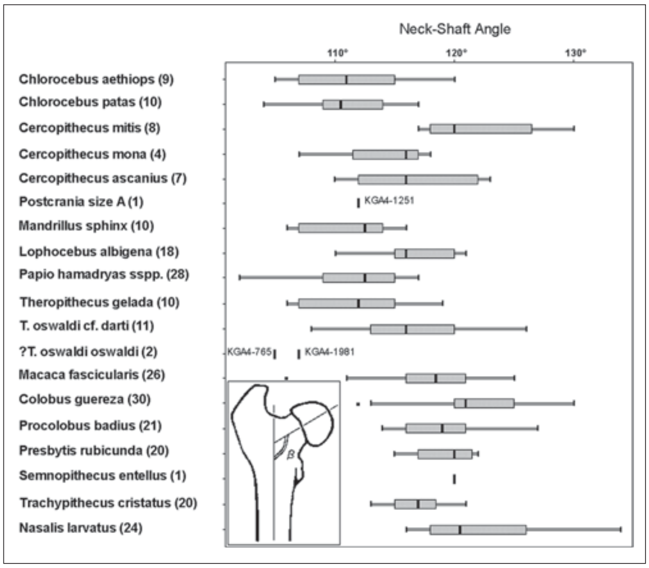


**Fig. 5.13.** Box and whisker plot of femoral neck-shaft angle. Some data from Ting (2001).

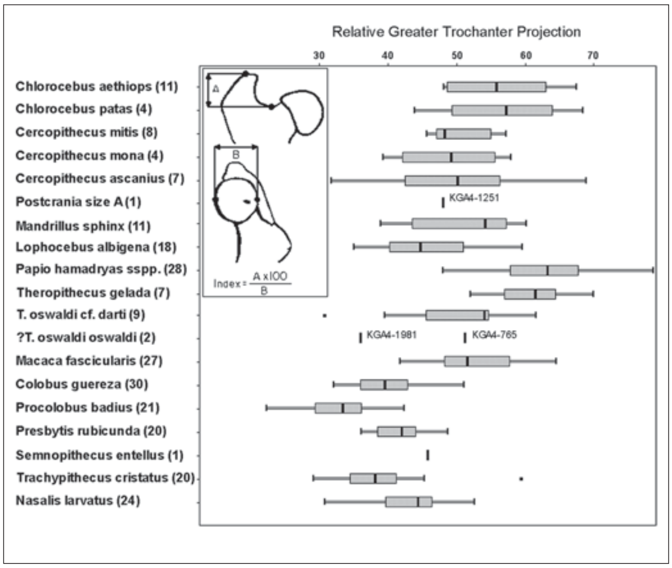


**Fig. 5.14.** Box and whisker plot of the height of the greater trochanter above the neck×100/anteroposterior diameter of the femoral head. Some data from Ting (2001).

**Postcrania size A**

There are two postcranial elements that are from significantly smaller individuals than the other material (Table 5.6). In size both are similar to extant *Chlorocebus aethiops*, to several species of *Cercopithecus*, and to *Macaca fascicularis*. Of the craniodental taxa, they may be compatible with Cercopithecinae tribe indet, but are too small for the others. The first, KGA10-2013 (~1.44 Ma), is a left distal humeral fragment, preserving the articular surface, epicondyles, and about 2 cm of the shaft (Figs. 5.6–5.9). Of the supra-articular fossae, the radial fossa is taller and deeper than the coronoid. The medial epicondyle is moderately retroflexed, but not as much as in most *Ch. aethiops*. The capitulum is relatively prominent and spherical. The lateral keel of the trochlea is well marked, but not as prominent as in some colobines, or most guenons (Gebo and Sargis, 1994). The medial keel of the trochlea is longer and sharper than most extant *Cercopithecus*, but similar to *Ch. aethiops* in its development. Posteriorly, the olecranon fossa is large, deep and relatively tall, occupying much of the posterior surface of the distal humerus.

The second specimen, KGA4-1251 (~1.6 Ma), is a right proximal femur from the Kayle Member (Figs. 5.12–5.14). The head is spherical with a large round fovea capitis. The articular surface extends onto the posterior surface of the neck. The neck is short and the neck-shaft angle is relatively high. The greater trochanter is slightly taller than the head, being slightly less projecting than is the case for most *Chlorocebus aethiops*. Its medial border is relatively straight, and the *m. quadratus femoris* insertion is not prominent. The lesser trochanter is relatively long and medially oriented.

