doi 10.4436/jass.90001

JASs Reports
Journal of Anthropological Sciences
Vol. 90 (2012), pp. 151-161

Refined age estimates and paleoanthropological investigation of the Manyara Beds, Tanzania

Stephen R. Frost[1], Hilde L. Schwartz[2], Liane Giemsch[3], Leah E. Morgan[4], Paul R. Renne[5], Maya Wildgoose[6], Charles Saanane[7], Friedemann Schrenk[8] & Katerina Harvati[9]

1) *Department of Anthropology, University of Oregon, Eugene, OR 97403-1218, USA*
email: sfrost@uoregon.edu

2) *Earth and Planetary Sciences, University of California, Santa Cruz, CA 95064, USA*

3) *LVR-Landesmuseum Bonn, Bachstr. 5-9, 53115 Bonn, Germany*

4) *Department of Petrology, Faculty of Earth; Life Sciences, Vrije Universiteit, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands*

5) *Department of Earth and Planetary Science, University of California, Berkeley, CA 94720, USA; Berkeley Geochronology Center, 2455 Ridge Rd., Berkeley, CA 94709, USA*

6) *Department of Geology, University of California, Davis, CA 95616, USA*

7) *Archeology Unit, History Department, Faculty of Arts and Sciences, University of Dar es Salaam, Tanzania*

8) *Goethe Universität, Siesmayerstr, 7060323 Frankfurt am Main, Germany*

9) *Paleoanthropology, Senckenberg Center for Human Evolution and Paleoecology; Department of Early Prehistory and Quaternary Ecology, Eberhard Karls Universität Tübingen, 72070 Tübingen, Germany*

Summary - *The Manyara Beds in the area of Makuyuni Village in the Lake Manyara Basin, Tanzania have been studied for nearly a century, but interpretations of their age have ranged from Middle Pleistocene to Late Pliocene. New geological, paleontological and archeological fieldwork was conducted at the site and has provided siginificant new evidence, including refined stratigraphy, radiometric age estimates, preliminary paleomagnetic analysis, significant new faunal collections, as well as stratigraphic context for some of the lithic artifacts in stratigraphic context. These efforts have succesfully constrained the geological age estimates for the Manyara Beds to between less than 0.63 to 1.3 Ma, and the age of the two hominin bearing localities to between ~0.63 and 0.78 Ma. This new chronology may impact the taxonomic interpretation of the hominin remains recovered from the site. They also suggest that two mammalian taxa,* Metridiochoerus compactus *and* Eurygnathohippus, *may have some of their youngest known occurences in the Manyara Beds. Acheulean lithics were also found in stratigraphic context during this more narrow time interval. Furthermore, the presence of potential cut-marks on the surface of a bovid mandible may represent the first evidence for human modification of bones from the Manyara Beds.*

Keywords - *Makuyuni, Manyara Beds, Tanzania, Pleistocene.*

Introduction

The fossiliferous deposits in the vicinity of Makuyuni Village, Tanzania (Fig. 1) were initially described in the early 20th century (Kent, 1941) and re-investigated in 1969-70 (Keller *et al.*, 1975) and 1994-95 (Kaiser *et al.*, 1995, 2010; Ring *et al.*, 2005). The latter expedition discovered two

