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News and Views

New primate remains from Mwenirondo, Chiwondo Beds in northern Malawi

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Introduction

The Hominid Corridor Research Project (HCRP) undertook its long-term paleontological survey of Plio-Pleistocene deposits of the Malawi Rift, the Chiwondo Beds, in 1983 (Bromage et al., 1985, 1995a). The project has recovered a vertebrate assemblage important for its geographic location between the well-known hominid-bearing sites of eastern and southern Africa. Primate remains are rare among the fauna of the Chiwondo Beds (<1% of total mammalian collection). To date, these include two hominins: a maxillary fragment of *Paranthropus boisei* from Malema locality RC 11, (Kullmer et al., 1999), and a mandible of *Homo rudolfensis* from Uraha locality U 18 (Schrenk et al., 1993; Bromage et al., 1995a), as well as 13 cercopithecoid primate cranio-dental remains, including three jaw fragments (Bromage and Schrenk, 1987; Frost and Kullmer, 2008). Here, we report on three new primate dentognathic specimens (one hominin and two cercopithecine) from the Mwenirondo localities in the vicinity of Malema.

Geology and biostratigraphy

The sedimentology and geology of the Northern Malawi Rift are described by Ring and Betzler (1995) and Betzler and Ring (1995). The Chiwondo Beds are separated into Units 1–4 (numbered stratigraphically from lowest to highest), which refer to lake-beds and fluviatile deposits. Unit 5 is distinguished as the Chitimwe Beds and consists of alluvial fan deposits.

The silty fine to middle sand deposits at Malema locality RC 11 where the *P. boisei* maxilla was found (Kullmer et al., 1999) have been previously described as part of a delta plain belonging to stratigraphic Unit 3A (Sandrock et al., 1999, 2007). The Mwenirondo area, including localities MR 10 and MR 11 where the new specimens come from, is located immediately to the north of Malema. Localities MR 10 and MR 11 are part of a tributary system further inland, and consist of fluviatile middle to coarse sands also belonging to Unit 3A. Further west of MR 10 and MR 11, the Mwenirondo sediments change to lake deposits with bioclastic beaches of high-energy ramp associations characteristic of Unit 2 (Betzler and Ring, 1995). No mammalian fossils have been recovered from Unit 2 at Mwenirondo.

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The Plio-Pleistocene age of the Chiwondo Beds relies on faunal correlation with radiometrically dated biostratigraphic units in eastern Africa (Bromage et al., 1995a; Kullmer, 2008). In general, the faunal assemblage is taphonomically biased toward the representation of large terrestrial mammals, crocodiles and fish (Sandrock et al., 1999). Unit 3A is dated to between 3.75 and 1.8 Ma (Bromage et al., 1995a; Sandrock et al., 2007). Analysis of fossil suids differentiates an older biozone 3A-1 (3.75–2.7 Ma) with *Notochoerus euilus*, from a younger biozone 3A-2 (2.7–1.8 Ma) yielding *Notochoerus scotti* and *Metridiochoerus andrewsi* I/II (Kullmer, 2008).

The Mwenirondo large mammal fauna consists of bovids, equids, suids, rhinos, giraffids, hippopotamids, cercopithecids (see Table 1, Sandrock et al., 2007) and a newly discovered hominid. A refined attribution of the Mwenirondo MR 10 and MR 11 fauna into biozone 3A-1 or 3A-2 is not possible at the present stage. Among the primates described so far, *Parapapio* sp. is known from the Mwenirondo area, whereas *Theropithecus* sp. and *Parapapio* sp. are known from adjacent Malema localities (Bromage and Schrenk, 1987; Sandrock et al., 2007; Frost and Kullmer, 2008).

Description

The new primate material consists of two isolated dental fragments and a partial mandible with teeth (Figs. 1–4) collected through surface survey at Mwenirondo localities in 2009 and 2010.