**Postcrania size B**

There are also two elements that are larger than those assigned to size A, but still significantly smaller than the remainder (Table 5.6). These two elements are comparable to extant *Colobus*

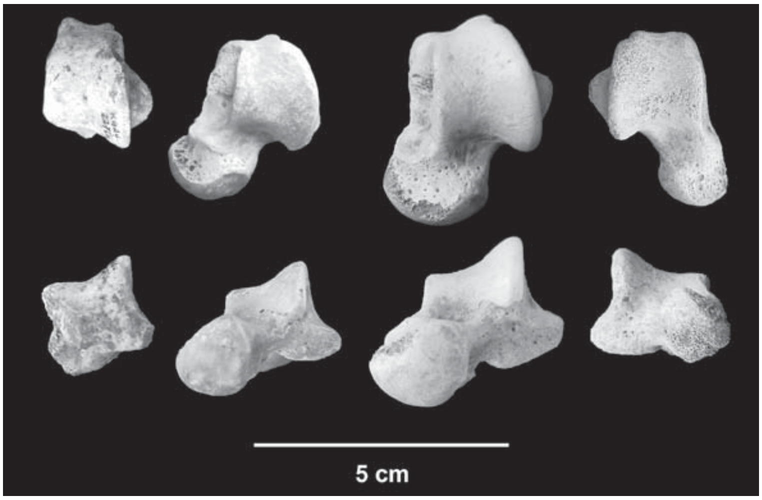


**Fig. 5.15.** Konso astragali, dorsal (above) and distal (below) views. Left to right: KGA4-2271 (?*Theropithecus oswaldi oswaldi*); KGA4-1618 (?*T. o. oswaldi*); KGA12-405 (?*T. o. leakeyi*); KGA10-1644 (Cercopithecidae indet. postcranial size C).


**Fig. 5.16.** Konso calcanei, dorsal view. Left to right: KGA4-388 (?*Theropithecus oswaldi oswaldi*); KGA4-913 (?*T. o. oswaldi*); KGA4-285 (?*T. o. oswaldi*); KGA5-151 (?*T. o. leakeyi*).

*guereza, Lophocebus albigena*, and several medium-sized species of *Macaca*. The first, KGA4-418 (~1.6 Ma), is from the middle part of the Kayle Member and is a proximal fragment of a right humerus (Fig. 5.17). The head is spherical and bulbous, being mediolaterally broad relative to its anteroposterior length. The greater tuberosity is slightly shorter than the head (depending on the exact angle of the shaft). The *m. infraspinatus* fossa on the lateral surface of the greater tubercle is large and deep. The bicipital groove is broad and shallow. All of these features are typical of relatively arboreally adapted cercopithecoids. This specimen is clearly not *Theropithecus* or any other large papionin. It is from a substantially larger individual than KGA4-1251 (also from the middle part of the Kayle Member), and most likely beyond the range expected in all but the most sexually dimorphic taxa.

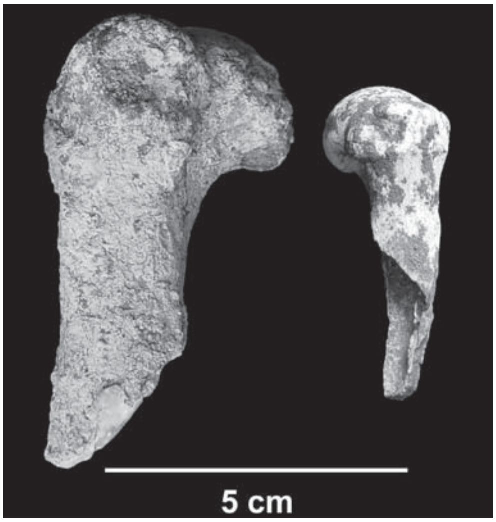


**Fig. 5.17.** Konso proximal humeri, lateral view. Left, KGA4-2294 (?*Theropithecus oswaldi* ssp. indet.); right, KGA4-418 (Cercopithecidae indet. postcranial size B).

KGA11-189 (~1.45 Ma) is a proximal fragment of a left tibia, with damage to the tuberosity and medial condyle. It is too small to represent *Theropithecus*, being similar to extant *Colobus guereza* in size. It could therefore potentially represent the same taxon as KGA4-418. Morphologically, the tibial tuberosity is flat and broad and the tibial plateau is short in the anteroposterior dimension and broad in the mediolateral (Table 5.6).