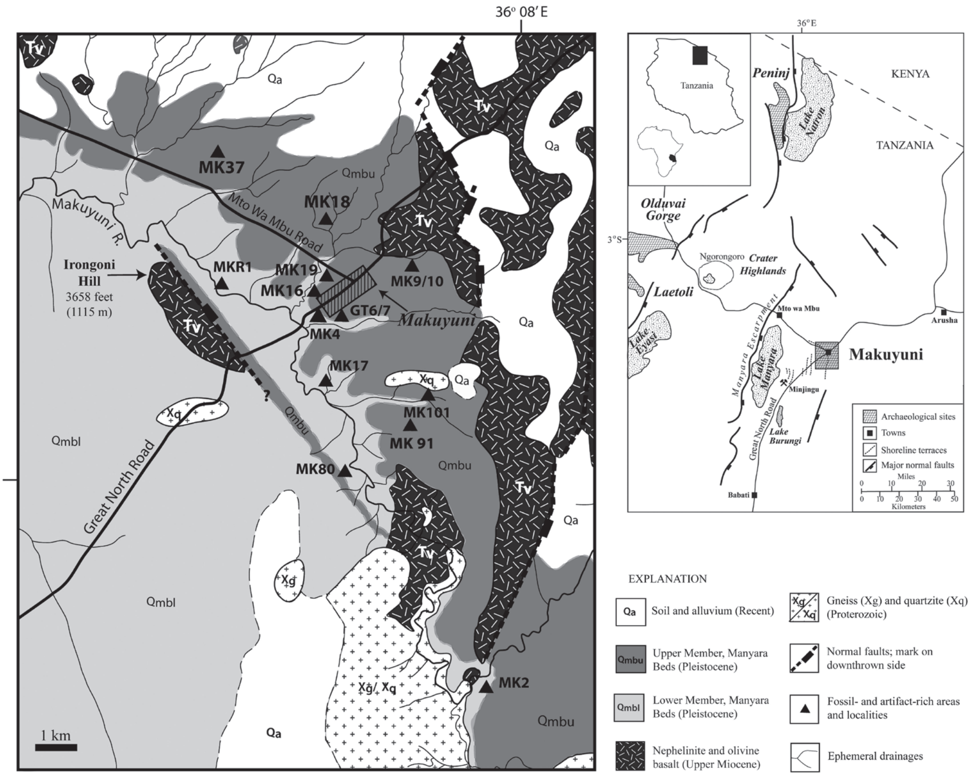

Fig. 1 - Left: geological map of the Lake Manyara Beds. The lower member represents the approximate high-stand of paleo-Lake Manyara. Important paleontological collecting areas and geological sections mentioned in the text are shown (MK37 is equivalent to MK 7/8 and 21/22 of Kaiser* et al.*, 2010). Right: Area Map showing the position of Makuyuni relative to other important Plio-Pleistocene paleoanthropological sites in Northern Tanzania. The approximate area represented by the geological map is indicated by cross-hatching in the area map. The colour version of this figure is available at the JASs website.

fragmentary fossils tentatively assigned to *Homo erectus,* and collected fauna and Acheulean lithics (Kaiser *et al.*, 1995, 2010; Kaiser, 2000; Ring *et al.*, 2005). Despite these important findings the chronology of these sediments has been uncertain, with previous age estimates for the Manyara Beds in the vicinity of Makuyuni village ranging from Middle Pleistocene to Late Pliocene (Kent, 1941; Kaiser *et al.*, 1995; Ring *et al.*, 2005). To address this situation, a joint Tanzanian, German and American team returned to Makuyuni in July 2008, with the primary goals of refining the stratigraphy of the Manyara Beds, constraining their age, collecting additional fauna, and locating the lithics within the stratigraphic context. The team systematically examined sedimentary exposures at both new and previously surveyed localities, collected fossil and lithic material, and conducted small test excavations in areas with high concentration of surface artifacts. Our refinement of the age estimates has implications for the interpretations of the hominins, the fauna, and the lithic artifacts.

Stratigraphy

Pleistocene lacustrine and alluvial sediments exposed for more than 200 km^2 around the town of Makuyuni are the most fossiliferous and artifact-rich strata in the Lake Manyara Basin. They unconformably overlie deeply weathered volcanic rocks (flows, agglomerate or coarse-grained conglomerate), and comprise a distinctively two-toned stratigraphic section that has been subdivided into two informal units. The 'lower member' (up to 15 m thick) contains greenish-grey to white mudstones, siltstone, sandstones, limestones and tephra deposited in a marginal lacustrine environment. The reddish-brown 'upper member' (8-10 m thick) contains concretionary mudstones, conglomerates, tuffaceous sandstones, tephra deposits and calcretes indicative of fluvial deposition and extensive paleosol development (Figs. 2,3; Ring *et al.*, 2005; Schwartz *et al.*, 2012). The lower member lacustrine beds are approximately 20 km east of the eastern shoreline of present-day Lake Manyara and mark a Pleistocene highstand for the paleolake (Fig. 1). A distinctively thick (and locally pumice rich) tuffaceous horizon (the "Hollywood Tuff") occurs at or just above the contact between the lower and upper members in the northwest and may be stratigraphically equivalent to the "Red Brick Tuff" in the southeast (Schwartz *et al.*, 2012). The transition between the two members is interdigitated and represents a change from lacustrine to fluvial deposition, marking a regression induced by rift faulting (Ring *et al.*, 2005), increased tephra deposition, climate change, or some combination thereof. The transition zone also includes the two localities, MK2 and MK4, where fragmentary hominid fossils were found in 1994-1995 (Ring *et al.*, 2005; Kaiser *et al.*, 2010).

Geochronology

During the 2008 field season we collected three samples of basal volcanic rock and 24 tephra samples from the lower and upper members for possible Ar^{40}/Ar^{39} dating. Most samples proved unusable: none appeared to be airfall and many showed evidence of extensive transport from the source. Ultimately, only two samples proved datable: the "Hollywood Tuff" from the base of the upper member (MK 16P) and a basaltic rock (probably nephelenite) that underlies the upper member (MK 9/10B) in the northeastern part of the project area (Figs. 2, 3). The MK16P crystals yield an average age of 0.633 ± 0.039 Ma (Schwartz *et al.*, 2012). The analyses from MK 9/10B yielded an average age of 6.00 ± 0.03 Ma. This date is consistent with the intensive weathering observed on the surfaces of basalts that directly underlie the Manyara Beds, and indicate that the basal nonconformity represents approximately five million years. No reliable radiometric ages have been determined for the lower member of the Manyara Beds, however preliminary magnetostratigraphic analysis suggests that the bottom of the Bruhnes Chron occurs in the lower member approximately 10.5 m from the base, and that the Jaramillo subchron is present approximately 4 m above the base of the lower member. This implies that:

a) the base of the section was deposited between 0.98 and 1.3 Ma and that the lower and upper members represent approximately 0.6 to 1.0 Ma of sedimentation,
b) that the top of the section was deposited between 0.27 and 0.44 Ma,
c) and that the main hominin-bearing localities MK2 and MK4 are between ~0.63 and 0.78 Ma (Fig. 2; Schwartz *et al.*, 2012).

