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New Fossil Cercopithecoids from the Late Miocene of As Sahabi, Libya

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ABSTRACT

A preliminary revision of the fossil cercopithecoids of As Sahabi is presented based on a well-preserved right half-mandible (1P25C) with minimally worn P3-M3 and a left distal humerus (514P28A) collected in 2007. The molar teeth of 1P25C are distinguished from similarly-aged *Macaca libyca* (Wadi Natrun, Egypt), cf. *Macaca* sp. (Menacer, Algeria), and cf. *Macaca* sp. (Casablanca, Spain) in having M_2s that are smaller, squarer, and more flared buccally. The As Sahabi papionin is distinguishable from *Parapapio lothagamensis* in having a less elongated and more steeply oriented mandibular symphysis, although the two monkeys share with *M. libyca* the presence of a P_3 metaconid. Differences in size between 1P25C and some of the previously collected papionins are here attributed to dental size sexual dimorphism, although the future discovery of new material might lead to recognition of two moderately small papionins from the site. The As Sahabi papionin belongs to a new species of either *Parapapio* or *Macaca*. A newly discovered distal humerus from As Sahabi exhibits clearly cercopithecine and terrestrial features, including a strongly retroflexed medial epicondyle. It may well belong to the same species as 1P25C. A previously collected distal humerus from As Sahabi 10P61A appears to be colobine due to its well-developed lateral trochlear keel and capitulum. None of the other postcrania can clearly be assigned to subfamily due to their poor preservation. Previously collected teeth from As Sahabi all exhibit lower cusp relief and greater buccal flare than is observed in modern colobines. Given that fossil papionins from this time range have greater occlusal relief than extant cercopithecines, it is possible that only papionins are represented in the As Sahabi dental sample. Such a monkey might have had an eclectic, but predominantly frugivorous diet.

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INTRODUCTION

The discovery of two new well-preserved Old World monkey specimens at As Sahabi by the East Libya Neogene Research Project during 2007 adds significantly to our knowledge of early stages in cercopithecoid evolution. Analysis of the 15 cercopithecoid specimens collected by the International Sahabi Research Project led by Boaz, Gaziry, and El-Arnauti between 1978 and 1981 indicated that they consist of at least one species of papionin referred to cf. *Macaca* sp. and one species of colobine monkey referred to Colobinae gen. sp. indet. (Boaz *et al.*, 1979; Boaz and Meikle, 1982; Meikle, 1987). They are part of a larger North African cercopithecoid radiation that includes fossils from the 6-7 million-year-old sites of Menacer in Algeria (Arambourg, 1959; Thomas and Petter, 1986), Wadi Natrun in Egypt (Stromer, 1913) and Toros-Menalla in Chad (Vignaud *et al.*, 2002). Like As Sahabi, Menacer and Wadi Natrun each preserves one papionin and one colobine monkey of moderate size (Table 1). Due to their geological age, these Late Miocene North African monkeys preserve early stages in the evolutionary history of papionins (baboons and macaques) which are estimated on the basis of molecular evidence to have diverged from cercopithecins (guenons) 11.5 million years ago. Macaque and baboon lineages are estimated to have split 7.6 million years ago. Early African Colobina are reconstructed as having split from Asian Presbytina by 9.6 million years ago (Disotell, 2000; Sterner *et al.*, 2006; Tosi, 2005; Ting, 2007).

Although their numbers are small, the North African fossils once represented much of what was known about Old World monkey evolution in Africa between 15 and 4 ma. Since 2003 the 5-8 ma deposits at Lothagam and Lemudong'o in Kenya and in the Middle Awash in Ethiopia have produced cercopithecoid fossils that demonstrate a greater number of species of varying body-size, locomotor, and dietary adaptations than was previously imagined (Table 1; Leakey *et al.*, 2003; Ambrose *et al.*, 2003; Haile-Selassie *et al.*, 2004; Hlusko 2007a, 2007b; Frost, 2007). The papionin species *Parapapio lothagamensis* from the lower member of the Nawata Formation has dental traits that were unexpected for a monkey of its geologic age, combining primitive features of the Middle Miocene victoriapithecids with those characterising modern papionins (Leakey *et al.*, 2003). The Lothagam cercopithecoid community resembles those from the North African sites which contain at least one papionin and one colobine species, and at which papionins make up a majority of the cercopithecoid fauna. In contrast, the abundant cercopithecoid fauna at the 6 ma site of Lemudong'o may consist entirely of three previously unknown colobine species (Hlusko, 2007a, 2007b). They demonstrate a greater diversity of body-size, dietary, and postcranial adaptations among Late Miocene Colobinae than was once predicted.

A preliminary description of the new As Sahabi fossil monkeys is provided here in the context of the new eastern African discoveries and a re-examination of previously collected fossils from North Africa. Fossil cercopithecoids from

Table 1. Fossil cercopithecoids from the Late Miocene of Africa, based on information in Stromer (1913), Szalay and Delson (1979), Delson (1980), Benefit and Pickford (1986),Thomas and Petter (1986), Meikle (1987), Senut (1994), Grine and Hendey (1981), Gundling and Hill (2000), Kingston *et al*. (2002),Vignaud *et al*. (2002),Leakey *et al*. (2003), Ambrose *et al.* (2003), Frost (2007), and Hlusko (2007).