Specimen HCRP-MR-1106 from locality MR 10 represents a strongly eroded and rounded fragment of a heavily and flatly worn hominin lower molar that is likely from the right side (Fig. 1) with a maximum preserved buccolingual width of 13.06 mm and maximum preserved mesio-distal length of 9.91 mm. The dental fragment comprises the anterior half of the crown and both branches of the mesial root. Dentine is exposed mesially on the occlusal surface due to *postmortem* enamel damage, although most of the visible dentine on the occlusal surface is from a large wear basin; this fact does not allow for any cusp delineation on the surface. There is a short dendritic remnant of a fissure traceable in the buccolingual direction along the enamel surface on the lingual occlusal aspect (Fig. 1e). The transverse break through the crown reveals a low pulp chamber surrounded by thick dentine towards the occlusal surface. Lateral enamel thickness along the middle third of the fracture through the lingual cusp (Fig. 1a) is on average 1.8 mm. While this measurement may not present the original thickness due to the diagenetic effects of transport and minor acid dissolution, the typical fading of Hunter-Schreger bands approximately 0.4 mm from the outer surface enamel suggests that the enamel thickness is reasonably intact. The plate-like root morphology and flatly worn and relatively thick enamel are typically hominin (Fig. 1). The transverse μCT cross-section halfway between the root bifurcation and the apex of HCRP-MR-1106 (Fig. 2) shows that the root has two near-circular lingual and buccal columns which are connected by a mesio-distally compressed bar (Fig. 3). Comparison of μCT radiographic cross-sections with other fossil hominins from eastern Africa, modern humans, great apes and cercopithecoids shows that the so-called dumbbell-shaped root outline (Ward et al., 1982) is characteristic for the M_1s and M_2s of early hominins such as *P. boisei* (KNM-ER-729) and *Homo habilis/rudolfensis* (HCRP-UR-501, KNM-ER-1802, KNM-ER-1805) (Figs. 2 and 3). Furthermore, dumbbell-shaped mandibular molar roots have been described in *P. robustus* from Swartkrans (Robinson, 1956) and *A. afarensis* from Hadar (Ward et al., 1982). Even though there is a considerable overlap in mesio-distal constriction of the mesial molar root in the comparative sample, it seems less

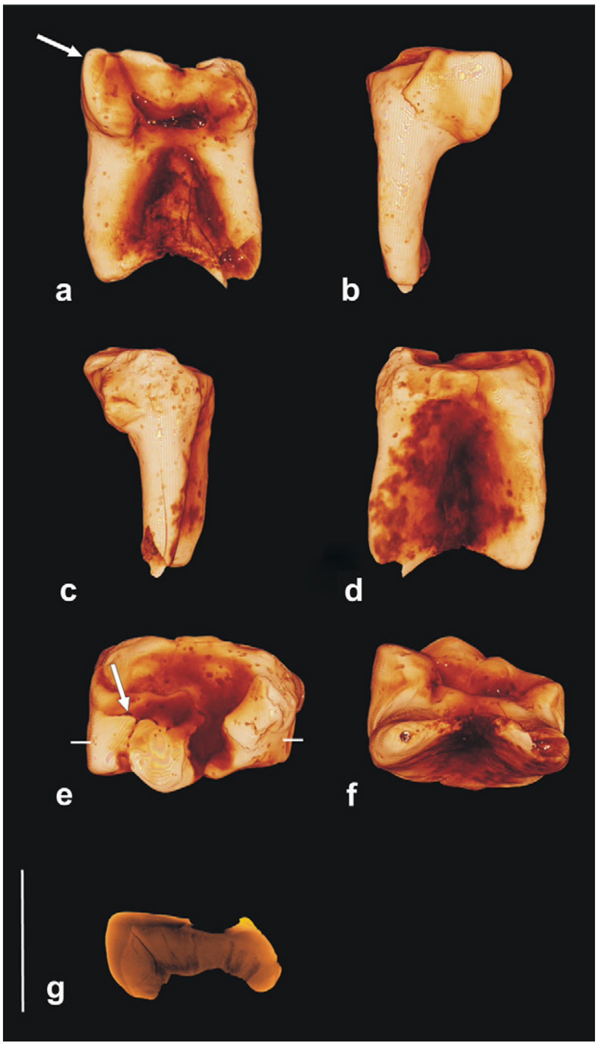

Figure 1. Virtual 3D reconstruction of the lower right molar fragment HCRP-MR-1106, *H. rudolfensis*, derived from μCT-data using the volume texture rendering "Voltex" in AMIRA® 5.3 (Visage Imaging GmbH), (a) distal view, arrow points to the location where enamel thickness and micro-anatomical measures were taken; (b) lingual view; (c) buccal view; (d) mesial view, (e) occlusal view (mesial above, lingual left), arrow points to fissure remnant; (f) apical view; (g) transverse crown cross-section taken as indicated in (e) by white lines; scale bar = 1 cm.

Table 1
Comparative enamel micro-anatomical measures of HCRP-MR-1106, HCRP-UR-501, *H. rudolfensis* and other East African hominids.