Paleontology

A total of 248 vertebrate fossils were collected (Fig. 3; Tab. 1). Eight mammalian families from four orders are present, along with cichlids (Perciformes: Ciclidae), catfish (Siluriformes: Clariidae), Crocodilidae, and Squamata. Among the mammalian fossils, bovids (59%), equids (22%), and suids (10%) predominate. The tribe Alcelaphini make up 75% of the bovid specimens, with all other tribes being comparatively rare. The occurrence of fish, *Crocodilus* and *Hippopotamus,* as well as reduncin bovids in both members indicate the presence of permanent water in the vicinity. The high overall abundance of grazers, such as alcelaphin bovids and equids, along with the rarity of tragelaphin bovids and primates, is consistent with an open and grass-dominated environment,

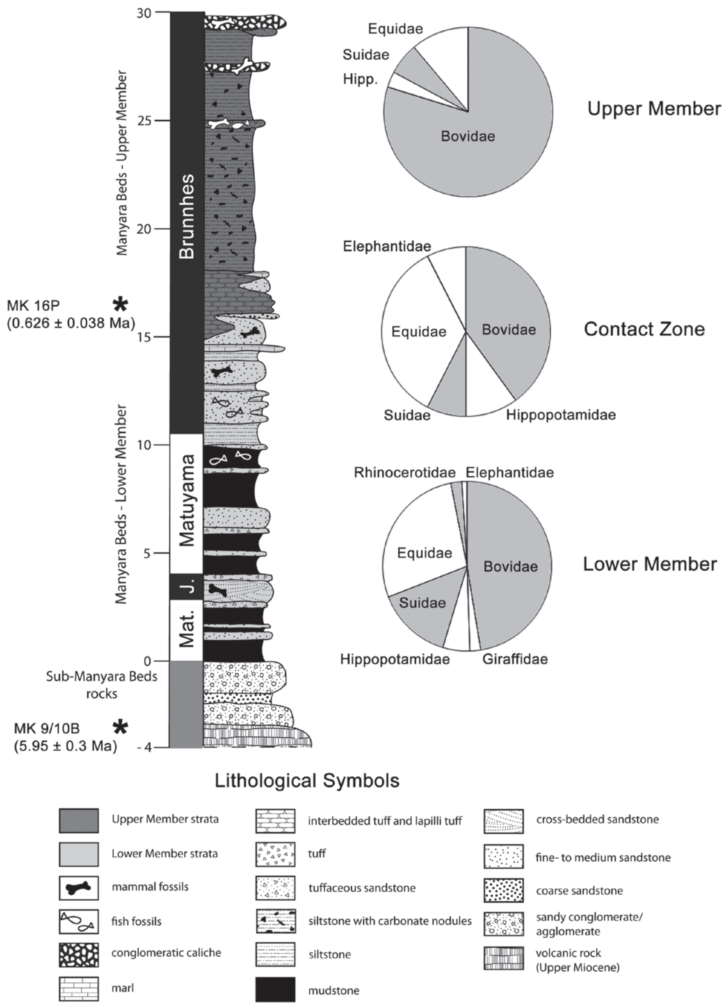

Fig. 2 - Composite stratigraphic column of the Manyara Beds near Makuyuni. Scale gives meters above / below the base of the Manyara Beds. Black and white bars represent normal / reversed polarity respectively and the gray zone adjacent to the sub-Manyara reds rocks indicates section not sampled for paleomagnetic analysis. The reversed interval labelled "J" Bed is the Jaramillo. The composite column does not reflect any one actual stratigraphic section: the Upper Member thickness and stratigraphy shown is representative of deposits in the eastern part of the field area, which overlie volcanic rocks rather than lower member strata. Note interfingering lower-upper member contact. Pie charts show relative abundance of mammalian families from different stratigraphic levels based on number of individual specimens. The colour version of this figure is available at the JASs website.

particularly in the upper member. The relative abundances of different faunal groups is consistent with that reported from the 1994-1995 field seasons (Kaiser *et al.*, 2010; Wolf *et al.*, 2010).

There are clear differences in the relative abundances of various faunal elements between the members (Fig. 2; Tab. 1), with bovids being much more common in the upper member and the lower member being significantly more diverse in terms of mammalian families. Furthermore, *Eurygnathohippus* and *Metridiochoerus* are absent from upper member above the contact zone, and *Phacochoerus* does not occur in the lower member below the contact zone. The presence of *Eurygnathohippus* and *Metridiochoerus compactus* in the contact zone places them among the youngest dated occurrences of these taxa between 0.63 and 0.78 Ma (White, 1995; Gilbert, 2008; Gilbert & Bernor, 2008; Wolf *et al.*, 2010).