NORTH AFRICA		
Menacer (Marceau)	*Macaca* sp. (n=31)	ca. 7 ma
	?*Colobus flandrini* (n=8)	
Wadi Natrun	*Macaca libyca*(n=?3)	ca. 6 ma
	Libypithecus markgrafi (n=?3)	
As Sahabi	*Macaca* sp. (n=6)	6-7 ma
	Colobinae sp. (n=1)	
	Cercopithecoidea indet. (n=13)	
Toros Menalla	Cercopithecidae	6-7 ma
EASTERN AFRICA		
Ngeringerowa, BPRP #25	*Microcolobus tugenensis* (n=1)	9.5-9.0 ma
Nakali	Colobinae indet (n=3)	9-7 ma
Mpesida, Rurmoch BPRP #85	Colobinae indet (n=2)	7-6.37 ma
Nawata Lower, Lothagam	*Parapapio lothagamensis* (n=76)	6.57-7.9 ma
	Colobinae sp. A (n=4)	
	Colobinae sp. B (n=7)	
	Colobinae indet (n=4)	
Nawata Upper, Lothagam	*Parapapio lothagamensis* (n=33)	6.24-5.5 ma
Colobinae sp. A (n=3)		
Colobinae sp. B (n=8)		
Colobinae indet (n=4)		
Nkondo Fm., Uganda	Colobinae, 2 M3s	6.5-6.2 ma
Lukeino	a few fragments	6.3-5.6 ma
Lemundong'o	*Paracolobus* sp. nov	6 ma
	Colobinae small taxon	
	Colobinae large taxon	
	(n=281 total cercopithecoid)	
Adu Asa and	*Pliopapio alemui*	5.2-5.8 ma
lower Sangatole	*Kuseracolobus aramisi*	
Formations, Ethiopia	Colobinae indet (larger species)	
	Cercopithecidae indet (small species)	
	(n-65+ total cercopithecoid)	
SOUTH AFRICA		
Laangebaanweg	Papionin (n=1)	6 ma

Menacer were studied at the Museum of Natural History in Paris and *Macaca libyca* at the American Museum of Natural History in New York.

COMPARATIVE DESCRIPTION

1P25C was found at Locality P25C in January of 2007 by Paris Pavlakis. The specimen is a right half-mandible with C-M_2 and erupting M_3 (Figure 1). The canine tip is broken, and a tiny flake of enamel is missing below the median buccal cleft of M_2, but otherwise the teeth are very well preserved. The large canine and well-developed P_3 honing facet indicate that the specimen is a male, and the erupting M_3 indicates that it is a subadult. The M_2 and P_3 show very slight wear on cusp tips. The P_4 and M_1 are more worn with small circles of dentin exposed on buccal cusps. The mandible preserves an intact corpus from C to M_3, a small portion of the lateral part of the symphysis, and a large portion of the ramus from gonial angle to about two-thirds of its height where it is broken well below the coronoid process and condyle.

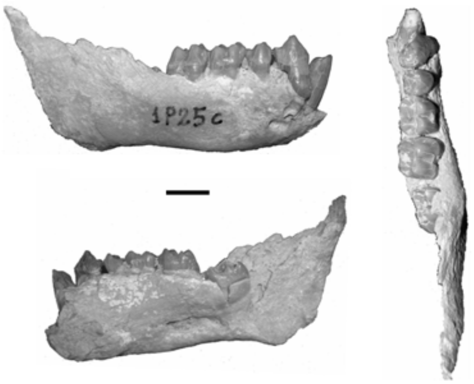


Figure 1. Mandible 1P25C. Scale is 1 cm.

Mandible

The new mandible 1P25C is one of three known from As Sahabi (Table 2). The three mandibles are attributed to Cercopithecinae based on the morphology of their associated dentition. 1P28A preserves a corpus from symphysis to M_3, but no ramus. Teeth associated with the specimen, a P_3 to fully erupted M_3 and canine root, are poorly preserved and missing enamel over much of their surface.

Table 2. As Sahabi cercopithecoid fossils. Attributions differ slightly from those described by Boaz and Meikle (1982) and Meikle (1987).

CF. *PARAPAPIO* OR *MACACA* SP.	
1P25C	Right half-mandible, male, with canine to partially erupted M3
1P28A	Right half-mandible, male, with canine root to fully erupted M3
57P99A	Right mandible fragment with P3 and M1
105P16A	Left I1 crown
841P34A	Left lower M1
514P28A	Left distal humerus
COLOBINAE GEN. INDET	
10P61A	Left distal humerus
CERCOPITHECOIDEA INDET	
151P81A	Right upper M2 or 3
244P16A	Lingual half of right lower P4
P61A	Left upper M1 collected by Jordi Agusti
P61A	Right lower I2 collected by Jordi Agusti
13P15A	Right distal humerus
34P30A	Left distal humerus
12P33A	Right distal humerus
24P11A	Right Proximal ulna
1P17B	Right proximal end and shaft of femur
121P87A	Right femoral head and neck
11P115A	Left calcaneus
21P87A	Proximal phalanx
P61A	Hallucial proximal phalanx collected by Jordi Agusti

The size of the root and development of the P_3 honing facet indicate it is a male. 57P99A preserves only the top half of the corpus from below I_2 to M_2 alveoli. It retains a P_3 that is missing enamel buccally and a well-preserved M_2 that is worn to a somewhat greater degree than that of 1P25C, with somewhat larger circles of dentine on its buccal cusps. The small size of the canine root and P_3 suggest it was probably female.

Of the three mandibles only 1P28A preserves the symphysis. The strong inferior transverse torus forms a distinct simian shelf that extends further posteriorly than the superior planum as in all Cercopithecinae. The anterior aspect of the symphysis slopes at an angle of close to 38^o as in *Pliopapio* from the Middle Awash, specimen YPM 21551 of *M. libyca*, and most living macaques including *Macaca fascicularis* (Frost, 2001). This trait differentiates the As Sahabi cercopithecines from specimen BSM I505 of *Macaca libyca*, *Parapapio lothagamensis*, and *Parapapio ado* which have more elongated and steeply sloping symphyses (25^o to the occlusal plane of the molar teeth in *P. lothagamensis* according to Leakey *et al* 2003; Figure 2), similar to larger bodied

