THE LARGE FOSSIL MAMMALS FROM BUIA (ERITREA): SYSTEMATICS, BIOCHRONOLOGY AND PALEOENVIRONMENTS

BIENVENIDO MARTÍNEZ-NAVARRO [1], LORENZO ROOK [2], AMAHA SEGID [3], DESSALE YOSIEF [4], MARCO P. FERRETTI [2], JEHESKEL SHOSHANI [4], TEWELDE M. TECLE [5], YOSIEF LIBSEKAL [3]

Abstract. This paper offers a preliminary overview on the large fossil mammals (Primates, Hyaenidae, Proboscidea, Rhinocerotidae, Equidae, Hippopotamidae, Suidae, Giraffidae, and Bovidae) from the Early Pleistocene sedimentary succession of the Dandiero (Buia) Basin (Danakil Depression, Eritrea). The 1995-1997 Eritrean-Italian fossil collection has been revised and studied. A few significant remains collected during the 2002-2004 field activities have also been included. Eighteen species of mammals have been identified, described and illustrated in the principal specimens. The systematic study allows general conclusions on the biochronologic and paleoenvironmental significance of the faunal assemblage. The study is completed by an analysis of "Genus Faunal Resemblance Index" (GFRI) with some well known faunal assemblages of Africa across the time span Late Pliocene – Middle Pleistocene.

Riassunto. Viene presentato uno studio preliminare dei grandi mammiferi (Primates, Hyaenidae, Rhinocerotidae, Equidae, Hippopotamidae, Suidae, Giraffidae, e Bovidae) provenienti dalla successione sedimentaria del Pleistocene Inferiore del Bacino del Dandiero (Buia, Depressione Dancala, Eritrea). La maggior parte dello studio si basa sulla collezione delle raccolte effettuate durante le campagne 1995-1997, i cui materiali sono stati restaurati, preparati ed analizzati nei locali del nuovo laboratorio geo-paleontologico allestito presso il "National Museum of Eritrea" di Asmara. Sono stati inclusi nello studio anche alcuni resti di particolare significato raccolti durante le campagne 2002-2004. Le 18 specie di mammiferi identificate sono descritte ed illustrate per i reperti più significativi. L'analisi tassonomica è affiancata da considerazioni riguardanti la biocronologia ed il paleoambiente. Lo studio è completato da una analisi sugli indici di similarità (GFRI) tra associazioni faunistiche Africane ben conosciute, attraverso un intervallo temporale dal Pliocene Superiore sino al Pleistocene Medio.

Introduction

The fossiliferous area of Buia (100 Km south of Massawa, northern Danakil Depression, Eritrea) was discovered in 1995 during a preliminary geological survey under the aegis of a collaborative research program between the Department of Mines, Eritrean Ministry for Energy and Water Resources and the Department of Earth Sciences, University of Florence. Further studies were carried out in the area during several field seasons in 1995-1997, also involving research teams from the National Museum of Eritrea, the Natural History Museum (Geology and Palaeontology section) of the University of Florence, as well as other Italian and European institutions.

These activities led to the discovery of a new important palaeoanthropological site at Buia (Abbate et al. 1998), the recovery of an abundant fossil vertebrate collection and the identification of a huge number of archaeological sites with extraordinarily abundant and magnificently preserved Mode 1 (Oldowan) and Mode 2 (Acheulean) tool industries (Martini et al. 2004).

In 1998- 1999 field research was interrupted due to the renewed Ethiopian-Eritrean conflict, but in early

1   ICREA, Grup d'Autoecologia Humana, Àrea de Prehistòria – Unitat Associada al CSIC - Universitad Rovira i Virgili, Plaça Imperial Tarraco 1, 43005 - Tarragona, Spain.
2   Dipartimento di Scienze della Terra e Museo di Storia Naturale (Sezione Geologia e Paleontologia), Università di Firenze, Via La Pira 4, I-50121 Florence, Italy. Corresponding author: lrook@geo.unifi.it
3   National Museum of Eritrea, University of Asmara, P.O. Box 5284, Asmara, Eritrea.
4   Department of Biology, University of Asmara, P.O. Box 1220, Asmara, Eritrea
5   Department of Mines, P.O. Box 212, Asmara, Eritrea

2000 the collaborative Italo-Eritrean research project was revived upon approval from the University of Asmara Research Committee (Rook et al. 2002).