The faunal age estimation is consistent with, but broader than, the obtained radiometric dates and paleomagnetic correlation. They indicate an Early - Middle Pleistocene age. Wolf *et al.* (2010) described the equids from the 1994-95 collection from Makuyuni and recognized two species of *Equus* based on size and a species of *Eurygnathohippus* consistent with *E. cornelianus* (Wolf *et al.,* 2010). Material from the sample described here is similar. The *Eurygnathohippus* material is consistent in molar size and morphology with *E.* cf. *cornelianus* from Daka, but no incisors diagnostic of this species have been found (Fig. 3d; Gilbert & Bernor, 2008; Wolf *et al.,* 2010). The presence of *Eurygnathohippus* in the lower member suggests a minimum age of approximately 0.6 Ma for the lower part of the Manyara Beds (Gilbert & Bernor, 2008; Wolf *et al.*, 2010). This age estimate is matched by the radiometric age estimate from MK 16P located just above the lower-upper member contact. A maximum age for the lower member is constrained by the presence of *Metridiochoerus compactus,* which is represented by several molar fragments that are large and hypsodont with Y-shaped lateral pillars (Fig. 3a). *M. compacuts* is known from approximately 1.6 – 0.78 Ma, with late occurrences in Olduvai Bed IV and the Daka Mb. of the Bouri Fm., but absent from younger deposits at Olduvai, the Middle Awash, and Asbole (White, 1995; Gilbert *et al.*, 2000; Geraads *et al.*, 2004; Gilbert, 2008). We have also tentatively identified *Phacochoerus* based on a second molar (Fig. 3b), whose earliest known occurrence is from Daka at 1.0 Ma, where it co-occurs with *M. compactus* (Gilbert, 2008). *Notochoerus euilus* was listed as present from the lower member by Ring *et al.* (2005), but was not found in any of the 2008 collections. The last appearance for *N. euilus* is approximately 2.0 Ma (White, 1995) and significantly older than any of the sediments found in the vicinity of Makuyuni, suggesting this identification may not be accurate. The *Hippopotamus* material is too fragmentary to confidently assign to species. However, one M^3 lacks enamel complexity and is larger than *H. amphibius* and within the size range for *H. gorgops. H. gorgops* is known from a number of Pleistocene sites (Boisserie & Gilbert, 2008). The *Elephas recki* material from Makuyuni is morphologically close to *E. r. ileretensis* and *E. recki recki* in terms of hypsodonty, hypsodonty index, enamel thickness, and plate frequency (Beden, 1983). *Theropithecus oswaldi* spans a very large time range, but the size of this specimen (a proximal tibia, Fig. 3e-f) is most consistent with *T. o. leakeyi* (Frost, *unpublished data*), which ranges in age from approximately 1.6 – 0.25 Ma (Frost & Delson, 2002). Therefore, the total faunal sample from the 2008 collection is consisted with an age of 1.6-0.6 ma.

The genus faunal resemblance index (GFRI) was used to compare the overall taxonomic composition of the Makuyuni mammalian fauna to that of other Pleistocene assemblages from East and North Africa as well as the Middle East (Simpson, 1960; Martinez-Navarro *et al.*, 2004). Using data from Martinez-Navarro *et al.* (2004), with *Theropithecus* added to the Olduvai assemblage, the Makuyuni fauna is most similar to the Olduvai Bed II, the Okote Mb. of Koobi Fora and Daka (GFRI 1.0 each, indicating they possess all of the genera found at Makuyuni). Buia was also very high (GFRI 0.9). Makuyuni was most different from Olduvai Bed III and Gesher Benot Ya'aqov (GRFI 0.3 each). The low GFRI between Makuyuni and Olduvai Bed III and Gesher Benot Ya'aqov is probably because these latter sites only have 16 and 13 mammalian genera in their samples respectively, yielding little opportunity to share genera. Whereas Okote, Olduvai Bed II and Daka have 32, 39, and 26 genera respectively.