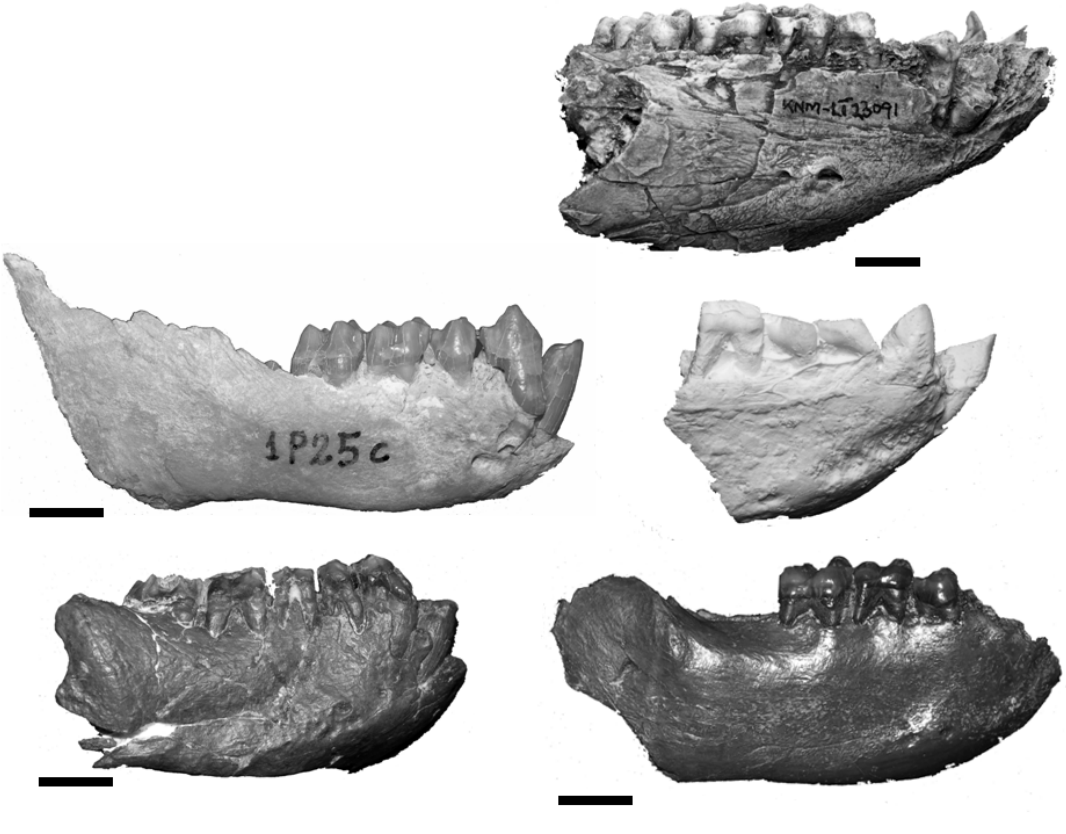


Figure 2. Left column: corpus and symphysis of 1P25C (center) and 1P28A (bottom); Right column: *P. lothagamensis* mandible KNM-LT 23091 (top), and *M. libyca* mandibles BSM I505 (middle) and YPM 21551 (bottom). Scale is 1 cm.

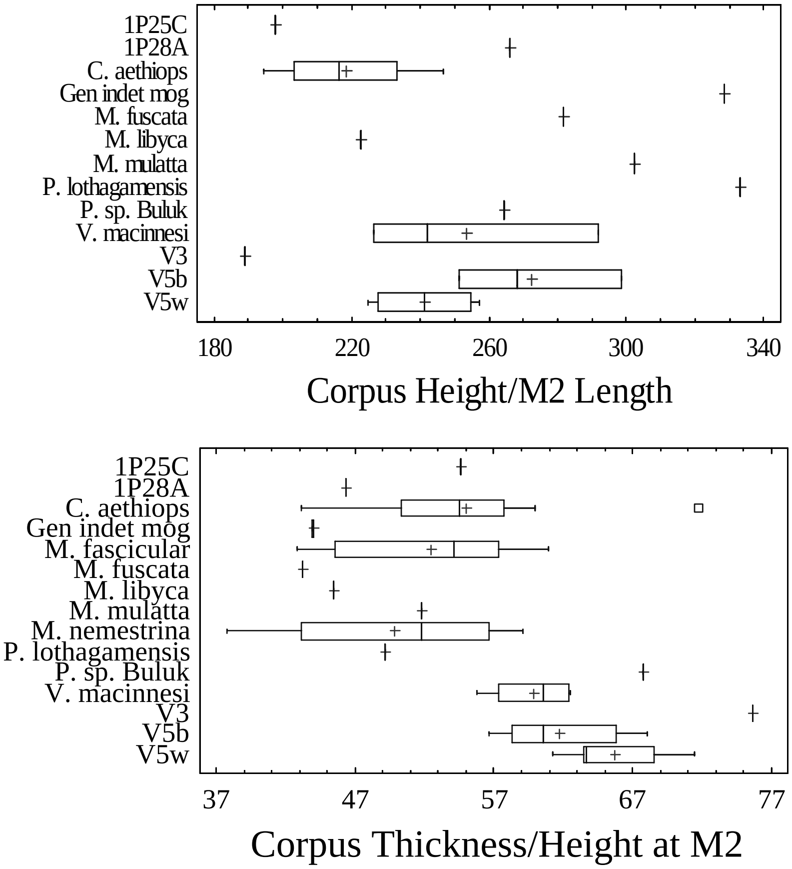


Figure 3. Plots of corpus height versus M2 length and thickness for dimensions of Middle Miocene victoriapithecids (*V. macinnesi)* at three stratigraphic levels at Maboko Island (V3, V5b, and V5w), specimens currently attributed to *Prohylobates* from Wadi Moghara (Gen indet mog) and Buluk (*P.* sp. Buluk), Late Miocene papionins *M. libyca, P. lothagamensis* and As Sahabi specimens, and extant vervets (*Chlorocebus aethiops*) and macaques (*Macaca mulatta, M. fascicularis,* and *M. fuscata*).

baboons and unlike other Old World monkeys. Differences between *M. libyca* specimens BSM I505 and YPM 21551 are difficult to reconcile and may exceed that expected within a single taxon. The ratio of symphysis height to thickness is 117 for 1P28A, but 75.4 for *M. libyca* (specimen BSM I505) and 84.3 for *P. lothagamensis*. Values of symphyseal height to thickness for *M. libyca* and *P. lothagamensis* are closest to baboons, whereas that of 1P28A is similar to extant macaques.