The first step of this revived project was the establishment of a laboratory for keeping fossil collections and for fossil cleaning and preparation at National Museum of Eritrea. All the fossil material collected during the 1995-1997 seasons was in fact temporary stored at the Department of Mines in Asmara, waiting the creation of proper space in the National Museum venues. Early in 2001, the new geo-paleontological laboratory was completed. The fossil material was transferred there and the long and delicate cleaning/restoration work began. This allowed us to further study and describe in some detail the faunal assemblage of Buia, whose faunal list was preliminarily published in Abbate et al. (1998).

The fossils came from sediments belonging to the Dandiero Group (formerly "upper Danakil Formation"; Sagri et al. 1998; Abbate et al. 2004). Most of the collecting sites are concentrated in the area from Wadi Aalad (to the north), across the Dandiero river to Wadi Maebele and Wadi Ghersaloita (to the south). Interpretations of the faunal assemblage and the magnetostratigraphic data allowed Abbate et al. (1998) to refer the *Homo*-bearing sediments to the top of the Jaramillo paleomagnetic event (sub-Chron C1r.1n), about one million years B.P. (for further data on chronology see also Albianelli & Napoleone 2004; Bigazzi et al. 2004).

This contribution represents the first study on the whole large mammal association from the Dandiero (Buia) Basin (the 1995-1997 collection, integrated with notes on some of the 2003-2004 findings). For systematics above species level we follow McKenna & Bell (1998). The only mammalian group that has been thus far studied in greater detail is the proboscideans (Ferretti et al. 2003). Also, a description of the fossil reptiles from the Dandiero Basin is given by Delfino et al. (2004).

The preliminary vertebrate faunal list published by Abbate et al. (1998) is updated as follows:

Homo "*erectus*-like", *Theropithecus* cf. *T. oswaldi* (Andrews, 1916), cf. *Crocuta crocuta* (Erxleben, 1777), *Elephas recki* Dietrich, 1916, *Ceratotherium simum* (Burchell, 1817), *Equus* cf. *E. grevyi* Oustalet, 1882, *Hippopotamus gorgops* Dietrich, 1926, *Hexaprotodon* sp., *Kolpochoerus olduvaiensis* (Leakey, 1942), *Kolpochoerus majus* (Hopwood, 1934), *Metridiochoerus* aff. *M. modestus* (Van Hoepen and Van Hoepen, 1932), *Giraffa* cf. *G. jumae* Leakey, 1965, *Tragelaphus* cf. *T. spekei* P.L. Sclater, 1863, *Pelorovis oldowayensis* Reck, 1928, *Kobus* cf. *K. ellipsiprymnus* (Ogilby, 1833), *Hippotragus gigas* Leakey, 1965, *Gazella* sp., Caprini indet., *Crocodylus niloticus* Laurenti, 1768, *Pelusios* cf. *P. sinuatus*

(Smith, 1838), *Varanus niloticus* (Linnaeus, 1766), and *Python* ex gr. *P. sebae* (Gmelin, 1789).

Abbreviations

Institutions

DSTF: Earth Sciences Dept, University of Florence, Italy; DME: Department of Mines, Eritrean Ministry for Energy and Water Resources, Eritrea; NME: National Museum of Eritrea; MGPF: Natural History Museum (Geology and Palaeontology section), University of Florence, Italy.

Collections. UA: Dandiero Basin, Wadi Aalad collection area (north of Wadi Dandiero), National Museum of Eritrea; DAN: Dandiero Basin, Dioli collection area (south of Wadi Dandiero, north of Wadi Maebele), National Museum of Eritrea; MHB: Dandiero Basin, Wadi Maebele collection area (south of Wadi Maebele, Wadi Ghersaloita), National Museum of Eritrea; ER: East Rudolf, National Museum of Kenya collections; WT: West Turkana, National Museum of Kenya collections; OM: Osteology Department, National Museum of Kenya collections.