Trait	*HCRP-UR-501, RM_2	**H. rudolfensis*	HCRP-MR-1106	**EAF ROB	**EAF HOM
Lateral enamel thickness (LT) (mm)	2.33	1.6–1.8	1.8	2.2	1.9
I degrees (°)	79		71	52	62
D degrees (°)	32		***11 (cervical third)	23	31
HSBW (μm) (middle third of lateral enamel)	56		61	52.8	62
HSBC (middle third of lateral enamel)	***4 (cuspal third)	1–2	1–2	1–2	4–5

*Bromage et al., 1995b; **Beynon and Wood, 1986; ***Measures for the other specimens in this trait category are taken from the middle third of lateral enamel and caution must be exercised in comparisons to other values in the row.

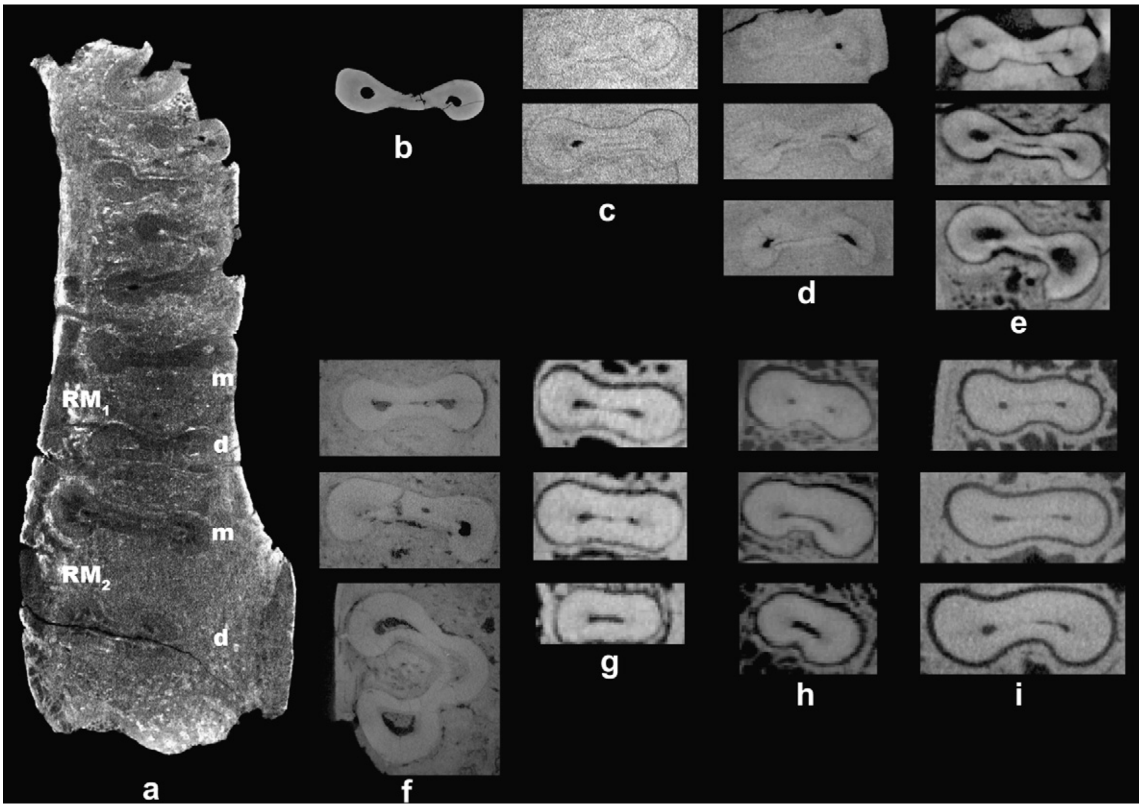

Figure 2. Transverse µCT cross-section images of hominin, great ape and cercopithecine mandibular molar roots taken halfway between the root bifurcation and the apex; (a) *H. rudolfensis* (HCRP-UR-501), right mandible C – M_2; (b) HCRP-MR-1106, right lower molar mesial root; (c) *H. rudolfensis* (KNM-ER-1802), right lower M_1 (top) and M_2 (bottom) mesial roots; (d) *H. habilis* (KNM-ER-1805), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots; (e) *P. boisei* (KNM-ER-729), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots; (f) *H. erectus* (KNM-ER-992), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots; (g) *H. sapiens* (recent), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots; (h) *P. troglodytes* (recent), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots; (i) *M. mulatta* (recent), right lower M_1 (top), M_2 (middle), M_3 (bottom) mesial roots. Not to scale.

