Note on the presence of *Hystrix* (Mammalia, Rodentia) in the Malawi Chiwondo Beds (Plio-Pleistocene): taphonomical and palaeoecological implications

Christiane DENYS
UMR CNRS-MNHN 7205 OSEB,
Muséum national d'Histoire naturelle,
Département Systematique et Évolution,
case postale 51, F-75231 Paris cedex 05 (France)
denys@mnhn.fr

Oliver SANDROCK
Department of Palaeontology, Hessiches Landesmuseum,
Friedensplatz 1, D-64283 Darmstadt (Germany)

Ottmar KULLMER
Palaeoanthropology, Forschungsinstitut Senckenberg,
Senckenberganlage, 25, D-60325 Frankfurt am Main (Germany)

Fernando RAMIREZ ROZZI
CNRS, UPR 2147, Dynamique de l'Évolution humaine,
44 rue de l'Amiral Mouchez, F-75014 Paris (France)

Timothy G. BROMAGE
Department of Biomaterials & Biomimetics,
New York University College of Dentistry,
345 East, 24th Street, New York, NY (USA)

Friedemann SCHRENK
Vertebrate Paleobiology, Johann Wolfgang Goethe University,
Siesmayerstrasse 70, D-60054 Frankfurt am Main (Germany)

ABSTRACT

We evaluate the taxonomic affinities of an Hystricid from the Plio-Pleistocene hominid site of Uraha (Chiwondo Beds), northern Malawi. At the cross roads between eastern and southern Africa, these deposits are both unique and interesting because of their age (they encompass a period of major climatic change and have yielded early *Homo* remains). We describe here the third upper molar found in Uraha and compare it with *Hystrix leakeyi* Denys, 1987 and *H. makapanensis* Greenwood, 1958 specimens. The new specimen is smaller

than *H. makapanensis* and *H. leakeyi*. It also differs from the fossil species by the absence of posteroloph and a smaller lingual sinus and oblique labial lophs. The new *Hystrix* Linnaeus, 1758 specimen has a small size and is bunodont, which differentiates it from the modern species found in Malawi today like *H. cristata* Linnaeus, 1758 and *H. africaeaustralis* Peters, 1852. It could belong either to a new species or enter into the variability of the described ones, but due to the low degree of knowledge of *Hystrix* molar morphology and variability as well as the very low number of specimens for comparison, we retain an indeterminate status for this specimen. Further, we ascribe the absence of small mammals and especially small rodents in these lake-shore deposits to taphonomic and palaeoecological phenomena.

RÉSUMÉ
*Note sur la présence d'*Hystrix *(Rodentia, Mammalia) dans les niveaux Plio-Pléistocènes des Chiwondo au Malawi : implications taphonomiques et paleoécologiques.*
Dans ce travail nous avons recherché les affinités taxonomiques d'un nouveau spécimen d'Hystricidae du site à Hominidae Plio-Pléistocène d'Uraha (Chiwondo Beds), du nord du Malawi. Par leur situation au carrefour entre l'Afrique de l'Est et l'Afrique du Sud et leur âge, ces dépôts sont à la fois uniques et intéressants car ils englobent un changement climatique majeur et ont livré les restes d'un des plus anciens représentant du genre *Homo*. Nous décrivons ici une M3 supérieure trouvée dans le site d'Uraha et la comparons à celles d'*Hystrix leakeyi* Denys, 1987 et *H. makapanensis* Greenwood, 1958. Le nouveau spécimen attribué à *Hystrix* Linnaeus, 1758 se caractérise par une plus petite taille que les espèces fossiles et est bunodonte, ce qui le différencie des espèces actuelles connues du Malawi telles que *H. cristata* Linnaeus, 1758 et *H. africaeaustralis* Peters, 1852. Il diffère des autres fossiles d'Afrique de l'Est et du Sud par l'absence de postérolophe et par un petit sinus lingual et des lophes obliques. Il pourrait appartenir à une nouvelle espèce ou entrer dans la variabilité des espèces fossiles décrites de la vallée du Rift, cependant en l'absence de connaissances concernant cette dernière et devant le peu de spécimens connus, nous conservons un statut d'espèce indéterminée pour ce spécimen. Enfin, nous émettons l'hypothèse que l'absence de petits mammifères et plus particulièrement de petits rongeurs soit liée aux conditions taphonomiques et paléoécologiques particulières régnant dans ce type de dépôts de bord de lac.

INTRODUCTION

Plio-Pleistocene rodents are well known in various part of Africa (Denys 1999; Winkler *et al.* 2010). Sometimes they are found in abundance, such as at Olduvai or in the South African cave deposits, and provide very useful palaeoecological and biogeographical indications. Despite intensive prospecting, the Plio-Pleistocene open air sites of the Chiwondo Beds in Malawi have yielded a poor and biased mammalian fauna, including mostly herbivores; primates and carnivores are rare (Sandrock *et al.* 2007). The only Chiwondo Beds rodent discovered to date is a porcupine of genus *Hystrix* sp. mentioned by Schrenk *et al.* (1995). Situated in the Rift valley in the corridor between East and South Africa, such a discovery is of great importance for knowledge of faunal and human evolution in that region.