The mandibular corpus of 1P25C resembles that of 1P28A, but is shallower relative to both M_2 length and corpus thickness at M_2 (Figure 3). Differences between the two specimens fall in the range of variation of *M. nemestrina,* and might be attributable to the subadult status and incomplete mandibular growth of 1P25C. *M. libyca* specimen YPM 21551 is intermediate between the two As Sahabi mandibles in terms of corpus height, but is thinner in cross-section than both specimens. The corpus of *P. lothagamensis* mandible KNM-LT 23901 is slightly deeper than 1P28A, although corpus height relative to M_2 length corpus height of the As Sahabi, Natrun, and Lothagam specimens fall within the range observed for *Macaca nemestrina*.

Development of a mandibular fossa is extremely slight in 1P28A and even shallower in 1P25C. This feature differentiates the As Sahabi, Lothagam, and Natrun cercopithecines from *Papio,* *Theropithecus, Mandrillus, Gorgopithecus,* and *Lophocebus* which have well-developed fossae, and makes them more similar to *Parapapio* and *Macaca* among papionins.

Dentition

The erupting male canine of 1P25C is the first known for a cercopithecoid from As Sahabi. It is 8.55 mm long mesiodistally, 5.43 mm wide labiolingually, and more than 12.4 mm tall to the point where the tip is broken away. These dimensions are slightly smaller than those observed for *P. lothagamensis*.

The P_3 of 1P25C is larger than the female P_3 associated with 57P99A, the length of the female P_3 being only 75% that of the male. A similar relationship is found in *P. lothagamensis* for which the average female P_3 length is 83% as large as the males. The male P_3 also has a much larger honing facet (for sharpening of the upper canine) than the female. Lingually the P_3s of 1P35C and 57P99A are very similar in morphology with small but distinct lingual metaconids set distal to the tip of the larger and taller protoconid (Figure 4). Metaconids are present on the P_3s of *P. lothagamensis, Victoriapithecus macinessi*, and undescribed papionins from Taung, but do not occur in *Macaca sp.* from Menacer. P_3 metaconids are extremely rare among

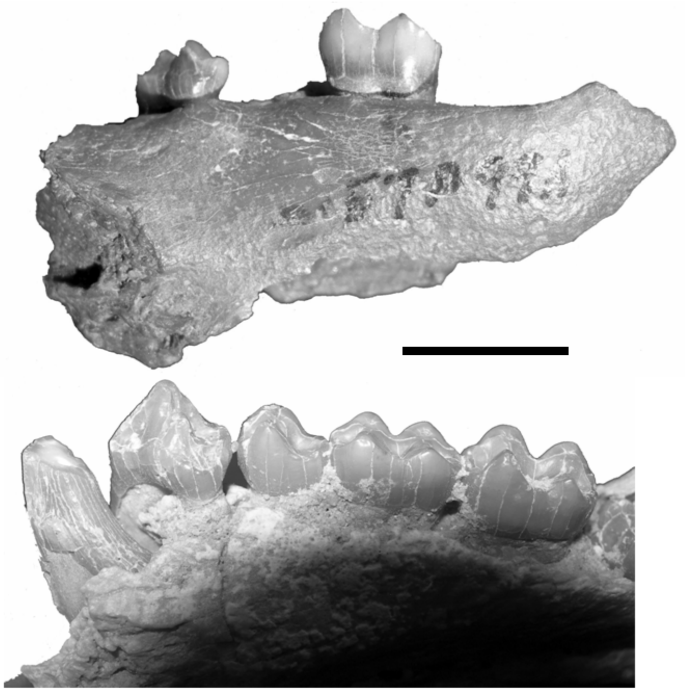


Figure 4. P3 metaconids from lingual view on 57P99A (top) and 1P25C (bottom). Scale is 1 cm.

modern Old World monkeys, although found on one (AMNH 19014) out of four *Macaca sylvanus* and in no other cercopithecine species surveyed at the American Museum of Natural History. Since no unworn P_3 is known for *M. libyca*, its resemblance to other species is not known. On both the male and the female P_3s from As Sahabi postmetacristids join the distolingual corner of the distal margin. The lingual surface of the crown of 1P25C has a deep dimple distally below the postmetacristid. The P_3 of 57P99A has a similar distal lingual dimple, but it is shallower in the female.

The P_4 of 1P25C has a metaconid that is slightly taller than the protoconid, and is broader mesially than distally. The crown is not obliquely rotated relative to the long axis of the molar row. The *P. lothagamensis* P_4 is described as being obliquely rotated as in *V. macinnesi* (Leakey *et al.*, 2003), but examination of casts and photographs indicate that the degree to which it is oblique is slight as in many macaques, and less than that seen in victoriapithecids. As Sahabi and *M. libyca* P_4s appear to have resembled those of *P. lothagamensis* in having been very slightly obliquely oriented, but the condition seems to have little phylogenetic value because it is widespread among cercopithecines.

The first molar of 1P25C is the largest known from As Sahabi. In comparison, the estimated length of the M_1 in mandible 1P28A is the smallest, and the M_1 associated with female partial mandible 57P99A is intermediate in length (Table 3). As Sahabi specimen 841P34A was previously identified as an isolated dp_4, but its length, cusp height, and overall proportions compare well with M_1s from the site. It is treated as an M_1 in this paper. The only well-preserved cercopithecoid M_2s and M_3s from As Sahabi are those of 1P25C. Only the M_3 hypoconulid of the molars in 1P28A has intact enamel. Estimated lengths of 1P28A molars are shorter than those of 1P25C, but within the range of variation expected for a single species.

Late Miocene papionins from Europe, eastern Africa, and northern Africa are all of moderate size, with those from Menacer being the largest (Table 3). M_2s of *M. libyca* are larger than 1P25C, but As Sahabi and Natrun monkeys overlap in M_1 size. M_1 and M_2 lengths of *M.* sp. from Menacer are larger than those from As Sahabi. *P. lothagamensis* is similar to *M. libyca* in M_1 length, but to 1P25C in M_2 length. The M_1 of *M.* sp from the Late Miocene of Spain is just larger than that of 1P25C.