Measurements. L: length; W: width; WAL: width at the anterior lobe; WPL: width at the posterior lobe; Trig: trigonid; oc ap: occlusal antero-posterior length; oc tr: occlusal transversal length; ptc: protocone length; PI: Protoconal Index; l pf: postfossette length; FI: Postflexidic Index; ap ext: length (antero-posterior) on the external side; ap int: length (antero-posterior) on the internal side; prot: width at protocone; met: width at metacone; EL: external length; IL: internal length; PTD: proximal transverse diameter; PAPD: proximal antero-posterior diameter; MTD: transverse diameter at the diaphisis; MAPD: antero-posterior diameter at the diaphisis; DTD: distal transverse diameter; DAPD: distal antero-posterior diameter. All measurements are given in millimeters.

Systematic Paleontology

Order **Primates** Linnaeus, 1758
Suborder Catarrhinii (Simpson, 1945)
Family Hominidae Gray, 1825
Genus *Homo* Linnaeus, 1758

Homo "*erectus*-like"

One mostly complete cranium (UA-31), one left ?I² and one left I₁ (UA-222 and UA-369, respectively), and one partial right hip-bone (UA-173 + UA-405), and a left pubic symphysis (UA-466), have been recovered from the so called *Homo* site in the Wadi Aalad area (UAHS). Preliminary morphological and size description of the UA 31 cranium and assessment of its "*erectus*-like" status have been based on the analysis of the original unrestored (Abbate et al. 1998; Rook et al 1999) and of the partially restored specimen (Macchiarelli et al. 2002, 2004). Based on the currently available evidence, a revision, refinement, and integration of our previous analytical work is in progress.

Family Cercopithecidae Gray, 1821
Genus *Theropithecus* Geoffroy Saint-Hillaire, 1843

Theropithecus cf. ***T. oswaldi*** (Andrews, 1916)

A large cercopithecid cranium fragment (UA-463) was collected in November 2004 in the area of Wadi Aalad, at a site identified as K003. It preserves the frontal and the anterior region of the parietals and, in a preliminary comparison, matches the anatomy of *Theropithecus oswaldi*, the largest Late Pliocene, Early Pleistocene and lowermost Middle Pleistocene African cercopithecid. This species is found at a number of Eurasian localities including: the Early Pleistocene site of 'Ubeidiya, Israel (Belmaker 2002); Mirzapur, India (Delson 1993), Cueva Victoria, Spain (Gibert et al. 1995) and Pirro Nord, Italy (Rook et al. in press).

Order **Carnivora** Bowdich, 1821
Suborder Fissipeda Simpson, 1945
Family Hyaenidae (Gray, 1869)
Genus cf. *Crocuta* Kaup, 1828

cf. *Crocuta crocuta* (Erxleben, 1777)

No skeletal remains were found ascribed to a large hyaenid nor other carnivores, but three coprolites of a large hyena have been identified in the fossil collection from Buia. The dimensions (in millimetres) of these fossil excrements are: UA-114 (Fig. 1): 56.0 x 27.1 x 23.6; UA-190: 23.3 x 36.0 x 35.5; UA-392: 47.1 x 43.0 x 36.0. The size and morphology of these coprolites matches those of the large African hyaenid *Crocuta crocuta*. A second "indirect" evidence of the occurrence of this large predator is found on a *Kolpochoerus* cranium (UA-20). The latter has gnaw marks on the nasals and the palate, which by their size are suggestive of gnawing by *Crocuta crocuta*.

Crocuta crocuta is the largest hyena recorded in eastern Africa after the extinction in the area of *Pachycrocuta* around 2.5 Ma (Werdelin 1999), although cf. *Pachycrocuta brevirostris* is cited at the site of Daka, Ethiopia, around 1.0 Ma (Asfaw et al. 2002).

Order **Proboscidea** Illiger, 1811
Family Elephantidae Gray, 1821
Genus *Elephas* Linnaeus, 1758

Elephas recki Dietrich, 1916

Material
See Ferretti et al. (2003); no new elephant material was collected during the 2002-2004 field work.