The Hystricid record for tropical Africa is not well documented and fossils are never abundant. If early occurence of Hystricidae in Africa dates from Vallesian (around 11 Ma) of Egypt (Mein & Pickford 2010) they are not well known from more recent periods of Neogene. Various fossil Hystricidae occur in the East and South African Mio-Pleistocene sites (Winkler *et al.* 2010) which have yielded representatives of three genera. Besides the large extinct *Xenohystrix crassidens* Greenwood, 1955, one finds specimens attributed to the modern *Atherurus* Cuvier, 1829 and *Hystrix* Linnaeus, 1758 genera, but unattributed to a species level, whose first occurrences have recently been recorded in East Africa as early as 6 Ma in Kenya (Lemudong'o, Lukeino) (Mein & Pickford 2006; Hlusko 2007) and around 5 Ma in Ethiopia (Adu Asa and Aramis sites [Wesselman *et al.* 2009]). During the middle Pliocene, two fossil species occur in Eastern and Southern Africa. *Hystrix leakeyi* Denys, 1987 is found only in Laetoli (Denys 1987, 2011), while *H. makapanensis* Greenwood, 1958 is known from Makapansgat, Olduvai Bed I (Sabatier 1979) and Laetoli (Denys 2011). In Ethiopia, the Omo Shungura Member B and Hadar (AL 132.27C) sites have yielded the oldest representatives of the modern *H. cristata* Linnaeus, 1758 (Sabatier 1979). However, in Africa today, *Hystrix* is represented by two species *H. cristata* and *H. africaeaustralis* Peters, 1852, whose distinction on the basis of tooth size and morphology is not very clear. Both modern species occur in sympatry in East and South Africa, including Malawi.

During a visit in October 1995, a *Hystrix* specimen was discovered at Uraha Hill, close to locality U18 at which a *Homo rudolfensis* Alexeev, 1986 jaw (UR 501) was discovered in 1991 (Schrenk *et al.* 1993). We report here the taxonomic analysis of this large rodent (*c.* 10-22 kg) in the Plio-Pliocene deposits of Malawi and we will also discuss the possible reasons for the rarity of small mammals in these deposits.

Locality: geological context and age
The Chiwondo Beds, situated along the north shore of the Lake Malawi in Malawi represent transgressive-regressive sedimentary cycles, consisting of five depositional units (Betzler & Ring 1995). According to Betzler & Ring (1995) the main sedimentary facies elements are braided and meandering river systems, delta deposits, lake beds, alluvial fans and aeolian sands. The overall thickness of the Chiwondo Beds is about 130 m. The sedimentary pattern within the Malawi Rift shows resemblance to other lacustrine sequences in the East African Rift system, e.g., Lake Turkana (Frostick & Reid 1989) or Lake Rukwa (Wescott *et al.* 1991).

The age of the Chiwondo Beds relies on faunal correlation with radiometrically dated biostratigraphic units in eastern Africa. The age range refers to radiometric well-dated volcanic tuffs within the Koobi Fora and Shungura Formations as described by Brown *et al.* (1985) and Brown & Feibel (1986). The age spectrum of significant fossiliferous Units 2 and 3 of the Chiwondo Beds lies between 4 Ma to 1.5 Ma (Schrenk *et al.* 1993; Bromage *et al.* 1995) and was recently refined by using Suids as biostratigraphic markers (Kullmer 2008).

Among the 145 fossiliferous localities, the Uraha region became famous for yielding a Hominid mandible (Schrenk *et al.* 1995). The Uraha hominid locality is situated in Unit 3A-2 composed of fluviatile sands and silts with calcimorphic soils and is equivalent in age with an other hominid site of the region (Malema, RC11) which yielded an other Hominid *Paranthropus boisei* Leakey, 1959 (Kullmer *et al.* 1999) found in 1996. Based upon the presence of *Notochoerus scotti* Leakey, 1943 and early *Metridiochoerus andrewsi* Hopwood, 1926, both localities are equivalent in age and can be correlated with Omo Shungura members C to F (2.7 to 1.8 Ma) according to Kullmer *et al.* (1999, 2008).

The new rodent was a surface find at Uraha Hill and has been discovered by one of us in 1996 (FRR). The aim of this note is to describe the Uraha porcupine molar, discuss its taxonomic affinities, and provide some taphonomical and palaeoecological implications of this discovery.

Material and methods
Morphological observations were made by using a microscope CETI at magnification × 6 and drawings with a camera lucida and measurements were taken with a calliper at 0.01 mm precision.