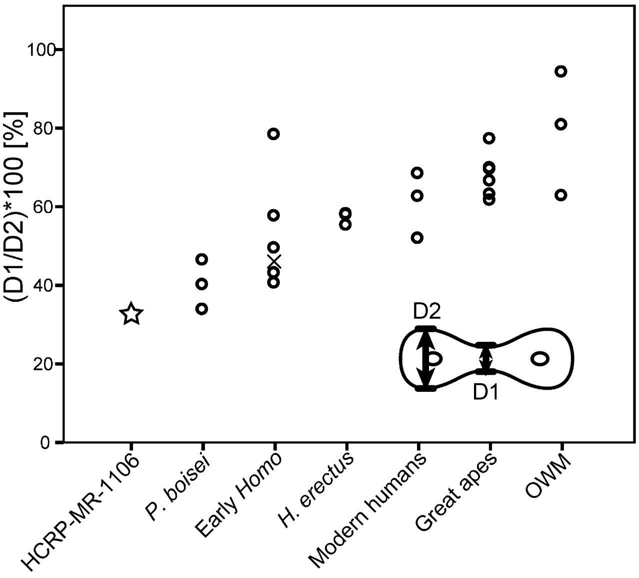

Figure 3. Comparison of mesio-distal constriction of mesial molar root of mandibular first molars. Measurements taken from µCT cross-section images halfway between the root bifurcation and the apex at minimum (D1) and maximum (D2) mesio-distal width (mesial is at the top). Specimen HCRP-MR-1106 shows close proximity to *P. boisei* and early *Homo*. The X indicates HCRP-UR-501. OWM = Old World Monkeys.

pronounced or absent in later *Homo* (*erectus* and *sapiens*) as well as in great apes and cercopithecoids, while in HCRP-MR-1106 it is noteworthy (Figs. 2 and 3). A definite identification of the tooth position (M_1, M_2 or M_3) of HCRP-MR-1106 is not possible due to the missing distal root. However, an attribution to M_3 is unlikely, because of the more variable root morphology of the latter compared to that of M_1 and M_2 (Robinson, 1956; Fig. 3).

Confocal and incident polarized light microscopy of enamel microstructure at the transversely fractured surface of the lingual crown (Fig. 1a) identifies characteristics of HCRP-MR-1106 typically associated with the UR 501 hominin from Malawi, *H. rudolfensis*, and *Paranthropus* (Table 1). The prism orientation, measured as the average angle at which Hunter-Schreger bands (HSB) meet the enamel–dentine junction (EDJ), or "I degree", is 71°. The average angle at which striae of Retzius meet the EDJ in lateral enamel, or "D degree", is 11°. The Hunter-Schreger band width (HSBW) at the middle third of the lateral enamel gives an average value of 61 µm. The Hunter-Schreger band curvature (HSBC), represented as the number of bands crossed from a line drawn along the HSB axis in outer surface enamel to the EDJ, measures 1–2 bands crossed. The enamel of HCRP-MR-1106 is similar to the UR 501 hominin from Malawi belonging to *H. rudolfensis*, and other *H. rudolfensis* and East African *Homo* (EAFHOM) specimens in two characters (I degree and HSBW), whilst two characters (LT and HSBC) share their affinities with early *H. rudolfensis* and only one (HSBC) with *Paranthropus* (Table 1). Admittedly, the opportunistic approach taken in the past to obtain micro-anatomical data, such as that presented here, may yield results that vary by section plane, tooth type, etc. However,