The M_2 of 1P25C is highly distinctive among living and fossil cercopithecoids in being more square due to its width being only slightly less than its length (L/MW=104%), and having more exaggerated buccal flare (MCP/MW=48%) (Figure 5). A rounded cingulum occurs above the cervix on the buccal cusps. Only Middle Miocene victoriapithecids, extant mangabeys, and Allen’s swamp monkey are similar to 1P25C in combining high M_2 buccal flare with nearly square crown dimensions. Worn specimens of *M. libyca* approach 1P25C in shape, but are far less flared. The only unworn specimen attributed to *M. libyca* is much more elongated (L/MW = 120), and moderately flared (MCP/MW=53%). The majority of

Table 3. Craniodental measurements. CD=corpus depth, CT=corpus thickness, L=mesiodistal length, W=buccolingual width, CH=labial crown height, and HF=honing facet height. Measurements for *P. lothagamensis* are from Leakey *et al.* (2003).

MANDIBLE	CDP4	CDM2	CT M2
1P25C	19	16.9	12.1
1P28A	23	22.1	10.2
57P99A			10.5
P. lothagamensis		25.5	12.4
M. libyca YPM 21551	21.84	21.3	9.7

ANTERIOR TEETH	I1L	I1W	I1CH	I2L	I2W	P3L	P3W	P3HF	P4L	P4W
105P16A	4.7	4.8	11.6							
1P25C (male)						7.7	6.25	13.5		
57P99A (female)						5.8			5.6	5.54
P61A				3.5	5.4					

MOLAR TEETH	M1			M2			M3		
LOWER	L	MW	DW	L	MW	DW	L	MW	DW
1P25C	8.2	7.1	7.1	8.9	8.45	7.5	11.2	7.5+	6.7+
57P99A	6.95	5.9	5.85						
1P28A	6.75			8.6			10.6		
841P34A	7.7	6.2	5.9						
M. libyca									
YPM 21551	7.75	6.95	7.25	9.56	8.6	8.3			
YPM 21552	7.45	8.1	7.4	9.9	9.55		13.0	9.9	9.0
cf. *M.* sp. Menacer									
Average	9.1	7.55	6.8	9.55	7.8	7.4	10.4	7.4	6.2
P. lothagamensis									
Average	7.6	6.2	6.4	9.0	7.7	7.2	11.4	7.7	6.8
M. sp. Almenara									
	6.2	6.1							
UPPER									
151P81A				7.15	7.1	6.6			
P61	6.25	6.85	6.0						
M. libyca									
Average	7.7	8.1	7.45	9.5	9.3	8.2	9.1	9.4	8.0
cf. *M.* sp. Menacer									
Average	7.75	7.9	7.25	9.0	8.8	8.05	8.1	8.6	8.5
P. lothagamensis									
Average	8.0	7.8	7.6	9.2	9.3	8.8	8.9	9.1	7.2

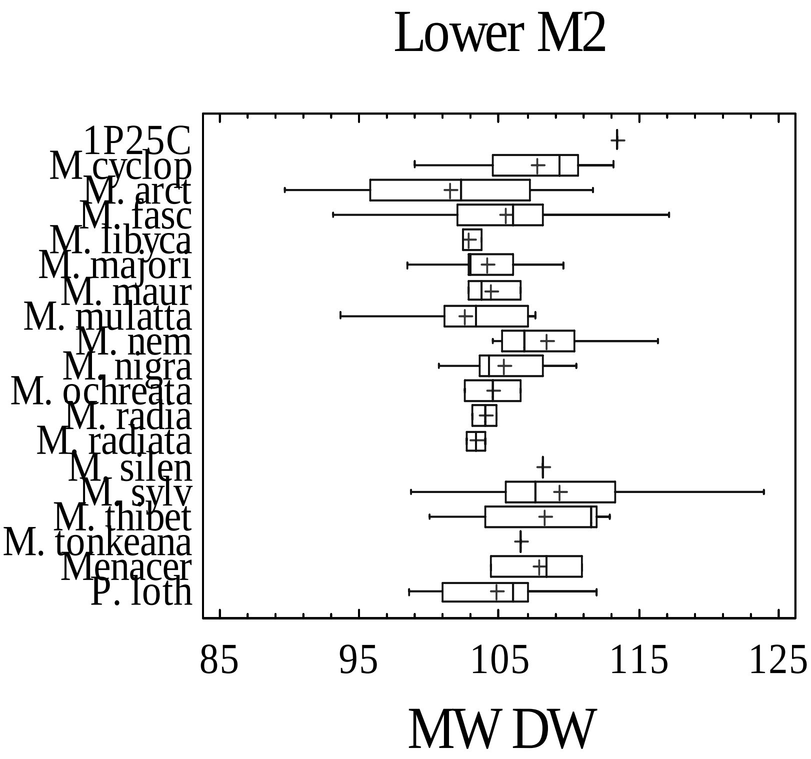
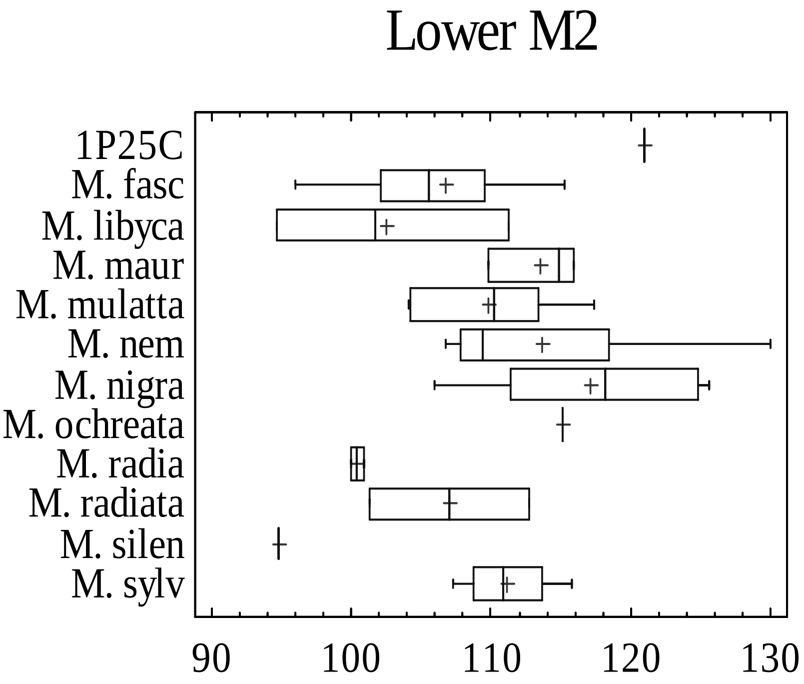


