



A new large Pliocene colobine species (Mammalia: Primates) from Asa Issie, Ethiopia

Une nouvelle espèce de grand colobiné (Mammalia : Primates) du Pliocène d'Asa Issie en Éthiopie

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Abstract

The Colobinae (Mammalia: Primates) are relatively unknown from the African middle to late Miocene. When they appear in the Pliocene they are unambiguous and already fairly diverse taxonomically, geographically, and ecologically. Discoveries from Pliocene sediments in eastern and southern Africa document a radiation of large-bodied colobines very different from those known today. Paleontological research in Ethiopia has recently led to the discovery and identification of another large-bodied colobine species from the early Pliocene site of Asa Issie, discovered in 2000. This new colobine is larger than but morphologically very similar to its sister taxon *Kuseracolobus aramisi*, an older taxon also described from the Middle Awash. This new species has significant implications for our understanding of the Pliocene colobine adaptive radiation.

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Résumé

Les Colobinae (Mammalia : Primates) sont très mal connus en Afrique au Miocène moyen et récent. Au cours du Pliocène, ils deviennent clairement identifiables et déjà relativement diversifiés sur les plans taxonomique, géographique et écologique. Les découvertes effectuées dans les sédiments pliocènes d'Afrique de l'Est et du Sud permettent de documenter une radiation de colobinés de grande taille, très différents de ceux connus aujourd'hui. Les recherches paléontologiques en Éthiopie ont récemment (en 2000) permis de découvrir et d'identifier une espèce supplémentaire de grand colobiné, provenant du site pliocène récent d'Asa Issie. Bien que morphologiquement similaire à son espèce sœur *Kuseracolobus aramisi* – un taxon plus ancien également décrit dans le Moyen Awache – ce nouveau colobiné est de plus grande taille. Cette nouvelle espèce a des implications significatives pour notre compréhension de la radiation adaptative des colobinés du Pliocène.

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Keywords: Pliocene; Cercopithecidae; Ethiopia; Paleontology; Colobinae; *Kuseracolobus*

Mots clés : Pliocène ; Cercopithecidae ; Éthiopie ; Paléontologie ; Colobinae ; *Kuseracolobus*

1. Introduction

Asa Issie (ASI) Vertebrate Paleontology (VP) localities 2 and 5 were discovered in December of 2000 and 2002,

respectively. Ongoing stratigraphic and geochronological work has placed these localities within the Middle Awash sequence below the VT-3 (= "Wargolo") tuff, dated at 3.75 Ma (White et al., 1993). Associated fauna at Asa Issie is ecologically similar to that documented from the nearby 4.4 Ma. Aramis localities (WoldeGabriel et al., 1994), but suid and proboscidean taxa appear to be more derived. Thus, a biochronological age estimate for these ASI localities is set

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between 3.8 and 4.4 Ma. The Asa Issie fauna assemblage is primarily terrestrial in origin, and is dominated (like Aramis) by primates and tragelaphine bovids.

The Asa Issie cercopithecoid fauna comprises at least one species of Cercopithecinae and two species of Colobinae. The most abundant primate taxon is a large colobine very similar in morphology to *Kuseracolobus aramisi* Frost, 2001 from Aramis, Ethiopia (Frost, 2001a, 2001b). The ASI localities 2 and 5 large colobine specimens display a few derived characters relative to the Aramis sister species, and they are dramatically larger. These Asa Issie colobine specimens are therefore described as a new species within the genus *Kuseracolobus* Frost, 2001.

2. Systematic paleontology

Order PRIMATES Linnaeus, 1758.

Suborder ANTHROPOIDEA Mivart, 1864.

Infraorder CATARRHINI E. Geoffroy, 1812.

Family CERCOPITHECIDAE Gray, 1821.

Subfamily COLOBINAE Jerdon, 1867.

Genus *Kuseracolobus* Frost, 2001.

Kuseracolobus hafu nov. sp.

Etymology: In recognition of the Afar people who live in the Middle Awash study area. “Hafu” is from the Afar language and is the name for the dominant male in a troop of baboons.

Holotype: ASI VP 2/242 (Fig. 1). A female partial left mandible with LM₁₋₃, inferior mandibular corpus from symphysis to M₂/M₃, and the lateral ramal eminence.

Paratypes/hypodigm: Listed in Table 1.

Locality/horizon: All specimens are from the Asa Issie area of the Middle Awash in Ethiopia. The horizon is biochronologically placed at 3.75–4.4 Ma and lies >10 km southwest of Aramis, at the southwestern margin of the Central Awash Complex (CAC; Renne et al., 1999).

Specific diagnosis: *K. hafu* is distinguished from *K. aramisi* primarily by size. Dental metrics of *K. hafu* are on average 4 standard deviations (S.D.) above the mean of *K. aramisi*. *K. hafu* is also distinguished from *K. aramisi* in that M₂ distal lophids are wider than the mesial lophids, whereas *K. aramisi* is characterized by more equal mesial and distal lophid buccolingual widths on M₂.

Description: *K. hafu* is known from fragmentary jaws, isolated teeth, and postcranial elements. None of the postcranial material was found in direct association with craniodental remains. However, because of their unusually large size and occurrence in the same horizon, within close proximity to the attributed craniodental material, the postcrania described below are considered conspecific.

Mandibles: The holotype specimen ASI VP 2/242 (Fig. 1) is a female left mandibular fragment preserving the inferior mandibular corpus from symphysis to M₂/M₃ and the LM₁₋₃ crowns. This specimen is small but with the same morphology as the larger specimens, and therefore is considered to be

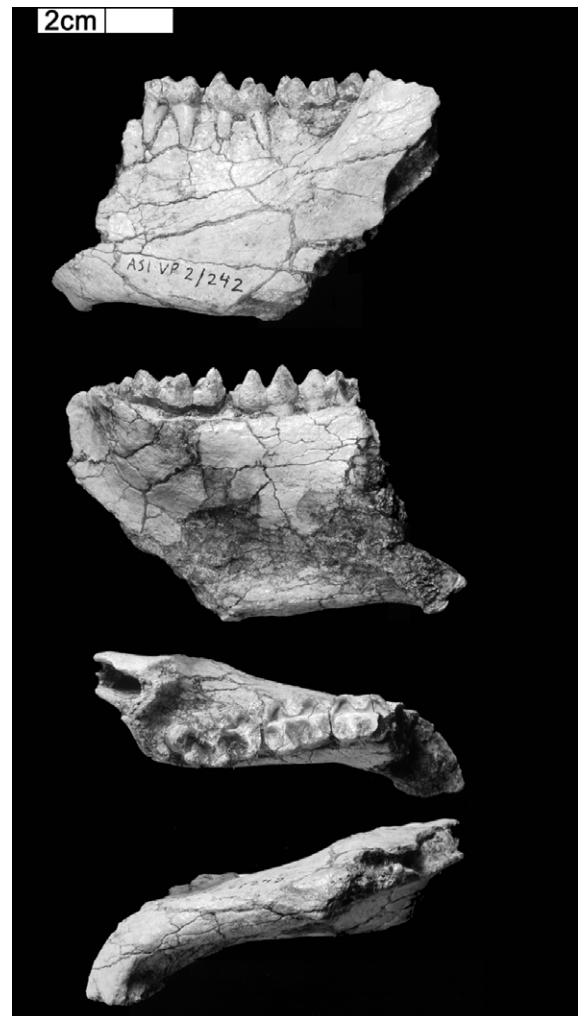


Fig. 1. Four views of ASI VP 2/242 type specimen of *Kuseracolobus hafu*, female left mandibular fragment with M1-3 crowns. From top to bottom: labial, lingual, occlusal, and inferior. Scale is 2 cm.