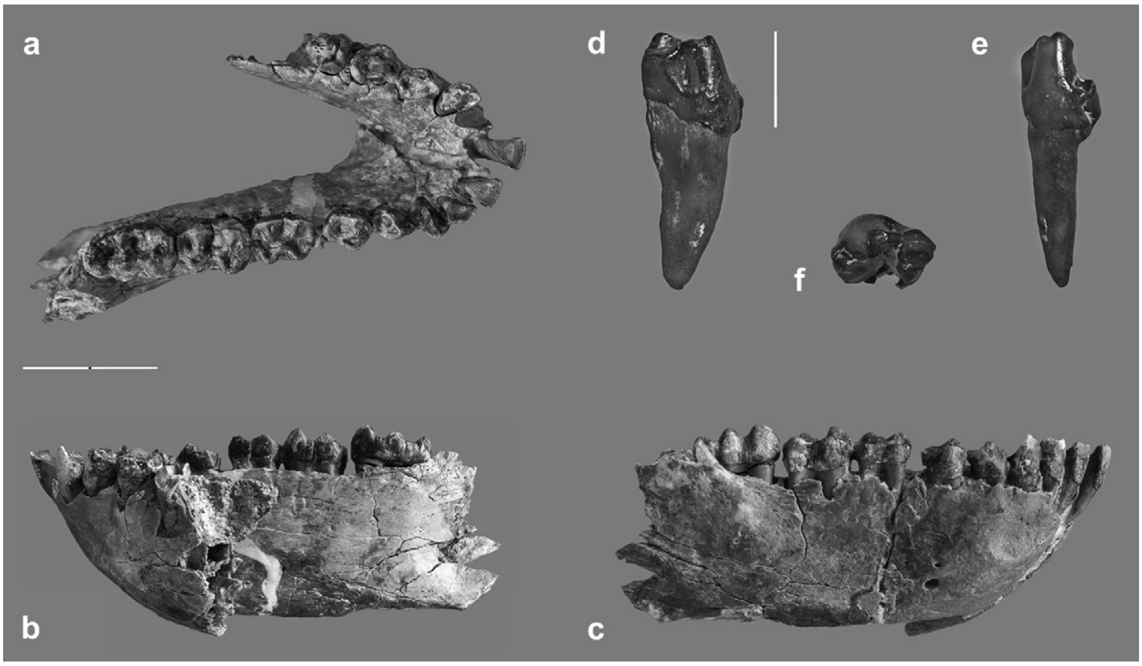

Figure 4. Partial mandible HCRP-MR-1043, *Parapapio* sp.; (a) occlusal view, (b) left view, (c) right view; scale bar = 2 cm. Molar fragment HCRP-MR-1166, *Theropithecus* sp. (d) distal view, (e) occlusal view, (f) buccal view; scale bar = 1 cm.

until such time as larger, controlled studies are made, we can only work with what is available. We thus note that the trait combination, which includes micro-anatomical similarities to *Homo* and *Paranthropus*, is typical for earliest *Homo* (Bromage et al., 1995b), and we tentatively assign the new hominin specimen to *H. rudolfensis*.

Specimen HCRP-MR-1043 is a cercopithecine female mandibular fragment with the right corpus and I_1-M_3, and left I_1, C, P_3, broken P_4 crown, and mesial M_1 root (Fig. 4). The left corpus is broken posterior to the M_1 roots. Both rami are lacking. The mandible shows breaks filled with sediment at the symphysis and a 2 mm interproximal gap between right P_4 and M_1 caused by *postmortem* breakage. The symphysis is marked by modest mental ridges. It is difficult to determine if a median mental foramen was present due to cracking in the midline. In lateral view, the symphysis is moderately receding similar to most papionins, but less so than in *Parapapio ado* and *Parapapio lothagamensis*, nor does it have the "sigmoidal" profile of *P. ado*. The incisors are vertically implanted. In overall depth the corpus is shallow and approximately even in depth from anterior to posterior; it is also relatively narrow, thinning towards its inferior margin. A shallow mandibular corpus fossa is present with the inferior border marked by modest ridges that are developed mesially on the lateral faces of the symphysis extending from I_1 towards the mesial P_3s. The corpus fossae are shallower than those of most African papionins and similar to those of *Macaca*, *Parapapio*, *Cercocebus,* and *Theropithecus oswaldi darti*. The dental arch was likely narrow. In superior view, the superior transverse torus extends posteriorly to the level of the P_3 and the inferior to the level of the P_4. Two very small and one large mental foramina are present on the right corpus externally. The most inferior foramen, situated below the P_4 crown, possesses the largest diameter. On the left corpus only one matrix-filled foramen can be identified.