Figure 5. Molar indices showing degree of elongation (crown length [L]/mesial width [MW]) and buccal flare (distance between tips of mesial cusps [MCP]/ mesial width [MW])



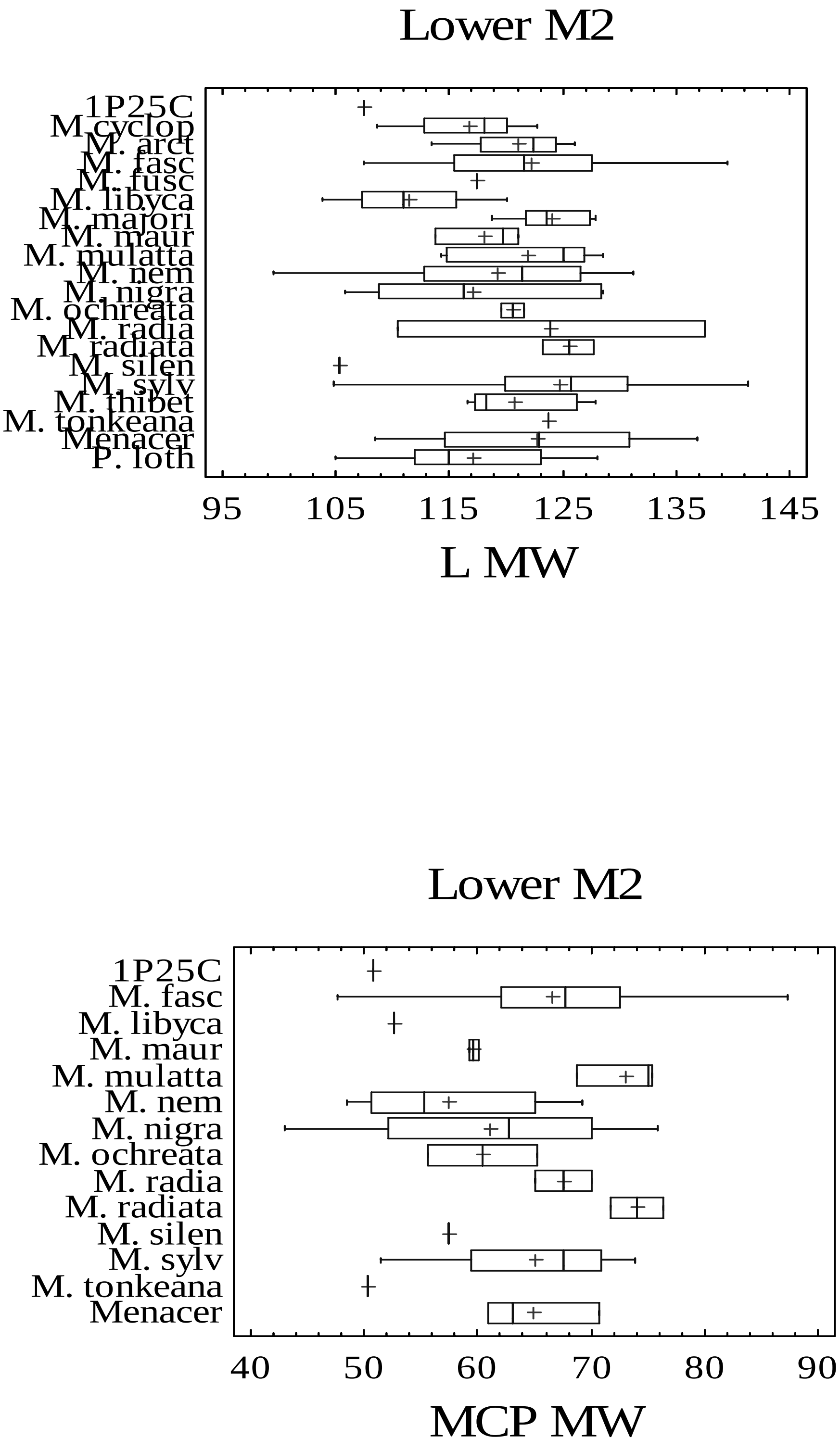


Figure 6. Molar indices showing relative height of the metaconid (MLCH/DLCH) and degree to which mesial width is greater than distal width (MW/DW).

P. lothagamensis M_2s are somewhat longer relative to width, although their molars are described as being highly flared (Leakey *et al*. 2003). *Macaca* sp. from Menacer is very different from 1P25C in being elongated (L/MW=121 on average) and having low buccal flare (MCP/MW=65%). Unworn As Sahabi M_1 841P34A shows the same pattern of high buccal flare as the M_2 (MCP/MW= 50.7), but is the most elongated of As Sahabi M_1s (L/MW=124, range=113-124). The M_1 of 1P25C is less flared due to wear (MC/MW=67), but more square (L/MW=115). M_1s of *P. lothagamensis*, cf. *Macaca* from Menacer, the isolated M_1 from Alemenara, *M. sylvanus*, and *M. majori* are more elongated but less flared than As Sahabi. Highly worn M_1s of *M. libyca* are the squarest of the Late Miocene papionins, but the unworn M_1 is more elongated (L/MW=127). Little flare (MCP/MW=72) is observed on the unworn M_{1s} and no flare is observed on the worn M_{1s} of *M. libyca*.