Fig. 1. Quatre vues du spécimen type ASI VP 2/242 de *Kuseracolobus hafu*, fragment mandibulaire gauche d'une femelle avec couronnes M1-3. De haut en bas: labiale, linguale, occlusale et inférieure. Échelle = 2 cm.

a female of *K. hafu*. This mandible has a wide extramolar sulcus and a prominent lateral ramal eminence that starts at midsection on the mandibular body and is positioned below the M₂₋₃ contact, similar to the morphology preserved on ARA VP 1/87, the type specimen of *K. aramisi* but different from modern baboons who are not as rugose. Height of the mandibular body increases distally, like most colobines including *Kuseracolobus*, but unlike *Cercopithecoides* Mollet, 1947. The holotype specimen also has slight lateral corpus hollowing below and mesial to M₁, and lateral bulging at the inferior margin of the corpus. The lingual molar cusps are high, as is typical for colobines, with deep lingual notches. The buccal cusps are moderately to very worn.

ASI VP 2/100 (Fig. 2a) is a male left mandibular fragment broken along the symphysis with LI₁₋₂ roots, LC broken at midcrown, LP₃₋₄ crowns, and LM₁ roots preserved. The specimen is broken at LM₂, with all of the mandibular body missing distal to this point. There is a mental foramen below the

Table 1

List of specimens assigned to *Kuseracolobus hafu*
Liste des spécimens attribuée à *Kuseracolobus hafu*

Specimen number	Element
ASI VP 2/53	Right proximal ulna
ASI VP 2/55	Right proximal ulnar shaft
ASI VP 2/59	A = radius, B = ulna, C = humerus
ASI VP 2/79	Phalanx
ASI VP 2/80	Intermediate phalanx
ASI VP 2/85	RM ₃
ASI VP 2/89	RM ₃
ASI VP 2/90	LM ₃
ASI VP 2/91	LM ₃
ASI VP 2/95	Right maxilla with RI ¹ -RC ¹ alveoli, RP ³ -RM ³ crowns
ASI VP 2/98	Left mandible with I ₂ roots, C ₁ -M ₁ crowns
ASI VP 2/99	Right mandible with RM ₁₋₃
ASI VP 2/100	Left mandible with LI ₁₋₂ roots, LC-P ₄ , LM ₁ roots, broken at M ₂
ASI VP 2/101	Mandible with RI ₁₋₂ roots, RC ₁ -RP ₃ crowns, and an associated LP ₃
ASI VP 2/114	Lateral condyle of right femur
ASI VP 2/232	Intermediate phalanx
ASI VP 2/242	Left mandible with LM ₁₋₃
ASI VP 2/243	Mandible with LI ₂ -RC ₁ alveoli and RP ₃₋₄ crowns
ASI VP 2/245	Right maxilla with RI ¹ -RM ³ crowns
ASI VP 2/246	LI ¹ w/maxillary bone
ASI VP 2/247	Right maxilla with P ⁴ -M ²
ASI VP 2/337	Associated LC ¹ -M ²
ASI VP 5/28	Right proximal radial shaft
ASI VP 5/37	Upper and midshaft of left humerus

P₄ mesial root. The superior transverse torus extends posteriorly to the distal portion of the P₃ and the inferior transverse torus extends to the distal aspect of P₄. ASI VP 2/243 and ASI VP 2/242 have the same configuration, which is also present in *K. aramisi*. ASI VP 2/100 has lateral corpus hollowing below P₃-M₁ and lateral bulging near the inferior margin. The P₃ has a long flange typical of male colobines. This specimen is similar in overall morphology to *K. aramisi* specimen ARA VP 6/796 but much larger. The symphysis is less sloping than is typical of many colobines, such as *Cercopithecoides*, and is thereby very similar to the morphology of the *K. aramisi* holotype, ARA VP 1/87 (Fig. 3).

ASI VP 2/98 (Fig. 2d) is a large left mandibular fragment broken at the I₁ alveolus. The I₂ roots and the C₁-P₄ crowns are present, although they are cracked and not well preserved. There is a fragment of the mesial portion of M1 with no enamel preserved. The mandibular bone is affected by expanding matrix distortion, EMD Stage 2 (White, 2003), and the corpus is missing at and below the level of the mental foramen, which is only partially preserved. ASI VP 2/98 has lateral corpus hollowing like ASI VP 2/100, again similar to the condition in *K. aramisi*. Because this specimen is quite large and the P₃ has a very long flange it is considered to be male.

ASI VP 2/99 (Fig. 2b) is a large male right mandibular fragment preserving RM₁₋₃ crowns. This specimen has a wide

extramolar sulcus like *K. aramisi*. The mandibular body is broken just mesial to M₁ and just distal to M₃. The molars have very high cusp relief characteristic of colobines, and the buccal cusps are moderately worn. The base of the corpus is missing. The M₃ has a prominent sixth cusp.

ASI VP 2/243 is a mandibular fragment preserving the symphysis (Fig. 2c). On the left side it is broken posterior/distal to the LC₁ alveolus. The LI₂-RC₁ alveoli and RP₃₋₄ crowns are preserved. It is broken just distal to RP₄. The symphysis has the same shape and midline cross-section as ASI VP 2/100 with no median mental foramen and rounded inferior morphology. However, ASI VP 2/243 is smaller than ASI 2/100. ASI VP 2/243 lacks mental ridges on the symphysis, as do most colobines except for *Procolobus* Rochebrune, 1887. The P₃ has female morphology and therefore is considered a female of *K. hafu*, compared to the conspecific ASI VP 2/100 male.

However, it is important to point out that ASI VP 2/243 is significantly smaller than ASI 2/100, exceeding the sexual dimorphism seen in most colobines. There are other isolated teeth and jaw fragments that are designated as Colobinae genus indeterminate from ASI VP 2 and 5. This female is at the high end of the size range and therefore is tentatively being attributed to *K. hafu* because it shares the same symphyseal morphology despite indicating an extreme amount of sexual dimorphism. More specimens of the other colobine taxa are needed to confirm or refute this attribution.

ASI VP 2/101 (not shown) is a mandibular fragment with the RI₁₋₂ roots, RC₁-RP₃ crowns, and an associated LP₃. The P_{3s} have well developed paraconid “shoulders” on the mesiobuccal flange, as is typical of colobines. The C₁ is small and has female morphology.

To summarize, the *K. hafu* mandible is large with a relatively deep mandibular corpus like *Colobus* Illiger, 1811, *Paracolobus* Leakey, 1969, *Rhinocolobus* Leakey, 1982, and *Kuseracolobus*. The symphysis has both superior and inferior transverse tori, like all colobine genera except for *Microcolobus* Benefit and Pickford, 1986 which lacks the inferior torus. The *K. hafu* symphyseal morphology is most similar to that seen in *K. aramisi*. Like *K. aramisi*, the *K. hafu* symphysis is gently curved, almost flat, in contrast to the break in slope on the anterior surface of the symphyses of *Paracolobus* and *Rhinocolobus*, and the more vertical symphysis of *Cercopithecoides*. The *Kuseracolobus* anterior symphyseal surface is smooth, lacking the mental ridges seen in *Procolobus* and the rugosity seen in *Rhinocolobus* and the median mental foramen known in *Rhinocolobus* and some species of *Cercopithecoides*. The *K. hafu* superior transverse torus extends posteriorly to the distal portion of P₃ (as demonstrated by ASI VP 2/100) and the inferior transverse torus extends to the distal portion of P₄ (ASI VP 2/100, ASI VP 2/243, and ASI VP 2/242), like *K. aramisi* and *Cercopithecoides kimeui* Leakey, 1982. The mandibular corpus of *K. hafu* deepens posteriorly (ASI VP 2/242), as is characteristic of *K. aramisi* and most other colobines, but quite different from the robust and shallow corpus of *Cercopithecoides* and