TABLE 1. — Upper M3 measurements (in mm) of fossil and modern *Hystrix* spp. specimens. Abbreviations: **HCRP**, Hominid Corridor Rift Project; **KNM**, Kenya National Museum; **MNHN.F**, Muséum national d'Histoire naturelle, Paris, collection of Paleontology.

Species	Origin	Number	Length	Width
Hystrix sp.	Uraha Hill	HCRP-1144	7.14	5.78
H. leakeyi Denys, 1987	Laetolil Beds	75/468	7.3	6
H. makapanensis Greenwood, 1958	Laetolil Beds	3354/00	7.86	6.88
H. cristata Linnaeus, 1758	Tunisia	MNHN.F.1971-690	7.75	6.75
	Senegal	MNHN.F.1962-2223	8.5	7.82
	Kenya	KNM 5324	7.32	5.45
	Kenya	KNM	7.25	5.49
	Kenya	KNM 5321	8.43	6.44
	Kenya	KNM 7190	7.76	6.52
	Senegal	MNHN.F.1995-3133	7.45	6
	Djibouti	MNHN.F.2007-356	7.39	6.55
	Djibouti	MNHN.F.2007-349	7.19	5.81
H. africaeaustralis Peters, 1852	Ethiopia	MNHN.F.1962-2227	8.01	5.58
	Ethiopia	MNHN.F.1962-2226	8.02	7.43

Pictures were made with a Nikon Coolpix camera. The nomenclature used here for molar lophs and cusps follows Denys (1987). We compared the material with specimens from Osteological department (Kenya Museums, Nairobi) and with MNHN porcupines collections.

SYSTEMATIC PALAEONTOLOGY

Order RODENTIA Bowdich, 1821
Family HYSTRICIDAE G. Fischer, 1817
Genus *Hystrix* Linnaeus, 1758

Hystrix sp.

MATERIAL EXAMINED. — Isolated left upper M3 (HCRP-1144).

DESCRIPTION
The molar is black with carbonate accretions. Some small breaks are observed in the crown and the intact enamel structure shows no signs of digestion. The crown is low with only one root and the molar is not very worn; some cusps are connected by lophs, and some cusps remain intact and are not individualized into small islands of enamel such as in aged specimens. The individual is probably a young adult (Fig. 1; Table 1). Due to its medium small size (smaller than in *Xenohystrix* Greenwood, 1955 and larger than in *Atherurus* Cuvier ,1829) this molar can be attributed to *Hystrix* genus.

The molar displays a typical *Hystrix* upper M3 pattern by being longer than wide. The first loph is long and convex following the anterior margin of the molar, and it ends in the middle of the labial side of the molar. The lingual sinus is deep and oblique but there is the trace of a protocone. The labial sinus is transverse and joins the ectoloph. The ectoloph is longitudinally oriented and short, and though its end is not well visible, a small cusp (hypocone?) is seen at the back of the molar, which lacks a posteroloph. The labial side of the posterior part of the molar is comprised of two lophs: a small transverse loph upon which one can see two cusps (mesoloph with entocone?) and a distal short oblique loph with one cusp. This molar displays one oblique curved root.