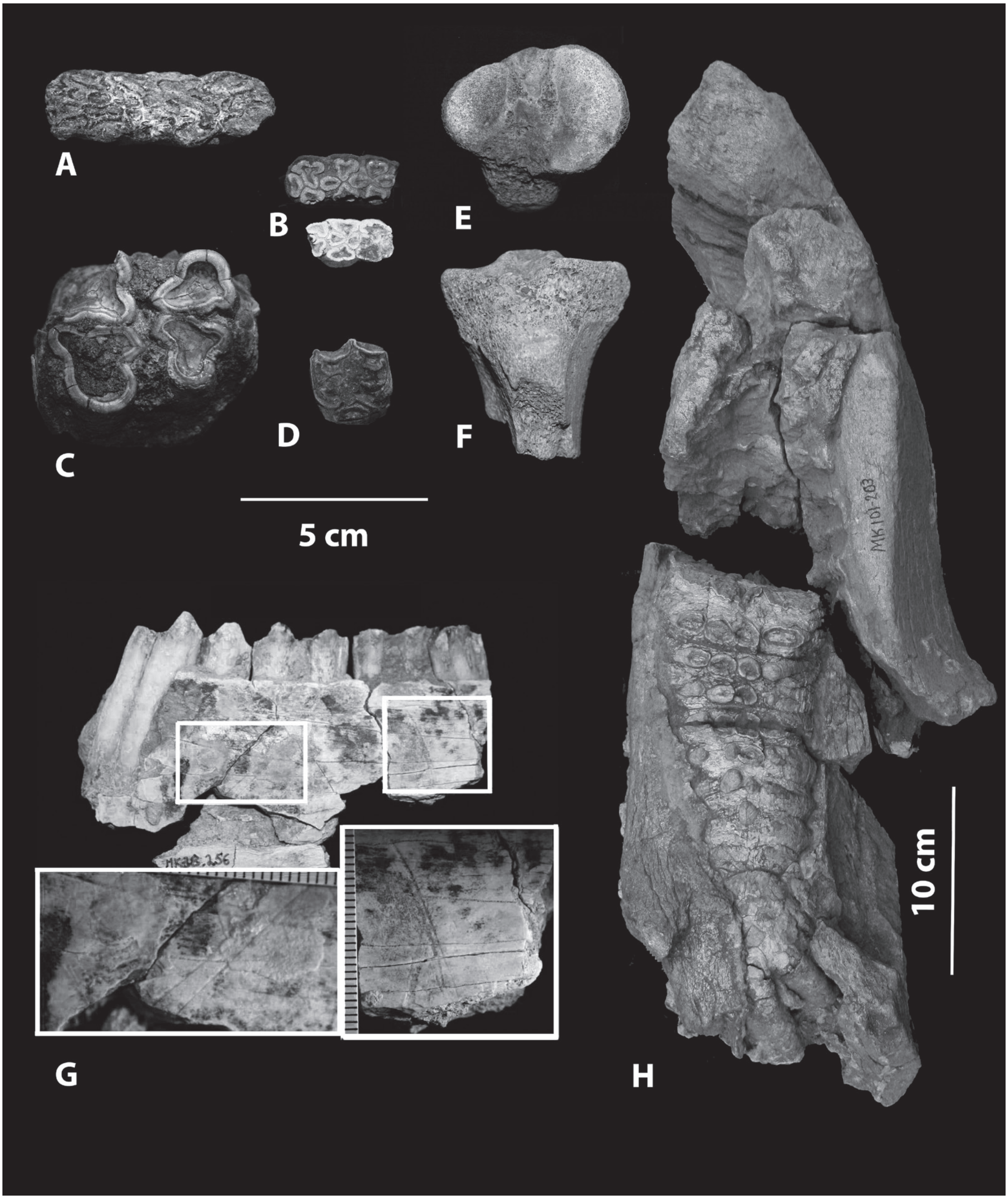

Fig. 3 - Fossil specimens recovered from the Makuyuni localities during the 2008 season. A. **Metridiochoerus compactus** *molar; B.* **Phacocheorus sp.** *molar fragments; C.* **Hippopotamus cf. gorgops** *upper third molar; D.* **Eurygnathohippus** *upper molar; E. Cercopithecidae cf.* **Theropithecus oswaldi***, right proximal tibia proximal view, F. anterior view; G. Alcelaphini, left mandibular corpus with P_4-M_3. Boxes show magnified views of two possible sets of cutmarks on the medial surface; H.* **Elephas recki** *partial mandible. The colour version of this figure is available at the JASs website.*

Tab. 1 - Faunal list from 2008 field seasons with number of individual specimens (NISP) by taxon for each member plus the area of contact between the two members.

CLASS	ORDER	FAMILY	TAXON	NISP BY MEMBER			TOTAL
				UPPER	CONTACT	LOWER	
MAMMALIA	ARTIODACTYLA	BOVIDAE		24	14	32	70
			ALCELAPHINI	41	2	10	53
			ANTILOPINAE/AEPICEROTINI	3		2	5
			BOVINI	4			4
			HIPPOTRAGINI	1			1
			REDUNCINI	4		1	5
			TRAGELAPHINI	2		1	3
		GIRAFFIDAE				2	2
		HIPPOPOTAMIDAE		2	3	4	9
			HIPPOPOTAMUS CF. *GORGOPS*	1	1	1	3
		SUIDAE		4	2	10	16
			KOLPOCHOERUS SP.			1	1
			METRIDIOCHOERUS COMPACTUS		1	3	4
			?*PHACOCHOERUS* SP.	2			2
	PERRISODACTYLA	EQUIDAE		3	10	16	29
			EURYGNATHOHIPPUS SP.		1	6	7
			EQUUS SPP.	8	3	5	16
		RHINOCEROTIDAE				2	2
	PRIMATES	CERCOPITHECIDAE	CF. *THEROPITHECUS OSWALDI*				1
	PROBOSCIDEA	ELEPHANTIDAE			1	1	2
			ELEPHAS RECKI SSP.		2		2
OSTEICHTHEYS	PERCIFORMES			3	1		4
		CICLIDAE				1	1
	SILURIFORMES	CLARIIDAE		1		1	2
REPTILIA	CROCODILIA	CROCODILIDAE		1		2	3
	SQUAMATA			1			1
TOTAL				105	41	101	248