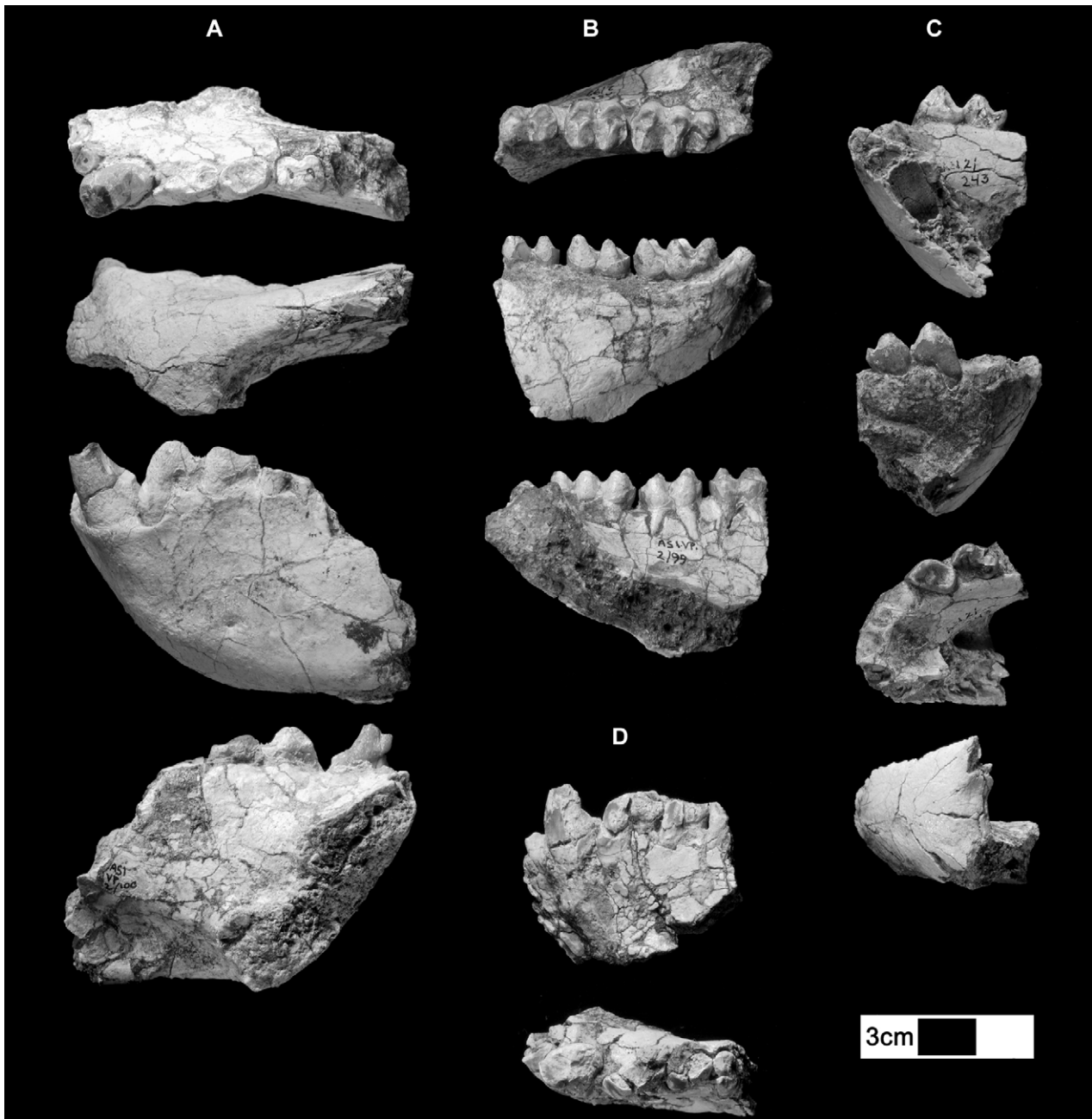


Fig. 2. Mandibular specimens included in the *Kuseracolobus hafu* hypodigm. **A.** ASI VP 2/100, male left mandibular fragment with broken C and P3-4 crowns. **B.** ASI VP 2/99, male right mandibular fragment with M1-2 crowns. **C.** ASI VP 2/243, mandibular fragment preserving symphysis and P3-4 crowns. **D.** ASI VP 2/98, left mandibular fragment with C-P4 crowns. Scale is 3 cm.

Fig. 2. Spécimens mandibulaires inclus dans l'hypodigme *Kuseracolobus hafu*. **A.** ASI VP 2/100, fragment mandibulaire gauche d'un mâle avec couronnes C cassée et P3-4. **B.** ASI VP 2/99, fragment mandibulaire droit d'un mâle avec couronnes M1-2. **C.** ASI VP 2/243, fragment mandibulaire préservant symphyses et couronnes P3-4. **D.** ASI VP 2/98, fragment mandibulaire gauche avec couronnes C-P4. Échelle = 3 cm.

Procolobus. *K. hafu* has a wide extramolar sulcus and prominent lateral ramal eminence (ASI VP 2/99, VP 2/242) as is seen on ARA VP 1/87 (*K. aramisi*) and unlike *Rhinocolobus turkanaensis* Leakey, 1982. The overall size and robusticity of the mandible is similar to *R. turkanaensis*, but in addition to the morphological differences already noted, the inferior edge of the *K. hafu* mandibular corpus is considerably more rounded compared to the thin, sharp inferior margin of *R. turkanaensis*.

Maxillae: ASI VP 2/95 (Fig. 4a) is a male right maxillary fragment broken approximately at midline in the premaxilla but missing much of the distal palate. The RI¹-RC¹ alveoli and RP³-RM³ crowns are preserved. The tooth row from P³-M³ is similar in length to male *Papio anubis* Lesson, 1827 but the premaxilla is significantly shorter, with less space between the C¹ and I² alveoli. The subnasal region is short and more vertically inclined (less prognathic) than *Paracolobus* or *Rhinocolobus* but very similar to *K. aramisi*. There is

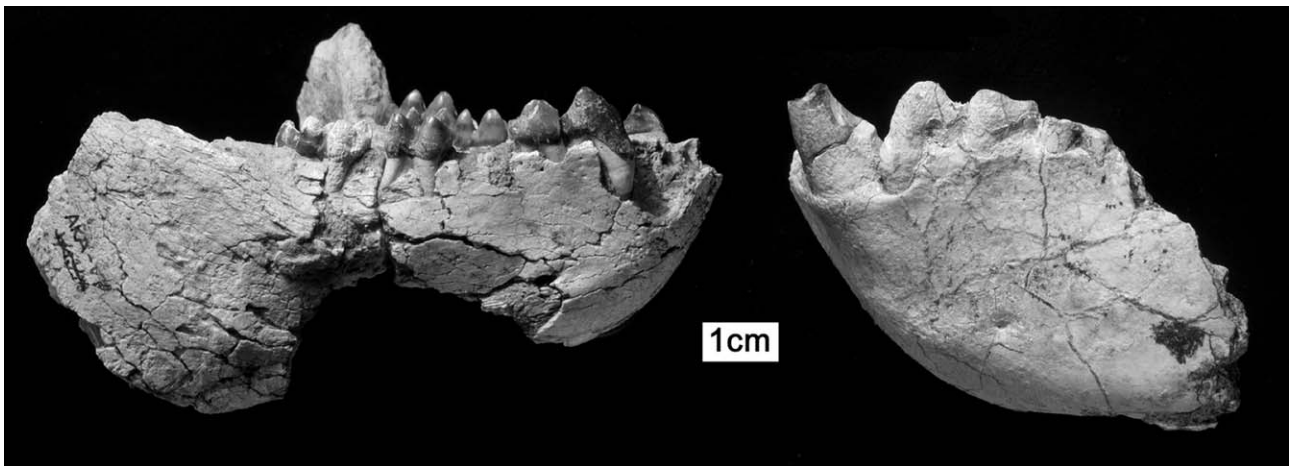


Fig. 3. Comparison of *Kuseracolobus aramisi* type specimen ARA VP 1/87 and *K. hafu* specimen ASI VP 2/100. Both seen in labial view with symphyses towards the center. Scale is 1 cm.