DISCUSSION
Comparison and taxonomic affinities
Upper hystricid molars are not frequently preserved in the fossil record which makes a comparisons to other fossil species difficult. In modern specimens, the upper M3 may be absent in very young specimens or be an erupted germ displaying only isolated cusps. Very old specimens have very worn crowns and only islands of enamel persist. Consequently we agree with Van Weers (2005) that in this taxonomic group of rodents, the morphology
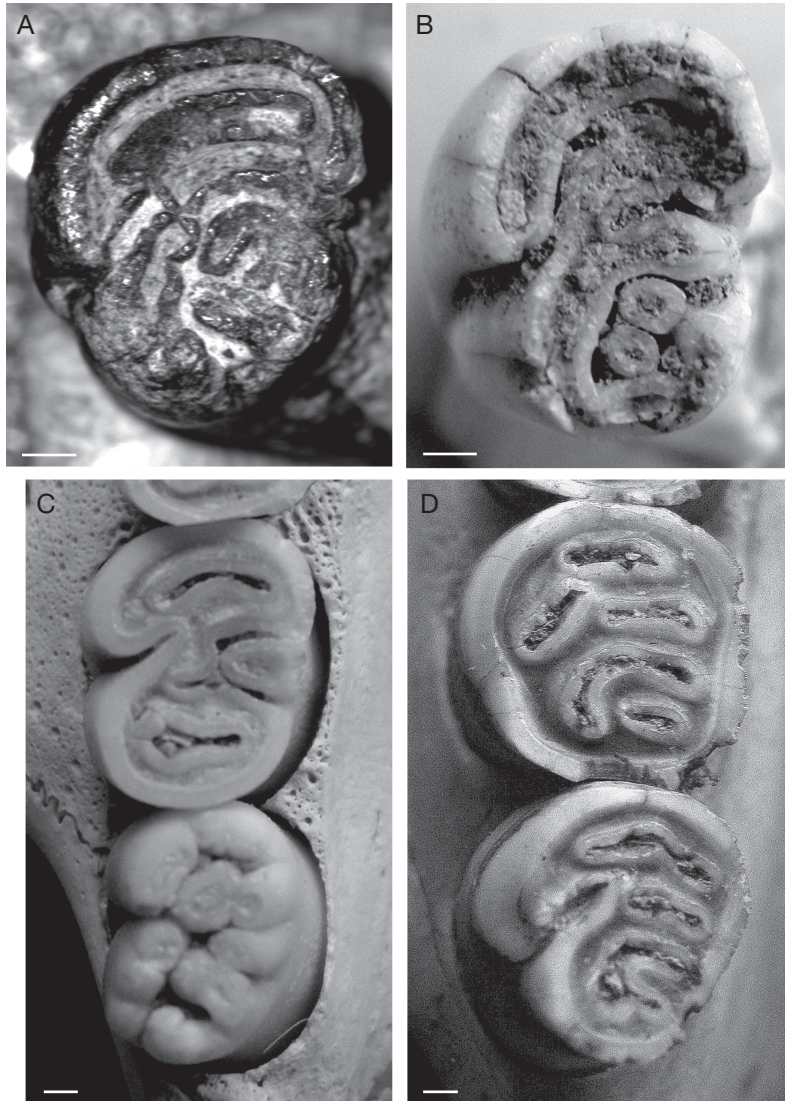
FIG. 1. — Fossil and modern *Hystrix* Linnaeus, 1758 specimens: **A**, *Hystrix* sp. upper left M3 Uraha (HCRP-1144); **B**, *Hystrix makapanensis* Greenwood, 1958 upper left M3 from Upper Laetolil Beds, Laetoli (EP3354/00- Loc.15); **C**, modern *H. cristata* Linnaeus, 1758 from Senegal (MNHN-CG1995-3133) juvenile with upper right M2 and M3 just erupted; **D**, modern *H. cristata* (MNHN-CG1962-2223) worn upper left M23. Scale bars: 1 mm.

of the cheek teeth may not be useful to distinguish between the species in the absence of comparisons between specimens at similar wear stages.

The Uraha molar is at an intermediate stage of wear, with lophs visible and connecting cusps, and it still has a relatively high crown. We did not found

any upper M3 in the fossil record corresponding to this wear stage but the comparison specimens are relatively close.

Two upper M3 fossils of *Hystrix leakeyi* and *H. makapanensis* have been recorded from Laetoli (Denys 1987, 2011) and one M3 from the FLKN1

site at Olduvai attributed to *H. makapanensis* (Sabatier 1979), which are used here for comparisons despite they do not correspond to the same wear stages. Due to the absence of a comprehensive revision of the modern African *Hystrix* species, the museum specimen identifications remain doubtful and the comparisons can be made only at the genus level.

The Uraha specimen is smaller than *H. leakeyi* (Fig. 2; Table 1) and fits into the lower limit of variability of modern *Hystrix* species. It is about same size than the *H. leakeyi* upper M3 (75/468) but the Laetoli specimen is a germ and thus the two molars display different wear stages. In comparison to *H. leakeyi*, the labial sinus is less transverse and not as well related to the ectoloph (Fig. 1).

In comparison to the upper M3 of *H. makapanensis* from Olduvai and Laetoli (00/3354)*,* which are slightly more worn, the Uraha specimen is smaller in size. The Uraha molar has a smaller lingual sinus and a narrower distal loph. Moreover, the Uraha specimen harbors a hypocone that is more longitudinal and less visible and the distal labial cusps are more oblique. The Olduvai and Laetoli M3 *H. makapanensis* also have more lophs visible than the Uraha and Laetoli *H. leakeyi* specimens, which may be due either to a more advanced wear or to a more lophodont pattern.

Compared to modern *Hystrix* spp. of Africa, the Uraha specimen is slightly smaller (Table 1) and is more bunodont, contains fewer connected cusps, and the crown is not completely circled by an enamel ring posteriorly. The lingual sinus of the Uraha M3 is, however, deeper and persists further toward the base of the crown than in modern *Hystrix* spp., indicating a rather lower stage of hypsodonty in the genus at around 2.5 Ma. The modern *Hystrix* upper M3s have more transverse labial lophs when they are visible and the labial sinus is absent in all wear stages (Fig. 1). There is a transversely long posteroloph at the back of the molar which is visible also in *H. leakeyi* and *H. makapanensis*, but not in the *Hystrix* sp. specimen from Uraha.