Discussion
The Buia elephants were described in a previous work (Ferretti et al. 2003). New field surveys in 2002-2004 did not contradict the conclusion that only one elephant species, namely an advanced form of *Elephas recki*, is represented in the Dandiero Basin. The specimens collected at several sites in the areas of Dioli (acronym DAN) and Wadi Aalad (acronym UA) docu-
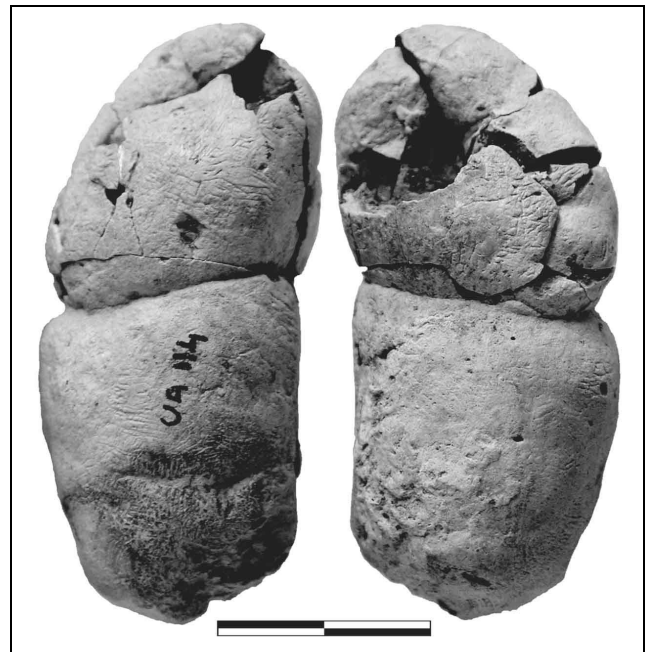

Fig. 1   - cf. *Crocuta crocuta*. UA-114, Coprolite. Bar scale in centimetres.

ment the occurrence at Buia of a very large form, characterized by extremely hypsodont molars and thin, highly folded enamel (Fig. 2). The molar features closely compare to those described by Beden (1987) for the subspecies *E. recki ileretensis* (comparable to *E. recki* stage 3 of Maglio 1973) from Koobi Fora and Ileret, Kenya. Nevertheless, specimens showing more derived features, similar to that of *E. r. recki* (stage 4 of Maglio 1973) from Beds III and IV at Olduvai, also occur within the sample. Rather than representing two different taxa, we believe the Buia sample to represents an *E. recki* population whose evolutionary stage is intermediate between *E. r. ileretensis* and *E.r. recki*. (Ferretti et al. 2003). This interpretation is consistent with the late Early Pleistocene age inferred from the magnetostratigraphic analysis of the Buia succession. *Elephas recki* is very common in the Plio-Pleistocene of East Africa. The species is best known from deposits in Ethiopia, Kenya and Tanzania (Maglio 1973; Beden 1987; Kalb & Mebrate 1994; Todd 1997), but has been also reported from Djibouti (Chavaillon et al. 1990), Chad, and Uganda (Maglio 1973). The Eritrean finding to date represents the northernmost occurrence of *E. recki*. The molars of the Buia *E. recki* show specific adaptation to grazing, which suggests this elephant preferred open environments.

Order **Perissodactyla** Owen, 1848
Family Rhinocerotidae Gray, 1821
Genus *Ceratotherium* Gray, 1867