**Postcrania size C**

Postcrania allocated to this size category are generally in the area of overlap between larger individuals of *Papio* or *Mandrillus* and the smaller part of the estimated range for *Theropithecus oswaldi*. Much of this material may well be of *Theropithecus*, but lacks sufficient morphological criteria to be tentatively allocated there.

KGA4-2575 (~1.45 Ma) is a fragment of a left scapula preserving the glenoid fossa and a small portion of the blade. In size it is similar to, but a little smaller than the scapulae from the Sorobo/Turoha Members, but the glenoid fossa is narrower (breadth 17 mm, length 28 mm) and lacks the medial bulging present in those specimens.

KGA12-1147 (~1.25 Ma) is a proximal fragment of a right ulna missing the proximal portion of the trochlear notch and the olecranon (Fig. 5.10). In size it is too small to articulate with the large humeri tentatively identified as *Theropithecus*. The radial notch is present, but damaged. It can be seen that it was relatively shallow. The medial side of the shaft is marked by a sharp interosseous border. KGA4-1303 (~1.45 Ma) is a proximal fragment of a left ulna, missing the proximal part of the notch and olecranon, and generally similar to KGA12-1147 in size and morphology (Fig. 5.10).

KGA4-390 (>~1.9 Ma) is a right radial fragment with the head and a small portion of the neck. At just under 17 mm diameter, this specimen is in the middle of the range for extant *Papio*. It is therefore likely within the lower part of the *Theropithecus oswaldi oswaldi* range, but also in the range for other taxa present at Konso.

KGA12-1181 (~1.25 Ma) is a proximal fragment of a right second metacarpal with the articular area and approximately 2 cm of the shaft preserved. In size, it is significantly smaller (Table 5.6) than any of the five measurable second metacarpals of *Theropithecus oswaldi leakeyi* from Olorgesailie, and KNM-ER 866ai a second metacarpal of a probable male of *T. o. oswaldi* from the Okote Member of Koobi Fora (pers. observation). It is also smaller than the equivalent element from male specimens of *T. brumpti* (NME L865-2 and KNM-WT 39368) a species comparable in size to *T. o. oswaldi* (Jablonski, 1986; Jablonski et al., 2002). KGA12-1181 may, therefore, be too small for *T. o. leakeyi*. It is possible, however, that this specimen is that of a small female.

KGA4-1253 (~1.6 Ma) is a left proximal femoral shaft fragment, from the middle part of the Kayle Member. It is at the upper extreme of the extant *Papio* range in size. It could potentially be a relatively small female *Theropithecus oswaldi leakeyi*, and is most likely too large to be from one of the other taxa known from Konso, but this can't be ruled out entirely.

KGA10-1644 (~1.44 Ma) is a right astragalus (Fig. 5.15). The head is highly rotated as described for the colobine morphotype by Strasser (1988). Additionally, the medial malleolar cup is widely separated from the calcaneal facet. The trochlea is tall and asymmetrical, but the proximal end is damaged so that it is hard to be certain if a sulcus for *m. flexor fibularis* is present.

KGA4-1501 (~1.9 Ma) is a large right cercopithecid navicular, most likely *Theropithecus* based on size. KGA4-236 (~1.9 Ma) is the distal articular end of a metapodial. KGA12-208 (~1.25 to ~1.4 Ma) is a lumbar vertebra that is probably too small to be *Theropithecus* or *Papio*.

## 5.4 DISCUSSION

Cercopithecids are relatively rare at Konso (Suwa et al., 2003), but the series is significant nonetheless as it samples a geographic region between the Turkana Basin and the Afar Depression, two of the best sampled major collecting regions in Africa, both of which have large and distinctive cercopithecid faunas (Frost, 2001, 2007b). While Konso is closer to the Turkana Basin, it is also separated from it by being in the Main Ethiopian Rift. Another interesting feature is that it samples a time span which covers an important transition between chronosubspecies of *Theropithecus oswaldi*, the most abundant cercopithecid lineage known.

While there are several taxa present at Konso, they are not evenly distributed through the stratigraphic sequence. *Theropithecus oswaldi* occurs throughout, though represented by two chronosubspecies. The other taxa are so rare in comparison, that their pattern of presence or absence at different times may well be the result of small sample sizes, the most diverse interval, stratigraphic interval 4, is also the best sampled. The second most common morph in the series, the non-*Theropithecus* papionin occurs from the Sorobo Member, upper part of the Kayle Member and the Karat Member. All of the other taxa are known only from the upper part of the Kayle Member and/or Karat Member. Interestingly, while there is only one tooth of *T. oswaldi* and four postcranial specimens known from the middle part of the Kayle Member, there is a minimum of three taxa present based on size alone (i.e., sizes A, B, and C/?*T. o. leakeyi*). This suggests that the possibility that the sample was equally diverse through time cannot be ruled out, and that stratigraphic interval 1 appears less diverse is due to its smaller sample size.