The Uraha specimen is close in size to a very young modern upper M3 germs and we do not have at the moment any equivalent fossil molar at a same stage to compare. Moreover, the variability related to age and sex in modern african *Hystrix* is still not well known. We can observe that the M3/3 are not visible on young specimens and they are always the smallest teeth as well as the latest to erupt. The African porcupine systematics must be revised and in the absence of such knowledge it is difficult to attribute the fossil species to a specific species on the basis of a unique specimen. However, our observations lead to the conclusions that the new Uraha specimen is a bunodont and small representative of the genus which is different in some respects from the modern *Hystrix* specimens and may be different from *H. leakeyi* and *H. makapanensis*. Due to an absence of knowledge of modern and fossil african *Hystrix* variability we cannot conclude upon size evolutionary trend. Van Weers (2005) in his revision of Eurasian Hystricids showed that all Miocene porcupines were low-crowned while high crowned specimens appear either during late Miocene or early Pliocene. If we assume similar evolutionary trend for tropical Africa, then the small size and bunodonty of the Uraha specimen could indicate an age earlier than 2.5 Ma. However, the scarcity of Hystricid upper molars fossil-record does not allow us to go further into phylogenetic, biochronological and biogeographical considerations for this specimen.

PALAEOENVIRONMENTAL AND TAPHONOMIC IMPLICATIONS

Porcupines today are nocturnal herbivore generalists; they eat roots, bulbs, fruits and bark (Kingdon 1974; De Graaff 1981). *Hystrix* lives in mostly non-desert habitats, including savanna woodlands, steppes and uplands. It is found sometimes along forest margins or galleries but avoids swamps and moist forest. This indicates that at around 2.5 to 2.33 Ma, the Uraha landscape was rather open. By the fact, based upon the proportions of bovids at Uraha, the habitat shared affinities of the fossil faunas of this locality fitted with the arid grasslands of Somali Masai region, which today is situated in the Zambezian phytochorion (Sandrock *et al.* 2007). Unfortunately, we cannot confirm here if the Uraha porcupine has more affinities with eastern or southern populations of the fossil species, which prevent us to assign the Uraha localities into Somali-Masai
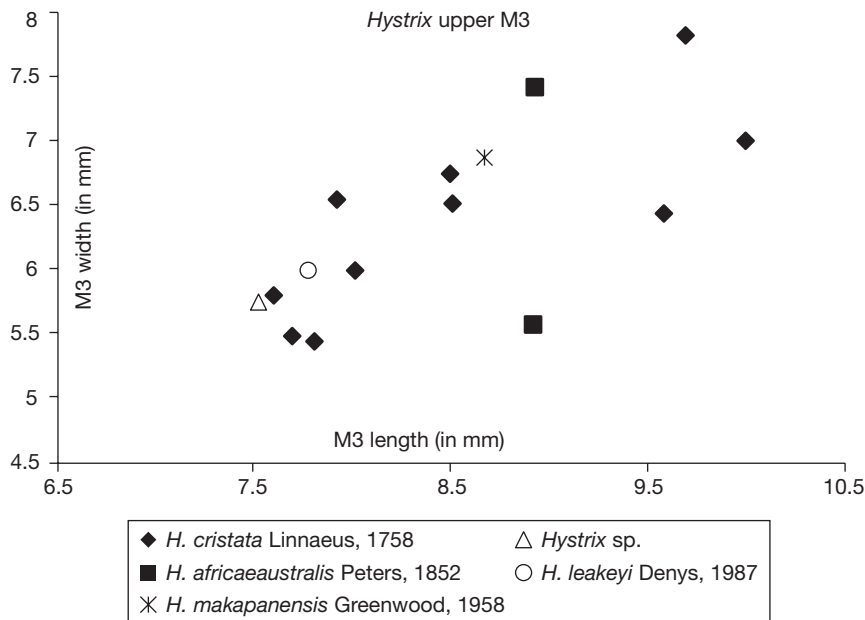
FIG. 2. — Scatter plot of the length versus width of the modern and fossil *Hystrix* M3 (after data in Table 1).

or Zambezian vegetation zones and define the type of savannas were early *Homo rudolfensis* and *Paranthropus boisei* lived. Modern *Hystrix* live generally in hilly or rocky landscape and hide during the day in caves or natural crevices with narrow entrances (De Graaff 1981). *Hystrix* is presently hunted by large felids (especially lion and leopard) and hyaenids, none of them being represented as fossils at Uraha. However porcupines are represented in low number of individuals in modern spotted hyaena and leopard dens studied (De Ruyter & Berger Lee 2007; Pokines & Kerbis 2007). In the leopard den, De Ruyter & Berger Lee (2007) mentioned two skulls of juvenile *Hystrix* deposited in 1991 and not recovered at the second visit in 1998 for unknown reasons. Today *Hystrix* is considered as a valuable bushmeat in some parts of Africa (Njiforthi 1996) and it could have also been hunted and consumed by early hominids.