Fig. 3. Comparaison d'un spécimen type *Kuseracolobus aramisi* ARA VP 1/87 et d'un spécimen *K. hafu* ASI VP 2/100. Les deux sont montrés d'un point de vue labial avec symphyses vers le centre. Échelle = 1 cm.

a small portion of the piriform aperture preserved above the I¹ alveoli. This indicates that the aperture was relatively narrow, similar to ARA VP 6/1686. The zygomatic root is positioned above M¹, also like ARA VP 6/1686. The C¹ alveolus is large, indicative of male status. The P³-M³ crowns are missing buccal/labial enamel and the M¹-M³ crowns lack some of their lingual enamel. However, from what is preserved it is clear that the molars have tall buccal cusps characteristic of colobines. The M³ has cingular remnants preserved, including a buccal pit between cusps and on the mesial and distal aspects of buccal cusps. The M² and M³ have protocone shelves, and the M² a slight pit and shelf in the lingual interconulus region. The incisor region forms a relatively straight line. The M³ is not distally reduced and has a pronounced fifth cuspule, as is often seen in *K. aramisi*.

ASI VP 2/247 (Fig. 4c) right maxillary fragment with P⁴-M². Its P⁴-M¹ crowns have slight mesiodistally oriented fractures bisecting the crowns. The M² is missing both the paracone and metacone. There is a deep buccal notch on M², as in colobines. The P⁴-M² are moderately worn. This specimen is similar in size and has very similar morphology to ASI VP 2/95 (although ASI VP 2/247 is a little smaller). Additionally, the zygomatic root is located above M¹, as in ASI VP 2/95 and ARA VP 6/1686, *K. aramisi*.

ASI VP 2/245 (Fig. 4b) is a right maxillary fragment larger than ASI VP 2/96 but smaller than ASI VP 2/95. This specimen preserves a broken RI¹, complete RI²-RM², and broken RM³. The canine tip is missing and the teeth are heavily worn, such that P³ is just a ring of enamel around dentine. Much of the P³-M³ enamel has spalled off, especially on the lingual and buccal surfaces. As is seen in the other *K. hafu* maxillary specimens, the zygomatic root is located above M¹. ASI VP 2/245 has a small canine, like a female, with a very shallow maxillary fossa behind the canine and anterior to the root of the zygomatic. The length of the snout from P³-I¹ is similar to what is seen in the male maxilla ASI VP 2/95, although the ASI VP 2/245 canine is much smaller as would be expected

in a female conspecific. There is no diastema between the canine and lateral incisor.

ASI VP 2/246 (not shown) is a left maxillary fragment with only a very worn LI¹ crown. This specimen preserves the inferior aspect and part of the left side of the nasal aperture, which is v-shaped along the inferior margin and relatively vertical like *K. aramisi* and different from *Rhinocolobus*. ASI VP 2/246 is relatively vertical and long from nasospinale to alveolare/infradentale superius, measuring more than twice the length of this region on ARA VP 6/1686. This corresponds to the larger size of *K. hafu* compared to *K. aramisi*.

ASI VP 2/337 is an associated set of isolated maxillary teeth, LC¹-LM² (not shown). The canine has a well developed honing facet but is otherwise complete. It is large with male morphology compared to the female *K. hafu* maxillary canine ASI VP 2/245. The two premolars are only slightly worn, and preserve well developed protocones that are mesially oriented. The molars are unworn or only slightly worn with very high cusp relief, as is characteristic of colobines. The lingual surfaces of both molars are marked by cingular remnants. A moderately developed shelf is located on the mesiolingual aspect of the protocone. M¹ has an interconulus of stage 2, and the M² an interconulus of stage 3 (Hlusko, 2002).

The overall maxillary morphology of *K. hafu* is remarkably similar to that of *K. aramisi*, although significantly larger. Both species have a short and vertically inclined subnasal region and a narrow nasal aperture. The root of the zygomatic in *K. hafu* and *K. aramisi* is positioned approximately above the M¹ in both species, suggesting that the snout may be short like *Procolobus*, *Cercopithecoidea*, *Colobus*, and *Rhinopithecus* É. Geoffroy Saint-Hilaire, 1812 but unlike *Paracolobus* and *Rhinocolobus*.

Dentition: The *K. hafu* dentition is approximately the same size as a female *R. turkanaensis* and smaller than *Paracolobus mutiwa* Leakey, 1982 in all dental measurements pub-