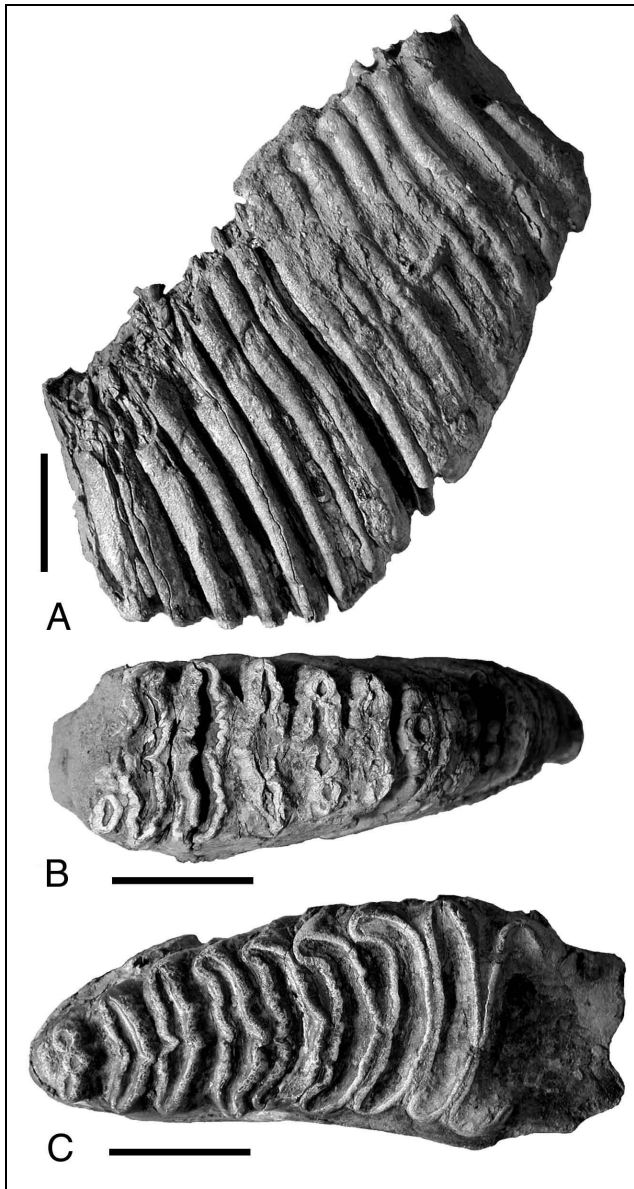*Ceratotherium simum* (Burchell, 1817)

Fig. 2 - *Elephas recki* (advanced form). A-B: DAN-243, right M³ in lateral (A, occlusal surface at bottom) and occlusal (B, anterior to the left) views; C: UA-41, right M₃ in occlusal view (anterior to the right). Bar scale represents 10 cm.

Material

One mostly complete cranium with right P³-M³ and left P⁴-M³ (DAN-150), 3 incomplete lower molars (DAN-81, DAN-180, DAN-214), 1 atlas fragment (UA-328), 1 cervical vertebra (UA-299), 2 humerus distal end fragments (UA-63, UA-126), 1 tibia distal end (DAN-49), 1 talus fragment (UA-47), 1 calcaneum (UA-458), 1 distal Mt-4 (DAN-170).

Description

At the moment, only one species of rhinoceros is recorded in the Buia sites, the white rhino *Ceratotherium simum,* which is entirely grazer (Foster 1967; Groves 1972). It is represented by a mostly complete cranium (DAN-150) (Fig. 3) and few poorly preserved teeth and postcranial elements. *Ceratotherium simum* is the only species of white rhino present in Africa after 3 Ma. It evolved from the Early Pliocene ancestor *C. praecox.* The species *C. simum* is represented by two successive subspecies, *C. simum germanoafricanum* from 3 to 2 Ma, and *C. simum simum* from 2 Ma until present. This lineage is characterised by a progressive decrease in size (Guerin 1985).

The cranium DAN-150 (Fig. 3) preserves a complete neurocranium, part of the muzzle (especially the right side), and most of the palate with right P³-M³ and left P⁴-M³. According to the tooth wear classes proposed by Hillman-Smith et al. (1986), DAN-150 represent a juvenile individual referable to the wear class "X", corresponding to an individual age of 8-11 years. The cranium is dolichocranial, with the occipital crest projecting posteriorward. The cheek teeth are hypsodont with much cement on the crown, and protoloph and metaloph are curved posteriorward. Comparison of the Buia specimen with *C. simum* fossil cranial remains from East Turkana (ER 328C, ER 329, ER 2320) and with one recent specimen (OM-2184), shows that the Eritrean specimen metrics fall within the normal range of variability of *Ceratotherium simum*, though, in general, the values are near the upper end of the range (Table 1).