The incisors show advanced wear with sharp edges, and clearly lack enamel as is typical of papionins. They are relatively vertically positioned in the symphysis with the left I_1 slightly offset due to *postmortem* alteration. The left I_2 is missing. They are fairly small in size relative to the molars, similar to *Parapapio*, *Paradolichopithecus*, and *Theropithecus*, but unlike most other papionins (Table 2; Frost, 2001a). The small size of the canines (mesio-distal 5.09 mm, buccolingual 5.92 mm, height 8.53 mm) identifies the specimen as female (Table 2). Crowns are slender and pointed with an elongate wear facet along the distal edge. A small posterior tubercle is present at its crown base. The P_3 is short with a reduced mesiobuccal flange likely accommodating a small upper canine. A talonid basin is present disto-lingually. The P_4 is larger than the P_3, with protoconid and metaconid cusps and an enlarged talonid basin. The P_4 is moderate in size with a P4/M1 ratio of 0.7; it is at the bottom of the range for *Mandrillus* and *Cercocebus*, but in the middle of the range for most other papionins, including *Parapapio* (Table 2; Fleagle and McGraw, 1999). The molars show a typical papionin relief and wear pattern with relatively low cusps, notches high above the cervical line, and poorly developed transverse lophids. The degree of crown flare is similar to that of most papionins, lower than that of *Cercocebus*, and greater than that of *Theropithecus* and possibly *Pliopapio*. The mesial lophids are wider than the distal, except in M_1. The M_1 is the smallest and M_3 is the longest with a prominent hypoconulid (Table 2).

In size, the molar teeth (Table 2) best fit the range of *P. ado* and *Parapapio jonesi* and are at the lower limit for *Parapapio broomi* (Freedman, 1957, 1976; Freedman and Stenhouse, 1972; Leakey and Delson, 1987; Frost and Delson, 2002; Harris et al., 2003). The M_3 dimensions are small and comparable with M 3051 and M 3061 from Makapansgat that overlap both *P. jonesi* and *P. broomi* in size and recognized as the former by Maier (1970) and the latter by Freedman (1976). The M2 is also considerably narrower than that of HCRP-RC-128b, though it is similar in length (Frost and Kullmer, 2008). Their differences are within the range expected for a single species, however (see several papionin species listed in Table 2). On the whole, the morphology of the HCRP-MR-1043 mandible is comparable with *P. ado* LAET 209 (Plate 4.1 p. 94, Leakey and Delson, 1987; Fig. 6.5 p. 94, Harrison, 2011), although the symphysis is less receding in the Mwenirondo specimen. It is also similar to SK573 a *P. jonesi* (Freedman, 1957), and KNM-WT

Table 2
Tooth crown measurements of *Parapapio* sp. mandible HCRP-MR-1043, other specimens from the Chiwondo Beds and various modern primates.