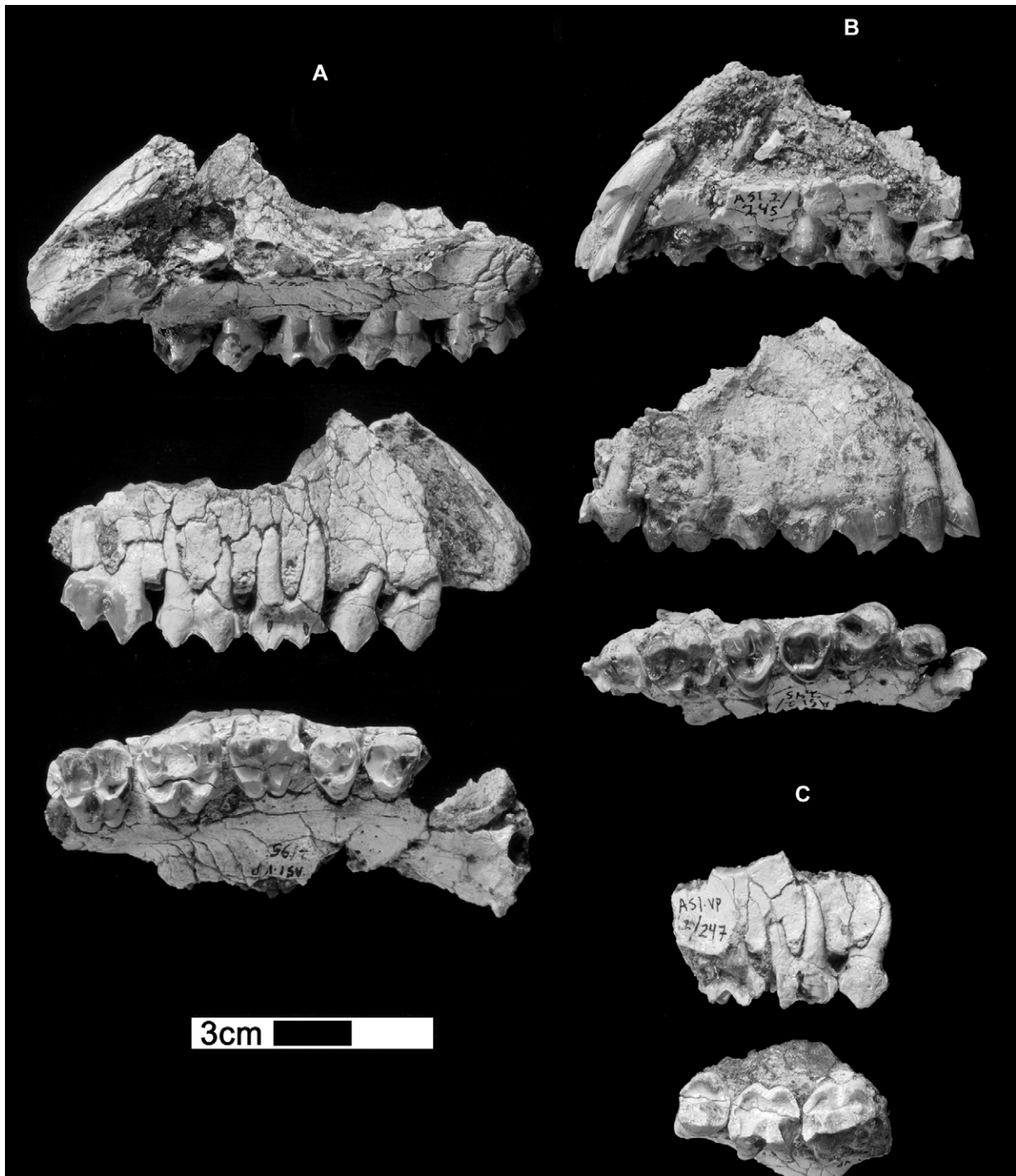


Fig. 4. Maxillary specimens included in the *Kuseracolobus hafu* hypodigm. A. ASI VP 2/95, male right maxillary fragment with P3-M3 crowns. B. ASI VP 2/245, right maxillary fragment with I2-M2, broken I1 and M3. C. ASI VP 2/247, right maxillary fragment with P4-M2. Scale is 3 cm.

Fig. 4. Spécimens maxillaires inclus dans l'hypodigme *Kuseracolobus hafu*. A. ASI VP 2/95, fragment maxillaire droit d'un mâle avec couronnes P3-M3. B. ASI VP 2/245, fragment maxillaire droit avec I2-M2, I1 et M3 cassés. C. ASI VP 2/247, fragment maxillaire droit avec P4-M2. Échelle = 3 cm.

lished in Delson et al. (2000); Leakey (1987) (Table 2), save for female P₃ length which is probably an artifact of measurement protocol. Researchers are inconsistent in how they measure P₃, often measuring from the paraconid or an estimate of where one might be, or from the P₃ articular facet with the canine to the distal edge. I find these inconsistent and therefore measure P₃ length as the maximum length parallel to the

occlusal plane from the mesial edge of the honing flange to the distal most aspect of the crown. This measurement does not always run directly along the mesiodistal axis of the tooththrow.

Mandibular canine mesiodistal length is measured as the maximum length of the crown, and buccolingual width as the diameter of the crown perpendicular to the mesiodistal length.

Table 2
Dental metrics for *Kuseracolobus hafu*
Dimensions dentaires pour *Kuseracolobus hafu*

Specimen number	Element	Sex	Length	Mesial width	Distal width	C height	P3 flange length	Length incisor MD	Width incisor LL
ASI VP 2/85	RM ₃	–	14.9	8.1	8.3				
ASI VP 2/89	RM ₃	–	13.8	7.9	8.1				
ASI VP 2/90	LM ₃	–	13.4	8.1	7.6				
ASI VP 2/91	LM ₃	–	14.0	7.9	8.3				
ASI VP 2/95	RP ³	Male	6.9	8.2					
ASI VP 2/95	RP ⁴	Male	6.3	8.6					
ASI VP 2/95	RM ¹	Male	10.1	Broken					
ASI VP 2/95	RM ²	Male	11	Broken					
ASI VP 2/95	RM ³	Male	11.8	Broken					
ASI VP 2/98	LC ₁	Male	10.5	7.4					
ASI VP 2/98	LP ₃	Male	12.9	6.9					
ASI VP 2/98	LP ₄	Male	8.2	7.1					
ASI VP 2/99	RM ₁	Male	10.2	7.5	7.2				
ASI VP 2/99	RM ₂	Male	10.9	8.7	8.9				
ASI VP 2/99	RM ₃	Male	14.7	8.4	8.5				
ASI VP 2/100	LC ₁	Male	11.1	7.8					
ASI VP 2/100	LP ₃	Male	13.3	6.2			14.9		
ASI VP 2/100	LP ₄	Male	9.4	6.8					
ASI VP 2/101	RC ₁	Female	7.6	4.9		9.5			
ASI VP 2/101	LP ₃	Female	9.9	5.3			10.2		
ASI VP 2/101	RP ₃	Female	10.1	5.5			10.1		
ASI VP 2/242	LM ₁	Female	9	Broken	7.3				
ASI VP 2/242	LM ₂	Female	9.9	8.1	8.4				
ASI VP 2/242	LM ₃	Female	13.6	8	8.0				
ASI VP 2/243	RP ₃	Female	9.9	6.2					
ASI VP 2/243	RP ₄	Female	8.6	Broken					
ASI VP 2/245	RI ¹	Female							6.6
ASI VP 2/245	RI ²	Female						5.5	5.9
ASI VP 2/245	RC ¹	Female	8.4	7.1					
ASI VP 2/245	RP ³	Female	6.7	7.4					
ASI VP 2/245	RP ⁴	Female	7.1	8.5					
ASI VP 2/245	RM ¹	Female	9.6e	Broken					
ASI VP 2/246	LI ¹	Male					7.1		6.4
ASI VP 2/247	RP ⁴	Female	6.3	8.7					
ASI VP 2/247	RM ¹	Female	8.8	Broken	8.6				
ASI VP 2/247	RM ²	Female	Broken	Broken					
ASI VP 2/337	LP ³	Male	8.2	8.0 (e)					
ASI VP 2/337	LP ⁴	Male	7.1	8.8					
ASI VP 2/337	LM ¹	Male	10.2	9.4	9.3				
ASI VP 2/337	LM ²	Male	11.0	9.4	8.8				
ASI VP 2/337	LC ¹	Male	13.2	9.4		25.7			

Measurements in mm; e = estimate

This measurement protocol is not dependent on how the tooth is oriented in the jaw, making it more replicable, and applicable to isolated as well as articulated teeth.

Overall, *K. hafu* is quite similar to *K. aramisi* in dental morphology. Aside from the typical colobine morphology of tall, pointed cusps, *K. hafu* has a high prevalence of a M₃ tuberculum sextum, as has also been described for *K. aramisi*. Four isolated M₃s are also included in the hypodigm of *K. hafu*. They are designated as *K. hafu* because of their very large size, colobine morphology, and presence of a tuberculum sextum. It is not possible to determine the sex of these specimens, although one (ASI VP 2/90) is smaller than the known female ASI VP 242 M3, one (ASI VP 2/85) is larger

than the known male ASI VP 2/99, and two (ASI VP 2/91 and ASI VP 2/89) are intermediate in size.

The spacing along the tooth row is tight in both *K. aramisi* and *K. hafu*, with all teeth in interproximal contact, contrasted with the diastemata seen between the canine and lateral incisors in the mandibles and maxillae of *Cercopithecoides meaveae* (Frost and Delson, 2002).