	DAN-150	ER-328C	ER-329	ER-2320	OM-2184
Maximum length	*740,0	800,0	-635,0	-500,0	825,0
Minimum length from nasal boss to nuchal crest	*610,0	733,0	633,0		756,0
Length from nasal boss to external auditory meatus	*530,0	652,0	540,0	459,0	
Basilar length	*570,0	752,0	-635,0		713,0
Length from palatonarial border to occipital condyles	365,0	431,0	400,0	-308,0	427,0
Width at nasal boss	193,0	182,0	161,0	82,0	194,0
Maximum width of cranium at orbits	328,0	302,0	-240,0	166,0	180,0
Minimum width of cranial vault at temporal fossa	127,0	120,0	115,0	103,0	112,0
Width of dorsal edge nuchal crest	320,0	275,0	-208,0		216,0
Maximum width of the occiput	263,0	283,0			216,0
Width of occipital condyles	165,0	151,0	-158,0		154,0
Depth foramen magnum to nuchal crest	169,0	156,0	-98,0		162,0
Maximum width cranium at zygoma	390,0	373,0	-320,0	-286,0	335,0
Width of the palate at M1	98,0	65,0	106,0	69,0	100,0
Width of the palate at M3	118,0	82,0		113,0	

* until P3

Tab. 1 - Measurements of the Buia *Ceratotherium simum* DAN-150, compared to Koobi Fora and extant specimens (data from Harris 1983a).
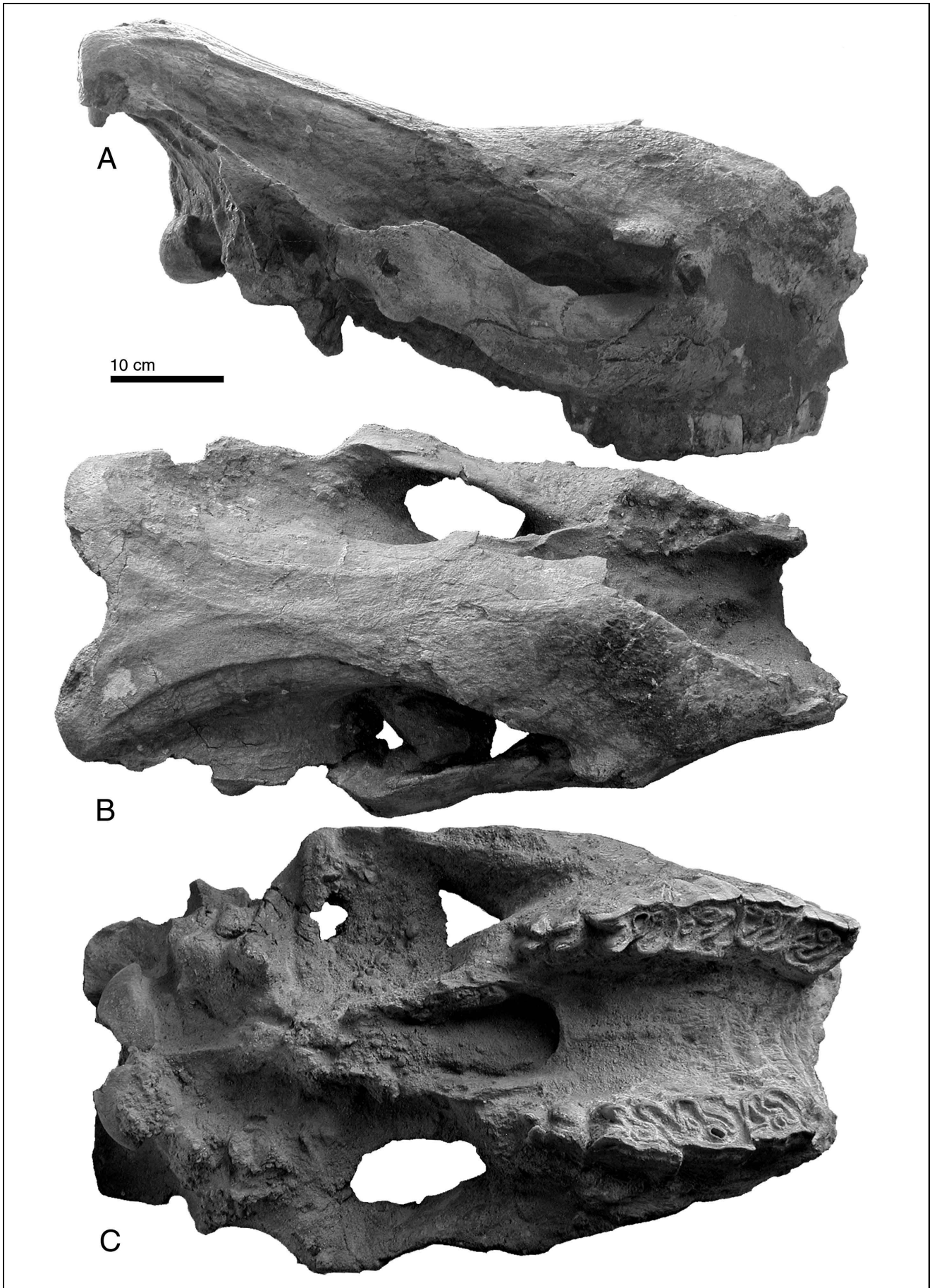
Fig. 3 - *Ceratotherium simum*. DAN-150, cranium in lateral (A), dorsal (B) and ventral (C) views. Bar scale represents 10 centimeters.