Discovery of the Uraha *Hystrix* raises an interesting taphonomic problem since Schrenk *et al.* (1995) report that micromammals and their predators carnivores are virtually absent from the Chiwondo Beds, despite intensive screening of the sediment.

Sandrock *et al.* (2007) also confirmed the low biodiversity and the ungulate-bias of the Chiwondo faunas. These authors suggested that such absences are likely the effects of destructive pre- and post-depositional taphonomic processes. Some taphonomic studies have noted numerous alterations and a rather complex taphonomic history for the Chiwondo Beds Malema site RC 11, equivalent in age to Uraha (Sandrock 1999; Sandrock *et al.* 1999, 2007). Geologically, the Uraha deposits are comprised of a ferruginous calcimorph palaeosol lying in siltsones to mudstones interbedded with lenticular sandstones. These deposits were assigned to a swamp to interchannel setting with no evidence of lacustrine condition (Betzler & Ring 1995). Sandrock (1999) suggests that the loss of information in the fossil record at Malema site RC 11 resulted from fluviatile reworking and post-burial destruction due to rapid oxidation of organic components combined with the pedogenic process of ferrolysis. Alternating wet and dry conditions plus plant decomposition and iron oxidation may be a source of acidification of soils and of bone destruction. Acid soil generally leaves typical corrosion marks at the

bone surface (Andrews 1990) and enamel is first affected by low pH (Fernández-Jalvo & Andrews 1992). This could result in a strong destruction of small mammal teeth and bones. Moreover the study of Malema bone diagenesis reveals the existence of strong chemical modifications with a high cristallinity index and enrichment in Ca, P, Al, Si and depleted in S, Mg, Cl, Na (Sandrock *et al.* 1999). The high rate of fragmentation and the existence of heavy weathering processes and crystallization indicate potential destructive effects for small mammal bones. However, taphonomic investigation at various sites in Africa and Europe have shown the existence of well preserved micromammal bones despite high diagenesis and complex taphonomic histories (Dauphin *et al.*1994; Denys *et al.* 1996).

Due to the selective preservation of large mammals at Uraha this suggests that other factors must account for the absence of small mammals. Generally, small mammals are concentrated in abundance by owls and small carnivores either in their regurgitation pellets or in their faeces (Andrews 1990). But, even in the case of the most destructive predator category, there are always bones left behind and it is not realistic to imagine the presence of only one predator at this time in the surroundings. Examples of such accumulations are well known at Olduvai bed I (Fernández-Jalvo *et al.* 1998) and at Tighenif (Dauphin *et al.* 1994) in open-air lacustrine environments. At Olduvai the alkaline conditions may have favoured exceptional preservation of all bone elements. But at Tighenif some levels show iron concentration and no signs of intense destruction of bones. In contrast, small mammals are nearly unknown from the fluviatile and deltaic deposits of East and West Turkana, except at Koobi Fora localities 103A, 130A and 131A, which, according to Behrensmeyer (1975), represent delta mudflats and delta margin settings. These deposits include rootcasts and coarse grained sands that fill the mudcracks and lack evidence of paleosoils. No small fossils have yet been found in the channels and river system and it seems that such types of high-energy and fluviatile deposits are poor environments for concentrating and preserving small mammals. Experiments by Fernández-Jalvo &

Andrews (2003) also demonstrated the damage made to small mammal bones by water and sediment action. Skulls can be rapidly disintegrated (within 48 hours) and silts and clay sediment have a strong capacity to abrade bones. Rapid breakage (1 to 4 hours) was also reported by Andrews (1990) in tumbling experiments.

Small mammal bones experimentally exposed to a pH1 HCl solution and pronase were destroyed in 23 hours but acid attack alone was insufficient to reach total destruction (Denys *et al.* 1995). Root growth and trampling in a densely covered vegetation landscape may alter bone by increasing breakage which could favour its destruction on long term (Sanchez *et al.* 1997; Fernández-Jalvo *et al.* 1998). But, for small mammal assemblages there is not any evidence of the total destruction by roots nor by weathering (Andrews 1990) because plenty fossil yielded rootmarks and display relatively advanced weathering stages. Another explanation for the absence of micromammals would be mechanical. After accumulation, the pellets or faeces of predators are removed by rain or dispersed during lacustrine episodes. According to Behrensmeyer (1975), bones display different behaviours to fluviatile transport and can be regrouped in different so-called Voorhies categories of dispersal in function of their shape and density. The dominance of some categories allows to extrapolate the presence of water transportation of some skeletal elements in a site. In Malema, Voorhies Group III elements are dominant indicating a removal of the lighter elements by water transportation. However, fluvial experiments by Korth (1979) have shown that even for small mammals the behaviour of bones is the same for small compared to large mammals, so micromammal bones of Voorhies Group categories III to V (including the denser identifiable teeth and molars) should have remained in situ. In contrast is the high energetic beach facies of the Chiwondo Beds Mwenerondo site, adjacent to Malema where most of the mammal bones are severely destroyed. Andrews (1990) and Korth (1979) have also shown that pellets can float a very long distancee (more than 500 m) before being degraded. This may explain not only the absence of small mammals at Uraha but all over Chiwondo beds in Malawi.