The maxillary dentition of *K. hafu* also demonstrates the characteristic colobine morphology. Neither *K. hafu* nor *K. aramisi* has distal reduction of the M³, and both species frequently express a pronounced fifth cusplule on the M³ (although it is important to note that this feature is variable within populations and has been noted to be more frequent in

female colobines; Swindler and Orlosky, 1974). Three of the four *K. hafu* maxillary P³s are heavily worn, but they appear to have protocones. The ASI VP 2/337 P³ is lightly worn and has an obvious mesially oriented protocone, as is characteristic of *K. aramisi*, *Paracolobus*, and *Rhinocolobus*, but different from extant African colobines.

There is one morphological difference noted to date that diagnostically differentiates the *K. hafu* dentition from that of *K. aramisi*. The overall shape of the M₂ is different between these two *Kuseracolobus* species, as *K. hafu* has slightly wider distal lophids on M₂ relative to mesial lophids, and the *K. aramisi* M₂ lophids are on average, equal in width.

A metric comparison of *K. aramisi* and *K. hafu* mandibular dentitions shows additional significant differences (Table 3). The *K. hafu* sample is relatively small, with sample sizes range from 1 to 6, and are typically sex-biased. Therefore, robust statistical comparisons between this new species and *K. aramisi* are constrained at this time. Nevertheless, *K. hafu* is clearly 2–5 S.D. above the mean of all of the *K. aramisi* dental metrics for which there are comparable teeth. The size of first molars is sometimes considered one of the more conserved, or least variable dental characters (Gingerich, 1974). In comparisons of this conservative tooth, the mandibular and maxillary M₁s of *K. hafu* are more than 3 S.D. above the *K. aramisi* means.

Several metric ratios also distinguish these two taxa (Table 3). Mandibular M₃s are relatively mesiodistally longer in *K. hafu* than *K. aramisi* (mesiodistal length/mesial buccolingual width: 1.75 vs. 1.64, respectively). *K. aramisi* P₄s are relatively longer (mesiodistal length/buccolingual width: *K. hafu* = 1.26; *K. aramisi* = 1.32), whereas *K. hafu* P⁴s are more mesiodistally compressed (mesiodistal length/buccolingual width, L/W: *K. hafu* = 0.76; *K. aramisi* = 0.85). The samples are particularly small for the canines, but *K. hafu* male man-

dibular and female maxillary canines appear to be more rounded in cross-section than are those of *K. aramisi* (male mandibular canine L/W: *K. hafu* = 1.4; *K. aramisi* = 1.53; female maxillary canine L/W: *K. hafu* = 1.19; *K. aramisi* = 1.34). Maxillary male canines appear to have similar proportions in both *K. hafu* and *K. aramisi*. As noted previously, statistical tests were not performed because of the small *K. hafu* sample size, see Table 3.

Postcrania: Attribution of the postcranial specimens is based on size. There is evidence of at least three cercopithecoid species at ASI VP 2, one cercopithecine and two colobines. Of the colobines, the predominant taxon is the very large species described herein. The other colobine is much smaller. The cercopithecine is also smaller than *K. hafu*, with the males approximately the same dental size as the *K. hafu* females. Therefore, only the largest postcranial specimens can confidently be associated with the new species of *Kuseracolobus*. The postcranial sample is therefore biased, as it only includes large male specimens.

Only nine specimens are confidently designated as *K. hafu*. However, their morphology does provide critical information as to the body size and locomotion of this species. Specimens are listed in Table 1 and shown in Fig. 5.

The most complete specimen is ASI VP 2/59, a left arm consisting of a radius (a), ulna (b), and humerus (c) (Table 4). The humerus is well preserved at the distal end. The proximal end was damaged by carnivore gnawing. The humeral shaft has a strong anterior deltoid tuberosity and associated cresting that extends inferiorly to midshaft. Distally, the medial epicondyle is relatively quite small and mediolaterally oriented. The trochlea is relatively flat with a very minimal lateral keel and only a slight medial keel extending approximately 2.4 mm below the inferior aspect of the capitulum, unlike what is seen in terrestrial cercopithecoids (Rose, 1993;

Table 3

Comparison of dental metrics for *Kuseracolobus hafu* and *K. aramisi*Comparaison des dimensions dentaires pour *Kuseracolobus hafu* et *K. aramisi*

Element	n	MD length		Mesial width		Distal width		P3 flange length		Labiolingual width	
		<i>hafu</i>	<i>aramisi</i>	<i>hafu</i>	<i>aramisi</i>	<i>hafu</i>	<i>aramisi</i>	<i>hafu</i>	<i>aramisi</i>	<i>hafu</i>	<i>aramisi</i>
C ₁ : ♂	2	10.8	8.4 (0.5)	7.6	5.5 (0.2)						
C ₁ : ♀	1	7.6	5.7	4.9	3.70						
P ₃ : ♂	2	13.1	7.3 (0.2)	6.6	4.7 (0.2)			14.9	11.6 (0.8)		
P ₃ : ♀	3	10	5.9 (0.5)	5.7	4.8 (0.5)			10.2	8.2		
P ₄	3	8.7	6.7 (0.5)	7	5.1 (0.2)						
M ₁	2	9.6	7.9 (0.5)	7.5*	6.1 (0.3)	7.3	6.2 (0.5)				
M ₂	2	10.4	8.8 (0.6)	8.4	7.2 (0.4)	8.7	7.3 (0.6)				
M ₃	6	14.1	11.8 (0.8)	8.1	7.2 (0.4)	8.2	7.1 (0.3)				
I ¹	2	7.1*	5.9 (0.3)							6.5	5.2 (0.3)
I ²	1	5.5**	5.2 (0.6)							5.9**	4.9 (0.5)
C ¹ : ♂	1	13.2	10.4 (0.3)	9.4	7.3 (0.3)						
C ¹ : ♀	1	8.4	6.7 (1.6)	7.1	5.0 (0.2)						
P ³	3	7.2	5.7 (0.6)	7.9	6.4 (0.5)						
P ⁴	4	6.7	5.5 (0.3)	8.7	6.5 (0.4)						
M ¹	4	9.7	7.9 (0.5)	9.4*	7.1 (0.4)	8.9	6.9 (0.3)				
M ²	2	11*	8.7 (0.2)	9.4*	8.0 (0.4)	8.8*	7.3 (0.3)				
M ³	1	11.8*	9.0 (0.3)	n/a		n/a					

All measurements in mm; (n) = S.D.; *K. aramisi* data from Frost, 2001a, 2001b; * male only; ** female only.



Fig. 5. Postcranial specimens included in the *Kuseracolobus hafu* hypodigm. Top and right of photograph is ASI VP 2/59 in articulation, ASI VP 2/59a = radius, ASI VP 2/59b = ulna, ASI VP 2/59c = humerus. Middle row, from left to right: ASI VP 5/37 upper and midshaft of left humerus; ASI VP 5/28 right proximal radial shaft. Bottom row, from left to right: ASI VP 2/114 lateral condyle of right femur; ASI VP 2/232 complete intermediate hand phalanx; ASI VP 2/80 proximal third of intermediate hand phalanx; ASI VP 2/79 proximal hand phalanx; ASI VP 2/55 fragment of proximal right ulnar shaft with radial notch; ASI VP 2/53 proximal right ulna. Scale is 10 cm.

Fig. 5. Spécimens post-crâniens inclus dans l'hypodigme *Kuseracolobus hafu*. En haut à droite de la photo se trouve ASI VP 2/59 en articulation, ASI VP 2/59a = radius, ASI VP 2/59b = ulna, ASI VP 2/59c = humérus. Rang du milieu, de gauche à droite : ASI VP 5/37 diaphyse du haut et centrale de l'humérus de gauche ; ASI VP 5/28 diaphyse radiale proximale de droite. Rang du bas, de gauche à droite : ASI VP 2/114 condyle latérale du fémur de droite ; ASI VP 2/232 phalange intermédiaire complète de la main ; ASI VP 2/80 troisième proximale de la phalange intermédiaire de la main ; ASI VP 2/79 phalange proximale de la main ; ASI VP 2/55 fragment de la diaphyse ulnaire proximale de droite avec entaille radiale ; ASI VP 2/53 ulna proximal de droite. Échelle = 10 cm.