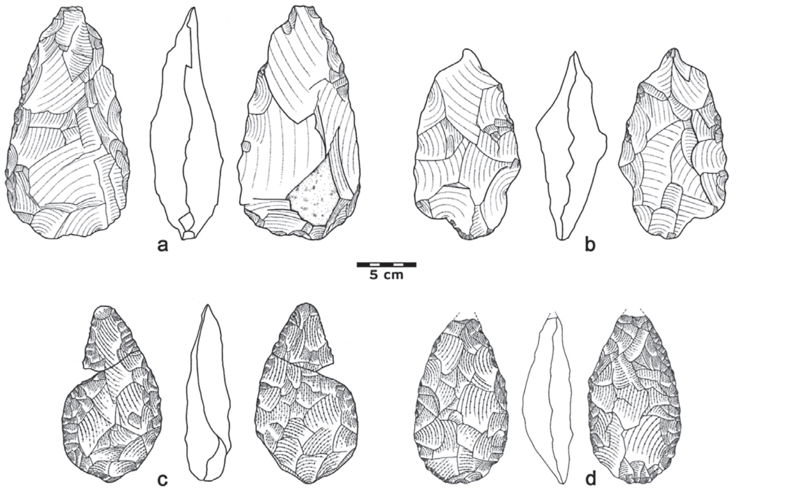

Fig. 4 - Representative Acheulean artifacts from Makuyuni. a-b basalt handaxes, c-d quartzite handaxes. c. Handaxe recovered in stratigraphic context from test excavation in locality MK 91.

Archaeology

Acheulean artifacts are abundant on the surface within the Makuyuni study area, with the majority of archeological sites found south of Makuyuni Village on both sides of a tributary of the Makuyuni River. A total of 588 artefacts were recovered and measured. Most (*n* = 522) derive from localities MK 4, MK 91 and MK 101 (Fig. 1). Almost all of the artefacts are made of locally available basalt (40 %) and quartzite (54 %). The artefact spectrum mainly comprises handaxes (38 %), cores and core tools (29 %), flakes and flake tools (27 %) and a small number of cleavers (4 %), as well as about a dozen manuports. All artifacts appear to have been produced using direct hard-hammer percussion.

Most handaxes from Makuyuni (Fig. 4) are similar in technology and shape to those from Olduvai Bed IV, which corresponds to an age of about 1.2-0.78 Ma (Hay, 1976) and from the middle Awash valley (DeHeinzelin *et al.*, 2000; Gilbert, 2008), where they have been attributed to *Homo erectus* (Asfaw *et al.*, 2002; Gilbert, 2008). However a subsample of the Makuyuni artifacts show similarities to handaxes from the Masek Beds at Olduvai Gorge, which date to a later age of approximately 0.5 Ma (Hay, 1976). The predominance of quartzite as raw material is also similar to the artefacts from the Masek Beds, where quartzite represents 94% of the sample (Leakey, 1994).

The context of the Makuyuni lithics was not established during previous research. In the excavations by Kaiser during the 1994/1995 season at locality MK 4, no Acheulean artifacts were found in stratigraphic context and the surface lithics were extremely rounded and weathered (Kaiser *et al.*, 2005). In order to clarify the Makuyuni artefacts' stratigraphic context we conducted small test excavations at the three artifact-rich localities near the lower - upper member transition, including locality MK 4, MK 91, and MK 101. Test pits were excavated in meter squares with quarter sub-squares. The positions of all finds were recorded in three-dimensions using a theodolite. Important specimens were additionally drawn and photographed. The excavated sediment was sieved and checked for small artefacts, microfauna, and other remains.

In spite of the abundance of surface lithic material, only two artefacts were recovered in stratigraphic context. One quartzite core was found at a depth of 20 cm at MK 101, and one broken quartzite handaxe was recovered at a depth of 25 cm at MK 91 (Fig. 4c). The latter is likely to be in its original context: its two pieces were found in close proximity and showed no abrasion and very sharp edges. The position of the handaxe near the lower-upper member contact suggests an age of approximately 700 ka for its deposit and points to the use of the near shore environment. The test trench at MK 4 yielded a number of predominantly Acheulean artefacts within the first 15 cm of depth. This sediment however seems to be mixed with surface material. Nothing further could be found down to a depth of 1.2 m, suggesting that the original cultural layer at MK 4 has been completely eroded and the finds accumulated on the surface over a period of time.