Sample	*N*	I_1		I_2		C			P_3		P_4		M_1			M_2			M_3			I_1L/M_2AW	LP_4/LM_1
		W	*L*	*W*	*L*	*W*	*L*	*H*	*W*	*L*	*W*	*L*	AW	PW	*L*	AW	PW	*L*	AW	PW	*L*		
HCRP-MR-1043 (L)		**5.1**	**5.5**			**5.7**	**5.0**	**8.5**	**5.5**	**6.4**	**6.5 (e)**	**7.1**										**0.54**	
HCRP-MR-1043 (R)		**5.0**	**4.7**	**4.6**	**4.5**	**5.9**	**5.1**	**8.3**	**5.6**	**6.2**	**6.7**	**7.2**	**7.1**	**7.9**	**9.1**	**8.8**	**8.5**	**11.0**	**8.4**	**8.0**	**13.7**	**0.62**	**0.70**
HCRP-RC1-128																10.0	8.8	11.1					
HCRP-RC11-870											7.0	7.4	7.6		9.5								0.72
HCRP-U39-476															9.1	9.4		11.2	9.7		14.2		
UCMP 97121		6.1	6.0																				
Parapapio jonesi	16	4.7–6.1	4.9–5.5	3.7–6.2	4.3–5.2	6.5–9.1	3.8–5.7	8.3–10.5	4.7–5.5		5.9–7.0	6.3–7.3	6.6–7.6	6.5–7.4	7.7–9.6	7.4–9.5	7.5–9.2	8.8–11.2	8.7–9.7	8.0–8.4	11.7–14.1	0.60–0.61	0.55–0.77
Parapapio broomi	37	5.9–6.2	4.5–6.0	5.7–5.8	3.9–5.6	6.7–8.7	4.3–5.4	7.5–11.3	4.6–6.1		5.6–8.2	6.0–8.2	7.2–9.0	7.2–8.8	7.6–10.5	8.8–10.8	8.5–10.3	9.7–12.4	8.2–10.9	8.0–10.2	12.1–15.8	0.57–0.60	0.54–0.90
Parapapio whitei	1	6,0	5,7	6,0	5,3	8,0	5,3	13,9	5,6		7,3	7,4	8,3	8,7	9,8	10,7	10,4	13,6	11,3	10,4	16,5	0,53	0.65–0.73
?Parapapio ado - Laetoli	9	4.5–5.6	4.5–6.3	4.6–5.9	4.3–5.4	5.1–7.1	3.0–5.0	8.0–11.1	3.6–5.0		5.5–6.5	5.8–7.5	6.3–7.5	6.5–8.0	7.7–9.6	8.2–9.1	7.8–9.4	9.7–11.3	7.8–9.5	6.5–8.7	12.5–14.3	0,69	0.58–0.69
Lophocebus sp. nov.	2										4.9–5.4	6.2–6.4	5.4–5.9	5.9–6.1	7.9–8.0	7,3	7,4	9,5					0.64–0.76
Taung Papionini	6	5.8–6.5	5.4–5.8	6.0–6.2	5.3–5.6	7.0–7.8	3.2–4.3	9.7–13.0	4.7–6.4		6.4–7.0	7.2–8.2	7.0–8.1	7.2–7.9	9.5–10.0	8.4–9.5	8.3–9.5	10.7–11.8	8.6–9.6	7.4–8.9	12.5–14.2	0.60–0.69	0.74
Cercocebus torquatus	11	5.6	4.7–4.9	4.7–4.8	4.3–4.7	4.9–5.5	3.5–4.1	7.0–9.8	3.9–4.4		5.0–5.9	5.3–6.8	5.7–6.4	5.6–6.7	6.2–7.5	7.0–7.9	6.4–7.9	7.4–8.9	6.0–7.8	5.7–7.2	7.6–10.0	0.63–0.70	0.70–0.80
Mandrillus sphinx	13	7.2–8.5	4.4–6.7	6.1–7.7	4.0–5.6	7.3–9.0	4.4–5.4	7.1–14.7	4.5–7.6		6.0–8.8	7.6–10.2	6.7–9.2	7.0–8.7	7.7–10.9	7.6–11.8	7.3–10.6	9.8–13.1	8.2–12.1	7.4–10.6	11.2–19.0	0.47–0.88	0.68–0.98
Lophocebus albigena	21	6.2*	6.5*	6.4*	4.6*				4.6*		4.0–5.0	4.3–5.8	4.8–5.6	4.9–5.8	5.4–6.8	5.6–6.9	5.4–6.4	6.0–7.5	5.2–6.9	4.5–5.8	5.7–8.0	0.88	0.55–0.83
Papio hamadryas	110	5.8–9.0	4.8–8.3	4.8–8.8	3.8–7.3	7.1–9.7	4.3–7.7	8.3–18.3	4.4–6.2		5.7–7.4	6.7–10.0	6.4–8.9	6.8–9.1	8.0–12.0	7.9–11.5	8.3–11.1	9.5–15.3	8.8–12.4	8.1–10.9	11.9–18	0.64–0.76	0.52–0.88
Theropithecus gelada	12		3.6–5.2						3.9–5.6		5.7–7.1	6.2–8.0	6.6–8.0	6.9–8.5	7.8–10.4	8.3–9.7	8.0–9.0	10.1–12.1	9.2–10.6	8.2–9.2	14.1–16.2	0.40–0.60	0.59–0.80

In all cases, W = either labiolingual or buccolingual width, and L = mesio-distal length. For canines, H = maximum crown height. All data are from specimens identified as female, except for *Lophocebus albigena* anterior dentition (*) for which in addition to the 21 female specimens a male individual was used. Taung Papioni material includes both *Procercocebus antiquus* and *Papio izodi* as mandibles and lower dentition of these species cannot be reliably distinguished in the Taung sample. *Papio hamadryas* includes all subspecies except *P. h. kindae*. No comparative data is provided on P3 length because of different ways this is measured by different sources. P4/M1 is calculated as the $P_4(L * W)/M_1$ $((AW + PW)/2) * L$. A large part of data courtesy of Eric Delson. Extant comparative data also provided by Michelle Singleton. Terry Harrison provided data on Laetoli Material. L. sp. nov. data from Jablonski et al. (2008). Data on other HCRP and UCMP material from Frost and Kullmer (2008).

16752 which is either *P. ado* or a papionin of undetermined affinity (Harris et al., 1988; Frost, 2001b). Since we have only a handful of cercopithecoid remains from the Chiwondo Beds, including a maxillary fragment (HCRP-MR-250) from Mwenirondo attributed to *Parapapio* sp., we do not have more reliable craniofacial parts for taxonomic determination. We allocate the specimen here to *Parapapio* sp. awaiting more material from surveys of the Chiwondo Beds.