Seventeen of the 36 specimens from the Sorobo/Turoha Members are cranial. Of these, 14 represent *Theropithecus* or approximately 82%. Similarly, 83 of the 107 specimens from the upper part of the Kayle Member and Karat Member are cranial, and fully 71 (i.e., 86%) of these are

**Table 5.6.** Dimensions taken on various postcranial elements (mm)

| Humeri | KGA4-389 | KGA4-550 | KGA8-433 | KGA8-540 | KGA10-2013 | KGA12-311 | KGA17-39 | KGA4-2294 | KGA4-418 |
|---|---|---|---|---|---|---|---|---|---|
| Proximal m-l dimension | | | | | | | | 40 | 21 |
| Proximal a-p dimension | | | | | | | | 39 | 21 |
| Biepicondylar breadth | 40 | 35 | 42 | 43 | 23 | 44 | 47 | | |
| Lateral epicondyle to medial edge of trochlea | 37 | 32 | 38 | 39 | 19 | 39 | 45 | | |
| Distal articular breadth | 29 | 25 | 27 | 30 | 16 | 31 | | | |
| Medial trochlear flange length | 20 | 19 | - | 21 | 11 | 20 | (18) | | |
| **Ulnae** | KGA4-391 | KGA4-1303 | KGA4-1352 | KGA4-1668 | KGA12-1147 | | | | |
| Height of olecranon above trochlear fossa | 15 | | | 14 | | | | | |
| P-d trochlear fossa length | 20 | | 17 | 16 | | | | | |
| M-l breadth across radial facet and trochlear notch | 26 | 17 | 23 | | 17 | | | | |
| **Radii** | KGA4-390 | KGA7-101 | | | | | | | |
| Maximum head diameter | 17 | 21 | | | | | | | |
| Perpendicular diameter | 16 | 21 | | | | | | | |
| P-d neck length | 9 | 7 | | | | | | | |
| P-d length from head to mid tuberosity | | 21 | | | | | | | |
| **Femora** | KGA4-281 | KGA4-765 | KGA4-1251 | KGA4-1253 | KGA4-1669 | KGA4-1981 | KGA4-2229 | | |
| A-p head diameter | | 25 | 11 | | | 26 | | | |
| Maximum m-l breadth | | 54 | 24 | | | 50 | | | |
| Greater trochanter projection | | 13 | 6 | | | 9 | | | |
| A-p shaft diameter | | | | 18 | 20 | | 22 | | |
| M-l shaft diameter | | | | 17 | 16 | | 18 | | |
| Bicondylar breadth | 42 | | | | | | | | |
| A-p condyle length | 35 | | | | (30) | | | | |
| **Tibiae** | KGA10-647 | KGA11-189 | | | | | | | |
| Proximal a-p depth | | 27 | | | | | | | |
| Proximal m-l breadth | | 35 | | | | | | | |
| Distal a-p depth | 26 | | | | | | | | |
| Distal m-l breadth | 33 | | | | | | | | |
| **Calcanei** | KGA4-285 | KGA4-388 | KGA4-913 | KGA5-151 | | | | | |
| P-d tuberosity length | 18 | 17 | 14 | 28 | | | | | |
| P-d proximal astragalar facet length | 16 | 16 | 13 | 20 | | | | | |
| Distal length | 15 | 15 | 14 | 16 | | | | | |
| Length | 49 | 47 | 40 | 61 | | | | | |
| **Metapodials** | KGA7-388 | KGA10-2365 | KGA12-1181 | KGA12-551 | KGA12-678 | | | | |
| Proximal m-l breadth | 12 | 15 | 7 | 13 | 14 | | | | |
| Proximal dorsoplantar depth | 10 | 11 | 10 | 12 | 15 | | | | |
| **Phalanges** | KGA12-794 | | | | | | | | |
| Proximal m-l breadth | 10 | | | | | | | | |
| Length | 25 | | | | | | | | |

A-p: Anteroposterior. M-l: Mediolateral. P-d: Proximodistal. See the text for further information.

*Theropithecus*. Also present in the sample from the upper part of the Kayle Member and Karat Member are six teeth of the larger non-*Theropithecus* papionin, the single specimen of the small cercopithecine, and the two colobine fossils. Thus, *Theropithecus* predominates throughout the sequence, with colobines comprising less than 2% of the sample (where present).