Table 4
Measurements of ASI VP2/59
Mesures de ASI VP2/59

ASI VP 2/59a	Radius head ap 17.9
	Head ml 20.1
	Mediolateral just below tuberosity 11.4
ASI VP 2/59b	Ulna radial notch width 14.6(e)
	Radial notch height 14(e)
	Trochlear notch/olecranon length 12.8
	Trochlear notch/olecranon width 15.8
ASI VP 2/59c	Humerus bicondylar width 40.5
	Mediolateral articular surface width 32
	Medial trochlea distal projection 19
	Olecranon fossa depth 11.3
	Olecranon fossa width 15.6
	Posterior trochlear articular surface width 15.9

Measurements in mm; e = estimate.

Birchette, 1982). The humerus has a minimally developed lateral keel that forms superior to the end of the capitulum, similar to that seen in *Nasalis* É. Geoffroy Saint-Hilaire, 1812 (Rose, 1993: Fig. 3.9c therein). The ASI VP 2/59c humeral capitulum is rounded but rather square in anterior view, flattened inferiorly, and extends onto the posterior surface. This morphology is unlike many terrestrial cercopithecids but similar to more arboreal species (Rose, 1993).

The ASI VP 2/59b left ulna is missing the distal end. The proximal end is preserved but the coronoid process is broken and the bone medial to it is missing. The olecranon process is also preserved and lacks the retroflexion typical of cercopithecines. A large crack runs mediolaterally through the trochlear notch.

The ASI VP 2/59a left radius is also missing the distal end but the proximal end is well preserved. The head is tilted proximally.

There are seven other forelimb specimens included in the *K. hafu* hypodigm. ASI VP 5/37 consists of the upper and middle shaft regions of a left humerus. This specimen is similar in size and morphology to ASI VP 2/59c and has a strong deltoid crest. A carnivore tooth puncture mark is located on the anterior surface. ASI VP 5/28 is a right proximal radial shaft broken at the neck and distal to the radial tuberosity.

There are two other partial ulnae, ASI VP 2/53 and ASI VP 2/55. ASI VP 2/53 is a right proximal ulna with cracked and missing cortical bone. This specimen is slightly smaller than ASI VP 2/59. ASI VP 2/55 is a fragment of a proximal right ulnar shaft with the radial notch. The distal–medial aspect of the trochlear notch is broken. ASI VP 2/55 is approximately the same size as ASI VP 2/59.

Three phalanges are recognized here as belonging to *K. hafu*, two intermediate and one proximal. ASI VP 2/79 is a proximal hand phalanx with strong ventral medial and lateral ridges. It is slightly curved, and preserves only the distal end and shaft; the proximal end is missing. ASI VP 2/80 and ASI VP 2/232 are both intermediate hand phalanges. The first is the proximal third of the phalanx with strong ventral medial and lateral crests. The second is a complete phalanx approximately 28 mm in length, with morphology similar to that of ASI VP 2/80.

The only hind limb element of *K. hafu* recovered to date is ASI VP 2/114, the lateral condyle of a right distal femur. This specimen is not well preserved, only part of the cortical bone on the dorsal and inferior surface of the condyle is present and the fragment is broken and distorted.

3. Discussion

The recognition and systematics of *K. hafu* rely on dentognathic characters. These show that this species has close morphological affinities to the older (4.4 Ma) *K. aramisi*, but is much larger in size. The associated postcranial material confirms the large size of the taxon and has functional and paleoecological implications.

Following Delson et al. (2000), body mass was estimated for *K. hafu* using both postcranial and dental metrics. The humeral midshaft anteroposterior dimension for *K. hafu* is 17.9 mm, which is slightly larger than that of a male *Paracolobus chemeroni* Leakey, 1969. Based on this humeral metric, *P. chemeroni* males are estimated to have had a body mass of approximately 39 kg (Delson et al., 2000). By comparison, *K. hafu* males may have been similar in size.

Dental metrics provide a rather different estimate, and on their basis *P. chemeroni* males were estimated to have had a body mass of approximately 46 kg (Delson et al., 2000). For dentally derived body size estimates, following Delson et al. (2000), *K. hafu* is most similar in size to *R. turkanaensis*, although there is variation depending on which metric is used. M_1 area estimates for *K. hafu* are most similar to *Parapapio jonesi* Patterson, 1968 and greater than those of either male or female *R. turkanaensis*. The *K. hafu* M_2 area estimate is

intermediate between *R. turkanaensis* males and females. M_3 area suggests that *K. hafu* body size was smaller than *R. turkanaensis* females but larger than *Dolichopithecus ruscinensis* males.

The lack of a consistent body mass estimate results from the differences in predictive value that various metrics offer (discussed further in Delson et al., 2000). Additionally, comparisons between taxa are complicated by their respective differences in dental proportions. For example, *R. turkanaensis* M_1 s and M_2 s have lophids of equal buccolingual widths whereas *K. hafu* M_1 mesial lophids are wider than the distal lophids, the opposite of the condition on the M_2 . *R. turkanaensis* M_3 s are also relatively wider than *K. hafu*, and the lophid width proportions are reversed. Therefore, consistency across body mass estimators is unlikely for any taxon.

However, despite these caveats, these comparisons do provide useful information about the body mass of *K. hafu*. Postcranial and dental metrics demonstrate that *K. hafu* was larger than any extant colobine species, with males probably weighing between 30 and 40 kg, and possibly more. A comparison between colobines and cercopithecines is complicated because of the fore- and hindlimb differences between these two subfamilies. Furthermore, colobines have been described as relatively microdont, where cercopithecine molars are larger at all positions than is seen in similarly sized colobines (Delson et al., 2000: 43–47). However, *K. hafu* males were probably about the same size as a modern male *Mandrillus sphinx* Linnaeus, 1758 at 35 kg.

This large body size for a colobine appears to be coupled with an arboreal lifestyle, much as is seen in *Rhinocolobus*. Animals are functionally integrated units, and therefore interpretations of locomotor patterns based on partial anatomical information are somewhat limited. However, morphological variation in the primate elbow joint has been demonstrated to correlate with habitual arboreality and terrestriality (Rose, 1993; Elton, 2001; Birchette, 1982). Cercopithecids are no exception. Three features, in particular, have been suggested to be relevant in previous studies: the inferior projection of the trochlear keel, the orientation of the medial epicondyle, and the length and retroflexion of the ulnar olecranon process. These three traits will be considered for ASI VP 2/59.

The amount of the projection of the humeral trochlear keel is associated with different locomotor patterns in cercopithecids. Rose (1993) has noted that strongly expressed medial and lateral keels appear to be associated with terrestriality. As previously noted, ASI VP 2/59c has a very slight medial trochlear keel and virtually no lateral keel. Following Rose's (1993) argument, ASI VP 2/59c medial and lateral keel expression is most similar to that of arboreal cercopithecoid. Frost and Delson (2002) calculated an index of medial trochlear flange length, or relative projection. Following their protocol, ASI VP 2/59c has an index of 59, placing it within the first interquartile of *Colobus guereza* Rüppell, 1835 and *Nasalis larvatus* Wurmmbach, 1787.