CONCLUSION

The *Hystrix* sp. indet. from Uraha is the first record of the genus at around 2.5-2.3 Ma in Malawi. Because little comparative material is available and the Malawi record so limited, this specimen cannot be related either to the Olduvai *H. makapanensis* or to Laetolil *H. leakeyi*, nor to the two modern species of the genus. Nevertheless, its presence confirms the absence of moist dense forest at Uraha. The absence of small mammals in Chiwondo Beds is likely the result of a combination of sedimentological factors (high energy system + hydraulic sorting + diagenesis) rather than because of predation or other environmental factors.

REFERENCES

ANDREWS P. 1990. — *Owls, Caves and Fossils*. Natural History Museum Publications, London, 231 p.

BEHRENSMEYER A. K. 1975. — The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology, Harvard* 146: 473-578.

BETZLER C. & RING U. 1995. — Sedimentology of the Malawi Rift: facies and stratigraphy of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* 28: 23-35.

BROMAGE T. G., SCHRENK F. & JUWAYEYI Y. M. 1995. — Palaeobiogeography of the Malawi Rift: age and vertebrate paleontology of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* 28: 37-59.

BROWN F. H., MCDOUGALL I., DAVIES T. & MAIER R. 1985. — An integrated Plio-Pleistocene chronology for the Turkana basin, *in* DELSON E. (ed.), *Ancestors: The Hard Evidence*. Alan R. Liss, New York: 82-90.

BROWN F. H. & FEIBEL C. S. 1986. — Revision of lithostratigraphic nomenclature in the Koobi Fora region, Kenya. *Journal of the Geological Society of London* 143: 297-310.

DAUPHIN Y., KOWALSKI K. & DENYS C. 1994. — Assemblage data and bone and teeth modifications as an aid to palaeoenvironmental interpretations of the open-air Pleistocene site of Tighenif (Algeria). *Quaternary Research* 42: 340-349.

DE GRAAFF G. 1981. — *The Rodents of Southern Africa*. Butterworths, Durban, Pretoria: 1-267.

DENYS C. 1987. — Fossil rodents (other than Pedetidae) from Laetoli, *in* LEAKEY M. D. & HARRIS J. M. (eds), *Laetoli: a Pliocene Site in Northern Tanzania*. Oxford Science Publications, London: 118-170.

DENYS C. 1999. — Of mice and men. Evolution in East and South Africa during Plio-Pleistocene times, *in* BROMAGE T. & SCHRENK F. (eds), *African Biogeography, Climate Change & Human Evolution*. The Human Evolution series, Oxford University Press, Oxford: 226-252.

DENYS C. 2011. — Rodents, *in* HARRISON T. (ed.), *Palaeontology and Geology of Laetoli: Human Evolution in Context*. Volume 2. *Fossil Hominins and the Associated Fauna*. Springer, Dordrechts: 15-53.

DENYS C., DAUPHIN Y. & FERNÁNDEZ-JALVO Y. 1995. — Experimental taphonomy: preliminary results of the digestion of micromammal bones in the laboratory. *Comptes Rendus de l'Académie des Sciences*, *Paris*, série II 321: 803-809.

DENYS C., WILLIAMS C. T., DAUPHIN Y., ANDREWS P. & FERNÁNDEZ-JALVO Y. 1996. — Diagenetical changes in Pleistocene small mammals bones from Olduvai Bed I. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126: 121-134.

DE RUYTER D. J. & BERGER LEE R. 2007. — Leopards as taphonomic agents in Dolomite caves – implications for bone accumulations in the Hominid-bearing deposits of South Africa. *Journal of Archaeological Science* 27: 665-684.

FERNÁNDEZ-JALVO Y. & ANDREWS P. 1992. — Small Mammal Taphonomy of Gran Dolina, Atapuerca (Burgos), Spain. *Journal of Archaeological Science* 19: 407-428.

FERNÁNDEZ-JALVO Y. & ANDREWS P. 2003. — Experimental effects of water abrasion on bone fragments. *Journal of Taphonomy* 1: 147-163.

FERNÁNDEZ-JALVO Y., DENYS C., ANDREWS P., WILLI-

AMS C. T., DAUPHIN Y. & HUMPHREY L. 1998. — Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). *Journal of Human Evolution* 34: 137-172.

FROSTICK L. E. & REID I. D. 1989. — Is structure the main control of river drainage and sedimentation in rifts? *Journal of African Earth Science* 8: 165-182.