Extensive work on the taphonomy of the site has been conducted previously on the material from the 1994-1995 field seasons (Kaiser, 1996; Saanane, 2002; Kaiser *et al.*, 2010). This research found that most of the fossil material from Makuyuni experienced significant surface exposure prior to fossilization, but no human modifications to the faunal material were observed. One specimen recovered from the surface during our research shows three sets of possible cutmarks. These were identified on the medial surface of a bovid mandible, an alcelaphine consistent in size with *Connochaetes sp*. (Fig. 3g). One set was located on the lingual side under the M_1, approximately 1 cm below the alveolar margin running superoposteriorly to anteroinferiorly to the broken edge of the specimen, with some cross hatching. The second set was located also on the lingual sitd approximately 1.5 cm from the alveolar margin and running superoanteriorly to posteroinferiorly from the M_2 to the M_3 level. They continue across a gap in the specimen, and measure 42 mm in total length. The last set of possible cutmarks is located on the buccal side near the inferior edge of the corpus. It runs superoposteriorly to anteroinferiorly for approximately 15 mm from the level of the M_3 to the middle part of the M_2. Discoloration evident on the surface of the specimen also affects the cutmarks, suggesting that they occurred either pre- or peri-fossilization.

Discussion and Conclusions

The 2008 fieldwork was able to produce important results filling previous gaps in our knowledge of the Manyara Beds. Importantly, we were able to establish a geochronolgical sequence and to revise and refine the chronology of the fossil-bearing sites. The new dates constrain the age of the lower member between 1.3 and 0.63 Ma and indicate a younger Middle Pleistocene age for the upper member. The recovered fauna is also in agreement with this assessment and confirms previous paleoecological interpretations of a relatively open and grass-dominated ecosystem, with the upper member being even more grassland dominated than the lower member (Ring *et al.*, 2005; Kaiser *et al.*, 2010). Furthermore, the hominid bearing localities of MK 2 and MK 4 which are near the lower-upper member contact can be constrained to between approximately 0.63 and 0.78 Ma. Given that the hominin fragments from Makuyuni are highly fragmentary (Ring *et al.*, 2005; Kaiser *et al.*, 2010), this younger chronology suggests that the hominin fragments recovered from the site may prepresent *Homo heidelbergensis* (s.l.) rather than *H. erectus* (s.l.), We were able to establish the stratigraphic context of some of the Acheulian material recovered near the lower-upper member contact, constraining at least some of this material to the same age as the hominins. The fact that both the hominins and some of the artifacts were found close to the contact zone suggest that hominins were exploiting the environment near the shore of paleolake Manyara in the early Middle Pleistocene.

Acknowledgments

We are grateful to the Tanzania Comission for Science and Technology (COSTECH), the Department of Antiquities for permission to conduct fieldwork at Makuyuni, and to Felista Mangalu for permission to work at the Arusha Museum of Natural History. We sincerely thank Jackson Njau for all of his kind assistance during our work in Tanzania, as well as Charles Bwaiye, Leslea Hlusko, Daniel Mainoya and Frank

Mataro. Olivia J. Straub drew the lithic artifacts. We thank Bienvenido Martínez-Navarro, Emiliano Bruner, and two anonymous reviewers for their helpful comments. Funding was provided by the Deutsche Forschungsgemeinschaft (HA 5258/2-1), the University of Oregon, and the Max Planck Society. Finally we thank Silvia Kunze-Ritter, the Ministry of Education of Baden-Württemberg and the Oregon University System for their additional support.

References

Asfaw B., Gilbert W.H., Beyene Y., Hart W.K., Renne P.R., Woldegabriel G., Vrba E.S. & White T.D. 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. *Nature*, 416: 317-320.

Beden M. 1983. Family Elephantidae. In J.M. Harris (ed): *Koobi Fora Research Project, Volume 2: the fossil ungulates: Proboscidea, Perissodactyla, and Suidae*, pp. 40-129. Clarendon Press, Oxford.

Boisserie J.-R. & Gilbert W.H. 2008. Hippopotamidae. In W.H. Gilbert & B. Asfaw (eds): Homo erectus: *Pleistocene evidence from the Middle Awash, Ethiopia*, pp. 179-191. U.C. Press, Berkeley.

DeHeinzelin J., Clark J.D., Schick K.D. & Gilbert W.H. 2000. The Acheulean and the Plio-Pleistocene deposits of the Middle Awash Valley, Ethiopia. *Belgium. Ann. Sci. Geol.*, 104. Royal Museum of Central Africa, Tervuren.

Frost S.R. & Delson E. 2002. Fossil cercopithecidae of the Hadar Formation and surrounding areas of the Afar depression, Ethiopia. *J. Hum. Evol.*, 43: 687-748.

Geraads D., Alemseged Z., Reed D., Wynn J. & Roman D.C. 2004. The Pleistocene fauna (other than Primates) from Asbole, lower Awash Valley, Ethiopia, and its environmental and biochronological implications. *Geobios*, 37: 697-718.

Gilbert W.H., Asfaw B. & White T.D. 2000. Paleontology. In J. de Heinzelin, J.D. Clark, K.D. Schick & W.H. Gilbert (eds.): *The Acheulean and Plio-Pleistocene Deposits of the Middle Awash Valley, Ethiopia.* Ann. Sci. Geol., 104., pp. 183-192. Royal Museum of Central Africa, Tervuren, Belgium.

Gilbert W.H. 2008. Suidae. In W.H. Gilbert & B. Asfaw (eds): Homo erectus: *Pleistocene evidence from the Middle Awash, Ethiopia*, pp. 231-260. U.C. Press, Berkeley.