Retroflexed olecranon processes are also associated with cercopithecoid terrestriality (Jolly, 1967, 1972; Rose, 1993; Bir-

chette, 1982), as are short ones (Fleagle, 1977). As described above and shown in Fig. 5, ASI VP 2/59 is quite long and not retroflexed, in line with the suite of anatomical features that are correlated with arboreality in some other primates.

The medial and distal projection of the medial epicondyle also appears to covary with substrate, with arboreal species tending to have more medially and less distally projecting medial epicondyles (Nakatsukasa, 1994a, 1994b; Fleagle, 1988; Frost and Delson, 2002; contra Senut, 1987). Frost and Delson's (2002) epicondyle ratio quantifies medial projection, and aligns ASI VP2/59 with more arboreal species. Following their protocol, medial epicondyle distal projection for ASI VP 2/59c is found to be 17, which places it within the first interquartile range of *Cercopithecus mitis* Wolf, 1822, *Theropithecus oswaldi* cf. *darti* Broom and Jensen, 1946, *C. guereza*, *Procolobus badius* Kerr, 1792, and *N. larvatus*. Additionally, the distal projection, or orientation of the medial epicondyle, can be calculated as an angle (Frost and Delson, 2002). The angle of the ASI VP 2/59 medial epicondyle is approximately 40°, similar to that seen in *C. mitis*, *C. guereza*, and the extinct *R. turkanaensis*, and considerably lower than the angle of medial epicondylar projection estimated for more terrestrial extant species such as *Theropithecus gelada* Rüppell, 1835 and the extinct species *Cercopithecoides williamsi* Mollet, 1947, *C. meaveae*, and *P. chemeroni* Leakey, 1969 (Frost and Delson, 2002).

Dentognathic features demonstrate the close affinities between *K. hafu* and *K. aramisi*, the type species of this genus, although *K. hafu* is considerably larger than *K. aramisi*. *K. hafu* is similar in size to *Rhinopithecus turkanensis*, probably smaller than *P. mutiwa*, and larger than *C. meaveae*. The new Asa Issie species appears to have had forelimb elements similar in morphology to more arboreal colobine species, suggesting that it spent a predominant amount of time in an arboreal substrate, despite its rather large size. If the functional assessments above are proven to be valid, then the Pliocene colobine radiation appears to have been characterized by several large-bodied arboreal species.

Colobines are relatively unknown in Africa from the middle to late Miocene in Africa, contrasting with their evolutionary record in Europe (i.e. *Mesopithecus*; Zapfe, 1991; Koufos et al., 2003). When colobine fossils appear in the African Pliocene they are unambiguous and already fairly diverse (Delson, 1994; Benefit, 1999; Jablonski, 2002). There are currently four widely recognized genera from the Pliocene of Africa: *Cercopithecoides* (3.4–1.2 Ma; Frost and Delson, 2002; Jablonski, 2002; Leakey, 1982; Frost et al., 2003), *Kuseracolobus* (4.4 Ma; Frost, 2001a, 2001b; WoldeGabriel et al., 1994), *Paracolobus* (3.36–1.88 Ma; Jablonski, 2002), and *Rhinocolobus* (3.4–1.88 Ma; Jablonski, 2002). The phylogenetic relationships among these four genera and modern colobines are largely unknown due to the relatively conserved dentognathic morphology of Old World monkeys, the unique adaptations seen in each species, the recency of the taxonomic radiation, and the biases inherent in the fossil record (Jablonski, 2002). Most smaller colobine specimens

are fragmentary and not yet diagnosable. As Jablonski noted, “The wealth of Old World monkey fossils has told us more about the niches and adaptations of cercopithecoid species, and about ancient primate communities, than it has about evolutionary relationships among species” (2002: 255).

Of these four genera, *Cercopithecoides* is the most taxonomically diverse, with four species. The genus is represented by specimens known from both eastern and southern Africa. *C. williamsi* (2.8–1.9 Ma; Leakey 1982; Bromage and Schrenk, 1999), *C. kimeui* (2.5–1.2 Ma; Frost et al., 2003) and *C. meaveae* (3.22–3.44 Ma; Frost and Delson, 2002) are medium to large-sized primates with a short rostrum and a shallow mandibular body (Frost and Delson, 2002). The postcrania have been characterized as terrestrial (Birchette, 1982; Leakey, 1982; Frost and Delson, 2002). *C. kerioensis* Leakey, Teaford and Ward, 2003 is smaller than the other congeneric species, but no postcrania are yet known. Unfortunately, provenience data were not recorded so the age of this species is also unknown (Leakey et al., 2003).

Paracolobus is also a large-bodied colobine with a broad muzzle. There are two known species, both from Kenya (Leakey, 1982). These species, *P. chemeroni* (3.5–2.5 Ma; Bromage and Schrenk, 1999; Leakey and Delson, 1987) and *P. mutiwa* (3.36–1.88 Ma; Jablonski, 2002) are described as having postcranial features that are more similar to arboreal colobines, although some aspects of their anatomy have been interpreted as limited terrestrial adaptations (Birchette, 1982; Leakey, 1982).

Several researchers have presumed that the earliest colobines were predominately terrestrial, in sharp contrast to the largely arboreal habitus of the extant representatives of this clade (Harris et al., 2003; Leakey et al., 2003). This presumption appears to have been made on the basis of two disparate lines of evidence. Two of the Pliocene colobine genera (*Cercopithecoides* and *Paracolobus*) are often described as having some terrestrial adaptations in their postcranial skeletons. This description has been coupled with the suggestion that the earliest known cercopithecoid, *Victoriapithecus* von Koenigswald, 1969 from the middle Miocene of Kenya was a terrestrial frugivore (Benefit, 1999 and references therein). The presumption that terrestrial substrate use was primitive for the colobine clade would suggest that arboreality in Asian and African colobines arose independently through parallel evolution.

However, this is not the only, or even the most parsimonious interpretation in light of the available evidence. For example, the third colobine genus from the African Pliocene, *Rhinocolobus*, appears in the record at 3.4 Ma, persists until 1.8 Ma (Jablonski, 2002), and has postcrania described as indistinguishable from modern arboreal colobines, suggesting that these large-bodied primates were not terrestrial (Leakey, 1982). Therefore, two of the three postcranially described genera are interpreted to be either fully or predominately arboreal and only one is described as terrestrial: *Rhinocolobus* is characterized as arboreal, *Paracolobus* as predominantly arboreal with some terrestrial characteristics, and

three of four species of *Cercopithecoides* are known to share a considerable number of features with typical terrestrial cercopithecids.

This latter genus may therefore represent the derived, rather than the primitive, condition. However, the relationships between the various species and specimens attributed to *Cercopithecoides* are not clear. The largest species (*C. kimeui*) appears later in the fossil record than the other congeneric species. The dentition of this latter species has been described as having cercopithecine-like features that are atypical for colobines (Leakey, 1982). However, if and when its postcrania are discovered, it is uncertain whether highly terrestrial features would indicate that the species is derived relative to its current conspecifics or represents a different genus.

The recent discovery and description of *K. aramisi* (Frost, 2001a, 2001b) and the large-bodied *K. hafu* described here, demonstrate that the Pliocene colobine radiation was even more expansive than previously known. Functional analysis of the postcranial anatomy of *K. hafu* suggests that this species was large-bodied and may also have been arboreal like *Rhinocolobus* and *Paracolobus*. The functional arguments outlined above suggest that the majority of the first African Pliocene colobines were arboreal rather than terrestrial. Colobine fossils from the late Miocene are needed to test this hypothesis and provide the outgroup taxa that will be necessary to elucidate the phylogenetics of Pliocene Colobinae.

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