Mesial width exceeds distal width on the M_2 of 1P25C by an even greater amount than is observed in all other cercopithecoid species sampled (MW/DW=113), and is slightly bigger than distal width for the M_1. Only M_1s from Menacer have even larger mesial than distal widths than is observed for As Sahabi. This difference may be related to an overall small size of the entoconid. The unworn M_1 and M_2 entoconids of 1P25C are much shorter and smaller than the metaconid, a condition seen in *V. macinnesi*, *P. lothagamensis*, and some extant macaques (Figure 6). Because the metaconid is positioned slightly mesial to the the protoconid, the mesial transverse lophid connecting these cusps is obliquely oriented relative to the distal lophid. Such skewing of the mesial lophid is not typical of cercopithecoid lower molars, but is seen among macaques.

Occlusal relief is similarly low for the As Sahabi, Natrun, and Menacer molars and overlaps that of several macaque species and greater than that of late Miocene colobines. The sum of M_2 shear crest lengths is 262% that of crown length for 1P25C as in extant *Macaca fascicularis* and *Macaca nemestrina*, indicating the As Sahabi monkey may have had a similarly frugivorous diet and that they did not feed on hard seeds like the extant mangabeys which have lower shear crest lengths. *M*. sp. from Menacer has higher shear crests similar to *M. radiata*.

What is visible of the erupting M_3 of 1P25C indicates that it would have had high buccal flare like the M_2 and similar occlusal relief. The hypoconulid is small and centrally positioned on both 1P25C and 1P28A. Entoconid size is very small in width and crown height. In contrast entoconids are well-developed, and hypoconulids are large and positioned buccally at the end of a long and transversely oriented postentoconid in both *P. lothagamensis* and *M. libyca*.

Other As Sahabi Teeth

In addition to the new specimens, the cercopithecoid collection includes an unworn lower central incisor, 105P16A. Its very thin lingual enamel indicates that it had papionin affinities and could easily belong to the same species as 1P25A. A very worn lower lateral incisor was collected by Jordi Agusti in 1999 and is of similar size.

Two upper molars are now known from As Sahabi, an upper right M^2 (or 3) 151P81A and an upper left M^2 (or 1) from P61A collected by Jordi Agusti. Both are smaller than upper molars of other North African papionins and *P. lothagamensis*, although they overlap in size with M^1s and M^3s of *Mesopithecus*. The tooth found by Agusti is wider than long, whereas 151P81A is as wide mesially as long. Both specimens are constricted distally with greater mesial than distal width, as in many colobine and cercopithecine species. Cusp relief on both specimens is lower than that observed in modern colobine species, but similar to that observed in the late Miocene colobines *Mesopithecus* and *Colobus flandrini*, and in many late Miocene and extant papionins. Specimen 151P85A has a lower degree of buccal flare (MCP/ MW=69) than most papionins and late Miocene colobines. A low degree of flare is observed on worn specimens of *M. libyca*, but the condition in unworn specimens is unknown. *M.* sp. from Menacer shows more flared upper molars than 151P81A although lower molars of the species are less flared than those from As Sahabi. Nothing aligns 151P85A definitively with either Colobinae or Cercopithecinae.

Distal Humerus

The new As Sahabi distal humerus 514P28A (Figure 7) was collected by Noel Boaz in 2007. It exhibits cercopithecine morphological features consistent with close affinities to cercopithecines in general

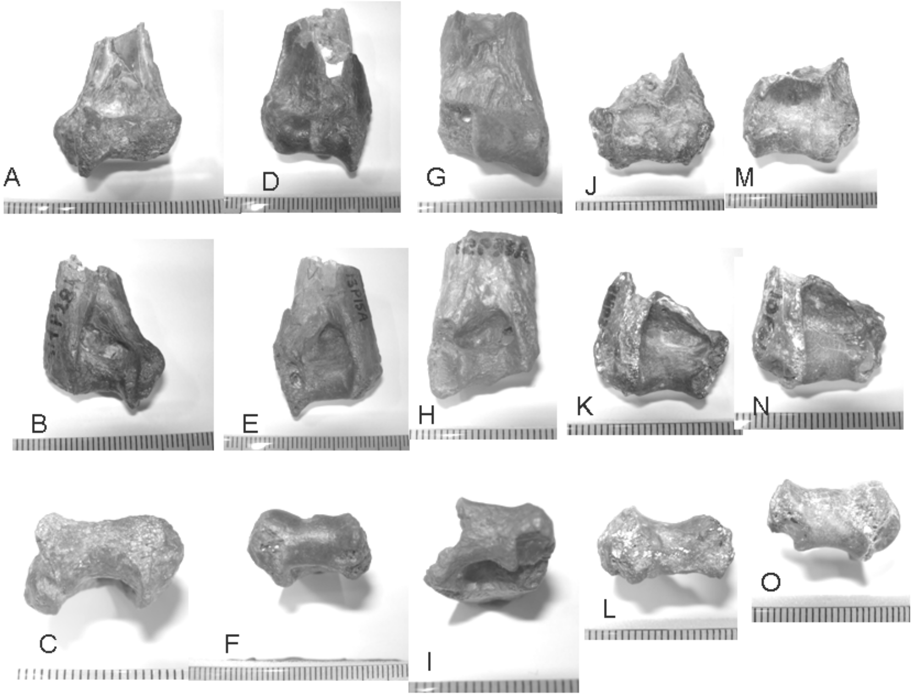


Figure 7. Cercopithecid distal humeri 514P28A (A-C), 13P15A (D-F), 12P33A (G-I), 34P30A (J-L), and 10P61A (M-O) in anterior (top row), posterior (middle row), and distal (bottom row) views. Scale divisions are mm.

and, with less certainty, to papionins in particular. Overall, the 514P28A distal humerus finds its greatest resemblance with semi-terrestrial and terrestrial cercopithecoids, such as the vervet monkey (*Chlorocebus aethiops*), macaques, and Middle Miocene *V. macinnesi*. Its size is consistent with the species represented by the new mandible 1P25C as well as 1P28A from the same locality. The dimensions of 514P28A are presented in Table 4. This specimen is reasonably complete and well-preserved in spite of some erosion. It is better preserved than the four cercopithecid distal humeri previously collected at As Sahabi (13P15A, 12P33A, 34P30A, 10P61A, see Figure 7; Meikle, 1987).