A disto-buccal tooth fragment HCRP-MR-1166 (Fig. 4), probably from a right lower M_1 or M_2, was collected in 2010 from the surface survey at the same locality where the hominin tooth fragment HCRP-MR-1106 was found in 2009. The specimen HCRP-MR-1166 represents a hypoconid cusp and a root fragment and part of the distal basin. Deep disto-buccal and median-buccal clefts are present. Morphology and tooth wear on the occlusal surface identify the fragment as cercopithecoid. Robustness, size, enamel infolding, root length and crown hypsodonty lead us to an attribution to *Theropithecus* sp., a taxon previously identified based on an upper molar, probably M^3 described from RC 1 (Frost and Kullmer, 2008) in the vicinity of the Malema hominin site, just 800 m across the Ruasho River.

Discussion

Primates are extremely rare in the Chiwondo Beds, and each specimen furthers our understanding of the relationships between eastern and southern African faunas and hominin evolution (Bromage et al., 1995a), at a crucial time when *Homo* and *Paranthropus* arose in Africa (Schrenk et al., 1995). Previously documented *P. boisei* from Malema is now joined by an *H. rudolfensis* representative from the adjacent Mwenirondo area. Mwenirondo and Malema are both dated by biostratigraphic correlation of suid material into the same biozone 3A-2, representing a time range between 2.7 and 1.8 Ma. At the Malema RC 11 hominin locality, however, primitive *N. scotti* specimens narrow the time estimation to 2.52–2.33 Ma (Kullmer, 2008). It is possible that MR 10 has the same age as RC 11, adding new evidence for an early occurrence of *Paranthropus* together with an early representative of *Homo* in the Malawi rift in southeast Africa (Kullmer et al., 1999). All other primate material from Unit 3A is allocated to the cercopithecid genera *Parapapio* and *Theropithecus*. Among southern African Pliocene sites, *Parapapio* generally predominates, and *Theropithecus* is often present but more rare, whereas in eastern African sites of middle and later Pliocene age, *Theropithecus* predominates and *Parapapio* is rare, if present at all. So in this sense the Chiwondo Unit 3A fossils are most similar to those from the southern African sites (Frost and Kullmer, 2008). In both regions outside of the Turkana basin, the same species of *Theropithecus* predominates: *Theropithecus oswaldi*. Unfortunately, the Chiwondo material cannot be allocated to species. For *Parapapio*, *P. ado* and *P.* cf. *jonesi* are known from slightly older deposits from eastern Africa (Leakey and Delson, 1987; Frost, 2001a,b; Frost and Delson, 2002; Harris et al., 2003; Harrison, 2011), whereas *P. jonesi*, *P. broomi*, and *P. whitei* are all known from roughly contemporary southern African sites (Freedman, 1957; Delson, 1984). The specific affinity of the Chiwondo *Parapapio* material is currently unknown. In dental size, the previously identified fossils were closest in size to *P. broomi*, whereas the new Mwenirondo mandible is closest to *P. jonesi*, though still at the lowest end of the *P. broomi* range. However, given the overlap in size between these species, and that the range of morphological variation in the total Chiwondo sample is consistent with a single species (Frost and Kullmer, 2008), recognition of multiple species is unwarranted at this point. If *Parapapio* sp. from the Chiwondo Beds, including the new mandible from Mwenirondo, belongs to *P. broomi* (which is possible but not definite) Mwenirondo would be the northernmost site where this species occurs, furthering the similarity of the Chiwondo fauna with aspects of the South African fauna.

There are no colobines present in the Chiwondo Beds, and while the primate sample is small, this suggests the Chiwondo habitats represent more open environmental conditions. Bovids show more affinities to the arid Somalia-Masai ecozone of Eastern Africa, than to the Zambezian ecozone to which the Malawi Rift belongs today (Sandrock et al., 2007). Alternatively, Schrenk et al. (1995) indicated a shared eastern and southern African fauna for the Chiwondo Beds.

Though the preservation of many Chiwondo specimens does not allow for a definite species-level determination, we hope that future surveys of this geographically intermediate region will continue to illuminate the paleoecological and paleobiogeographical role of the Malawi rift in the evolution and distribution of monkeys and early hominins of the African Plio-Pleistocene.

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