HLUSKO L. 2007. — Earliest evidence for *Atherurus* and *Xenohystrix* (Hystricidae, Rodentia) in Africa from the Late Miocene site of Lemudong'o, Kenya. *Kirtlandia* 56: 86-91.

KINGDON J. 1974. — *East African Mammals.* Volume 2. *(Hares and Rodents)*. The University Chicago Press, Chicago, Academic Press, London: 343-703.

KORTH W. W. 1979. — Taphonomy of microvertebrate fossil assemblages. *Annals of the Carnegie Museum* 48: 235-285.

KULLMER O., SANDROCK O., ABEL R., SCHRENK F., BROMAGE T. & JUWAYEYI Y. M. 1999. — The first *Paranthropus* from the Malawi Rift. *Journal of Human Evolution* 37: 121-127.

KULLMER O. 2008. — The fossil Suidae from the Plio-Pleistocene Chiwondo Beds of northern Malawi Africa. *Journal of Vertebrate Palaeontology* 28: 208-216.

MEIN P. & PICKFORD M. 2006. — Late Miocene micromammals from the Lukeino Formation (6.1 to 5.8 Ma), Kenya. *Bulletin mensuel de la Société linnéenne de Lyon* 75: 183-223

MEIN P. & PICKFORD M. 2010. — Vallesian Mammals from Sheik Abdallah Western desert, Egypt. *Historical Biology* 22: 229-259.

NJIFORTHI L. 1996. — Preferences and present demand for bushmeat in north Cameroon: some implications for wildlife conservation. *Environmental Conservation* 23: 149-155.

POKINES J. T. & KERBIS PETERHANS J. C. 2007. — Spotted hyaena (*Crocuta crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. *Journal of Archaeological Science* 34:1914-1931.

SABATIER M. 1979. — *Les rongeurs des sites à Hominidés de Hadar et Melka-Kunturé (Éthiopie).* Unpublished thesis, Université des Sciences et Techniques du Languedoc, Montpellier, 122 p.

SANCHEZ V., DENYS C. & FERNÁNDEZ-JALVO Y. 1997. — Origine et formation des accumulations de microverté-

brés de la couche 1a du site du Monté di Tuda (Corse, Holocène). Contribution à l'étude taphonomique des micromammifères. *Geodiversitas* 19 (1): 129-157.

SANDROCK O. 1999. — *The Taphonomy and Paleoecology of the Malema Hominid Site, Northern Malawi.* Ph.D. dissertation, Johannes Gutenberg Universität Mainz, 276 p.

SANDROCK O., DAUPHIN Y., KULLMER O., ABEL R., SCHRENK F. & DENYS C. 1999. — Malema: Preliminary taphonomic analysis of an African hominid locality. *Comptes Rendus de l'Académie des Sciences, Paris* 328: 133-139.

SANDROCK O., KULLMER O., SCHRENK F., YUWAYEYI Y. M. & BROMAGE T. G. 2007. — Fauna, taphonomy, and ecology of the Plio-Pleistocene Chiwondo Beds, Northern Malawi, *in* BOBE R., ALEMSEGED Z. & BEHRENSMEYER A. K. (eds), *Hominin Environments in the East African Pliocene: An Assessment of the Faunal Evidence*. Springer, Dordrechts, The Netherlands: 315-332.

SCHRENK F., BROMAGE T. G., BETZLER C. G., RING U. & JUWAYEYI Y. 1993. — Oldest *Homo* and Pliocene biogeography of the Malawi Rift. *Nature* 365: 833-836.

SCHRENK F., BROMAGE T. G., GORTHNER A. & SANDROCK O. 1995. — Paleoecology of the Malawi Rift: Vertebrate and invertebrate faunal contexts of the Chiwondo Beds, northern Malawi. *Journal of Human Evolution* 28: 59-70.

VAN WEERS J. D. 2005. — A taxonomic revision of the Pleistocene *Hystrix* (Hystricidae, Rodentia) from Eurasia with notes on the evolution of the family. *Contributions to Zoology* 74: 301-312.

WESTCOTT W. A., KREBS W. N., ENGELHARDT D. W. & CUNNINGHAM S. M. 1991. — New biostratigraphic age dates from the Rukwa rift basin in western Tanzania. *American Association Petroleum Geology Bulletin* 75: 1255-1263.

WESSELMAN H. B., BLACK M. T. & ASNAKE M. 2009. — Small mammals, *in* HAILE-SELASSIE Y. & WOLDE-GABRIEL G. (eds), Ardipithecus kaddaba*: Late Miocene Evidence from the Middle Awash, Ethiopia*. University of California Press, Berkeley: 105-134 .

WINKLER A. J., DENYS C. & AVERY M. 2010. — Rodentia, *in* WERDELIN L. & SANDERS W. J. (eds), *Cenozoic Mammals of Africa* 17. University of California Press, Berkeley, Los Angeles, London: 263-304.