The new distal humerus from As Sahabi exhibits a fundamentally cercopithecoid morphology in several respects. The medial trochlear keel is strongly developed, compared with its weaker expression in primitive catarrhines and hominoids, and projects both anteriorly and distally from the remainder of the humeral-ulnar articulation. The anterior surface of the capitulum is flattened, compared with the spheroidal convexity of the humero-radial articulation in hominoids. The medial epicondyle, which forms the area of origin of the carpal and digital flexors, is abbreviated and posteriorly oriented, compared with the longer and more medially directed medial epicondyle of hominoids. Moreover, 514P28A lacks the well-developed median (or lateral) trochlear keel and *zona conoidea* of hominoids.

To a great extent, the cercopithecine-like features of 514P28A probably relate to adaptations for a semi-terrestrial/terrestrial substrate preference. The medial trochlear keel of 514P28A is very strongly developed so that it extends as a distinct flange distally and anteriorly. Extant colobines, in contrast, typically have a less well-developed trochlear keel. The strongly posterior orientation of the medial epicondyle of 514P28A is also like that of terrestrial cercopithecines. Extant colobine medial epicondyles are usually more medially oriented. The deep and narrow humero-ulnar articulation of semi-terrestrial/terrestrial cercopithecines, tightly limiting elbow motions to flexion and extension, is mirrored in the structure of 514P28A. The new specimen also has strong development of a flange on the lateral margin of a deep olecranon fossa. This lateral flange would have articulated with a proximal extension of the anconeal process of the ulna (a condition present on 179P15A, a cercopithecine-like ulna previously collected at As Sahabi [Meikle, 1987]).

Two conditions of 514P28A are unusual. First, the medial surface of the distal humerus (between the medial trochlear keel and the medial epicondyle) is marked by a very deep and well-defined fossa. Second, both the coronoid and radial fossae (but especially the former) are deeply hollowed. This latter condition is also clearly expressed in 34P30A, a much less complete cercopithecid distal humerus from As Sahabi.

Most of the distal humeri from As Sahabi lack sufficient morphology to be certain which subfamily they represent. 10P61A is probably colobine because it has strong development of the lateral trochlear keel and a more spheroidal capitulum than 514P28A. 13P15A also appears to differ from other distal humeri due to its more

Table 4. Measurements of As Sahabi cercopithecoid distal humerus 514P28A

Maximum medio-lateral breadth of distal end	24.8
Maximum antero-posterior thickness of distal end	15.1
Antero-posterior thickness of medial trochlear keel	12.5
Proximo-distal length of medial trochlear keel	12.9
Maximum medio-lateral breadth of trochlea	ca. 11.5
Maximum medio-lateral breadth of capitulum	ca. 8.4
Medio-lateral breadth of coronoid fossa	7.4
Medio-lateral breadth of radial fossa	4.3
Proximo-distal length of mid-trochlea	7.6
Proximo-distal length of capitulum	9.0
Medio-lateral breadth of olecranon fossa	9.9
Medio-lateral breadth of trochlea posteriorly	9.5
Maximum antero-posterior depth of olecranon fossa	7.9
Medio-lateral breadth of lateral supracondylar crest (from olecranon fossa)	8.5
Orientation of medial epicondyle	71 degrees

expansive lateral trochlear keel and spheroidal capitulum. It too may have colobine affinities. The absence of a medial epicondyle makes it difficult to test whether either of these possible colobines had a more arboreal adaptation as is indicated by the more expansive trochlear keel and spheroidal capitulum.

CONCLUSIONS

Both the new cercopithecoid mandible and distal humerus from As Sahabi are cercopithecines and may belong to the same species. The mandible and other papionin teeth from As Sahabi are readily distinguished from fossil macaques from the site of Menacer. They are more similar to *M. libyca* from Wadi Natrun, although differences exist between the Natrun and As Sahabi fossils. Both have similarities to the eastern African Late Miocene species *P. lothagamensis*. The unusually high degree of buccal flare on the molars is sufficient to place them in a new species, but deciding whether to place it in the genus *Macaca* or *Parapapio* is more difficult to determine. In the past, placement of the North African fossil papionins into *Macaca* rather than *Parapapio* rested solely on their geographic location, primitive dentition, and the assumption that *Macaca* had its origins in North Africa (Delson, 1980). Fossil papionins that may be ancestral to *M. sylvanus* first occur at Casablanca in Spain 6 million years ago (Kohler *et al*., 2000). It is equally possible that the Natrun and As Sahabi specimens belong to a widespread African radiation of Miocene *Parapapio*. The squarish shape and the unusually high buccal flare of the As Sahabi molars and the elongated and steeply sloping symphysis of

M. libyca make their connection to *Parapapio,* especially to *P. lothagamensis,* highly tenable.

Reexamination of previously collected specimens from As Sahabi indicates that colobines were extremely rare at the site and may only be represented by one or two postcranial elements and upper molars that are difficult to distinguish from Miocene papionins. In contrast, the complete skull of *Libypithecus markgrafi* from Wadi Natrun is clearly colobine and distinct from that of the European *Mesopithecus*. Its long shear crest and high frequency of microwear scratches on its molars indicate that *Libypithecus* was the oldest known committed folivore in the colobine fossil record (Reitz, 2002; Reitz and Benefit, 2001). It is more likely related to the new colobines from Lemudong'o or to the Pliocene large-bodied colobines from eastern Africa, such as *Paracolobus* and *Rhinocolobus*. If colobine, the As Sahabi upper molars exhibit a much lower degree of shearing potential and cusp relief than *Libypithecus* and would have consumed as many leaves as fruits, similar to the diet predicted for *Mesopithecus* and *C. flandrini*. Its affinities might have been with the Miocene colobines of Europe. More evidence is needed to test this hypothesis.

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