In spite of *Theropithecus oswaldi* being well known across Africa, the Konso material is informative. The material from the upper part of the Kayle Member and Karat Member is the oldest sample of *T. o. leakeyi* other than the series from Upper Bed II Olduvai, and adds considerably to what was known from that site. The Konso material shows important transitional morphology between "classic" *T. o. oswaldi* (e.g., Kanjera, Olduvai Bed I, Swartkrans, Koobi Fora, and Sorobo/Turoha Members) morphology to the highly distinctive morphology of later Middle Pleistocene *T. o. leakeyi* (e.g., Olorgesailie, Dawaitoli Formation, Asbole, Daka, Hopefield, Tighenif). Nonetheless some distinctive *T. o. leakeyi* features were already well established, thus the assignment to the latter subspecies. These include: the extremely small lower incisors and the development of a fossa on the mental surface between the canines as result; the presence of lingual enamel on the lower incisors; the extreme superstructures on the male calvaria; relatively short mesiobuccal flange length of the $P_3$s; and the more complexly folded molar enamel.

The *Theropithecus oswaldi* material samples the lineages across approximately one half million years, and captures the transition between chronosubspecies. The two populations show morphology and body size in line with expectations for their ages. It has been shown by Leakey (1993) that there is a trend towards decreasing male relative canine size in *T. oswaldi*. As Konso *T. o. leakeyi* is an early population of the subspecies, male canines are still large compared to those from later samples such as Olorgesailie, Olduvai Bed IV, Tighenif, and the Dawaitoli Formation (Jolly, 1972; Delson and Hoffstetter, 1993; Frost, 2001).

Functional morphology of the Konso postcrania corroborates the view of *Theropithecus oswaldi oswaldi* and *T. o. leakeyi* as terrestrial cercopithecines (Jolly, 1972; Krentz, 1993; Elton, 2002; Guthrie, 2011). The elbow, hip, and ankle joints all show features that increase stability and decrease mobility, although not all of these are developed to the same degree seen in extant *T. gelada* or *Papio hamadryas*. The elbow also has features that maintain muscular efficiency when in it is in an extended posture, as would be expected of a terrestrial quadruped (Jolly, 1972; Rose, 1988). Additionally, metatarsal and phalangeal proportions are short and robust as is typical of cercopithecoids that frequently utilize terrestrial substrates (Jolly, 1972). The features associated with use of the forelimb for manual foraging, as described by Guthrie (2011) are not well represented in this sample, but the broad and flaring scapular glenoid and relatively long (even if retroflexed) humeral medial epicondyle may be examples.

The Konso cercopithecids are also important from a biogeographic perspective. In general, the sample from Konso is similar to most Middle Pliocene and Pleistocene East African sites, and different from South African sites, in that *Theropithecus* greatly predominates (Benefit, 1999; Frost, 2007b). *Theropithecus brumpti* is apparently absent from the Konso Formation, but is common in Middle to Late Pliocene sediments of the Turkana Basin and Tugen Hills older than approximately 2.0 Ma (Eck, 1976; 1977; Eck and Jablonski, 1987; Harris et al., 1988, 2003; Jablonski et al., 2008; Gilbert et al., 2011). If sampling is adequate, then there are two possible explanations for this absence, though they are not mutually exclusive. The first is that the 2.0 Ma last appearance of *T. brumpti* is accurate and all of the Konso material is younger than this. Alternatively, *T. brumpti* may have been endemic to the Turkana Basin and Tugen Hills, as in spite of large samples from sediments of the Pliocene age, there are no confirmed occurrences of *T. brumpti* from the Afar Region (Kalb et al., 1982; White et al., 1993; de Heinzelin et al., 1999; Frost, 2001; Frost and Delson, 2002) or South Africa (Freedman, 1957; Maier, 1970; Eisenhart, 1974; Delson, 1984). Furthermore, the relatively advanced morphology of the Konso *T. oswaldi leakeyi* material may be more similar to early but morphologically derived *T. o. leakeyi* series from

Upper Bed II of Olduvai Gorge than to the similarly aged material from the Okote Member of Koobi Fora which retains more *T. o. oswaldi* features. If this is accurate, it suggests that the transition between subspecies was slightly diachronous.

The non-*Theropithecus* material is too fragmentary to provide accurate identifications, but does show that while *Theropithecus* predominates, a diversity of cercopithecid species was present, including at least two other cercopithecines and a colobine.

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