Gilbert W.H. & Bernor R.L. 2008. Equidae. In W.H. Gilbert & B. Asfaw (eds): Homo erectus: *Pleistocene evidence from the Middle Awash, Ethiopia*, pp. 133-166. U.C. Press, Berkeley.

Hay R.L. 1976. *Geology of Olduvai Gorge*. U.C. Press, Berkeley.

Kaiser T. 1996. *Die Taphonomie plio-pleistozäner Hominidenfundstellen Ostafrikas: mit besonderer Berücksichtigung der Säugetierfaunen des Laetoli- und Lake Manyara-Gebietes in Nordtansania*. Unpublished PhD-Thesis, Technische Hochschule Darmstadt, Darmstadt.

Kaiser T.M. 2000. Die Taphonomie plio-pleistozäner Hominidenfundstellen Ostafrikas mit besonderer Berücksichtigung der Säugetierfaunen des Laetoli- und Lake Manyara-Gebietes in Nordtansania. *Archäologische Informationen*, 23: 139-142.

Kaiser T.M., Bromage T.G. & Schrenk F. 1995. Hominid Corridor Research Project update: New Pliocene fossil localities at Lake Manyara and putative oldest Early Stone Age occurrences at Laetoli (Upper Ndolanya Beds), northern Tanzania. *J. Hum. Evol., 28: 117-120.*

Kaiser T.M., Fiedler L., Schrenk F., Schwartz H., Bromage T., Seiffert C., Saanane C., Kaletsch B., Arnhold S., Busch S., Hüser A., Junger B., Steinmaetz S., Stötzel K. & Tschirschnitz C. 2005. Makuyuni, eine neue altpaläolithische Hominidenfundstelle in Tansania. *Jahrb. Röm. Germ. Zentralmus*, 52: 1–42.

Kaiser T.M., Seiffert C., Hertler C., Fiedler L., Schwartz H.L., Frost S.R., Giemsch L., Bernor R.L., Wolf D., Semprebon G., Nelson S.V., Schrenck F., Harvati K., Bromage T.G. & Saanane C. 2010. Makuyuni, a new Lower Paleolithic hominid site in Tanzania. *Mitt. Hamb. Zool. Mus. Inst.*, 106: 69-110.

Kent P.E. 1941. The recent history and pleistocene deposits of the plateau North of Lake Eyasi, Tanganyika. *Geol. Mag.*, 78: 173-184.

Kent P.E. 1942. A Note on Pleistocene Deposits Near Lake Manyara, Tanganyika. *Geol. Mag.*, 79: 72-77.

Keller C.M., Hansen C. & Alexander C.S. 1975. Archaeology and paleoenvironments in the Manyara and Engaruka Basins, Northern Tanzania. *Geogr. Rev.*, 65: 365-376.

Leakey M.D. 1994. The Masek Beds and sites in uncertain stratigraphic positions. In M.D. Leakey & D.A. Roe (eds): *Olduvai Gorge, Vol. 5, Excavations in Beds III, IV, and the Masek Beds 1968-1971*, pp. 116-129. Cambridge University Press, Cambridge and New York.

Manega PC. 1993. *Geochronology, geochemistry and isotopic study of the Plio-Pleistocene hominid sites and the Ngorongoro volcanic highland in Northern Tanzania.* PhD Dissertation, University of Colorado.

Martínez-Navarro B., Rook L., Segid A., Yosief D., Ferretti M.P., Shoshani J., Tecle T.M., Libsekal Y. 2004. The large fossil mammals from Buia (Eritrea): systematic, biochronology, and paleoenvironments. *Riv. It. di Paleont. Stratig.*, 110 (suppliment): 61-88.

Ring U., Schwartz H.L., Bromage T.G. & Saanane C. 2005. Kinematic and sedimentological evolution of the Manyara Rift in Northern Tanzania, East Africa. *Geol. Mag.*, 142: 355-368.

Schwartz H., Renne P.R., Morgan L.E., Wildgoose M.M., Lippert P.C., Frost S.R., Harvati K.H., Schrenk F. & Saanane C. 2012. Geochronology of the Manyara Beds, northern Tanzania: stratigraphy and new magnetostratigraphy and $^{40}Ar/^{39}Ar$ ages. *Quat. Geochronol.*, 7:48-66.

Simpson G.G. 1960. Notes on the measurement of faunal resemblances. *Am. J. Sci.*, 258A:300-311.

White T.D. 1995. African omnivores: global climatic change and Plio-Pleistocene hominids and suids. In E.S. Vrba, G.H. Denton, T.C. Partridge & L.H. Burckel (eds): *Paleoclimate and Evolution, with emphasis on human origins,* pp. 369-384. Yale University Press, New Haven.

Wolf D., Nelson S.V., Schwartz H.L., Semprebon G.M., Kaiser T.M. & Bernor R.L. 2010. Taxonomy and paleoecology of the Equidae from Makuyuni, Northern Tanzania. *Paleodiversity,* 3: 247-267.

Associate Editor, Emiliano Bruner