The teeth (Table 2) and the scanty postcranial elements fall within the normal variability of *Ceratotherium simum*.

<div style="text-align: center">

Family Equidae Gray, 1821
Genus *Equus* Linnaeus, 1758

Equus cf. *E. grevyi* Oustalet, 1882

</div>

Material

One P^4 (UA-301), 1 M^1 (DAN-230), 1 right mandibular fragment with P$_4$ (DAN-140), 2 M$_2$ (DAN-153, UA-13), 2 P$_2$ (UA-254, DAN-185), 1 cervical vertebra (UA-455), 1 lumbar vertebra (UA-119), 1 humerus distal end (DAN-124), 1 tibia distal end (UA-96), 1 right magnum (UA-14), 1 pisiform (UA-455), 1 talus (UA-277), 1 medial phalanx (UA-333).

Description

Although scanty, the study of the equid material in the collection allow us to exclude the occurrence of the genus *Hipparion* (the genus was reported erroneously in the 1998 faunal list) and to attribute all the equid remains to the genus *Equus* (Fig. 4). They probably correspond to a species similar to the large zebra inhabitant of the semidesertic areas, *Equus grevyi*. The Buia dental remains include large molars with moderate protoconal indices in the upper series, and show stenonine morphology in the lower one. Only 15 specimens have been ascribed to this form of equid, including two maxillary and five mandibular cheek teeth, although one, the lower M$_2$ DAN-153, is not measurable (Table 3). In the upper series, as in the Koobi Fora specimens ascribed to *Equus* cf. *E. grevyi* (Eisenmann 1983), the P^4 UA-301 shows a developed caballine fold, and the protoconal indices (PI) is shorter in this specimen than in the M^1 DAN-230. (35.0 and 46.1, respectively), suggesting an increase in the PI from the premolars to the molars. The lower cheek teeth show deep lingual groove in the premolars and very deep labial groove in the only one molar of the collection (M$_2$ UA-13, Fig.4). Their measurements fall in the variability of those of *E.* cf. *E. grevyi* from Koobi Fora.

These specimens have also been compared to *Equus tabeti* from Koobi Fora (Eisenmann 1983) and 'Ubeidiya, Israel (Eisenmann 1986). In general, the teeth anatomy of *E. tabeti* shows some similarities to the Buia specimens, especially in the upper cheek teeth series, but
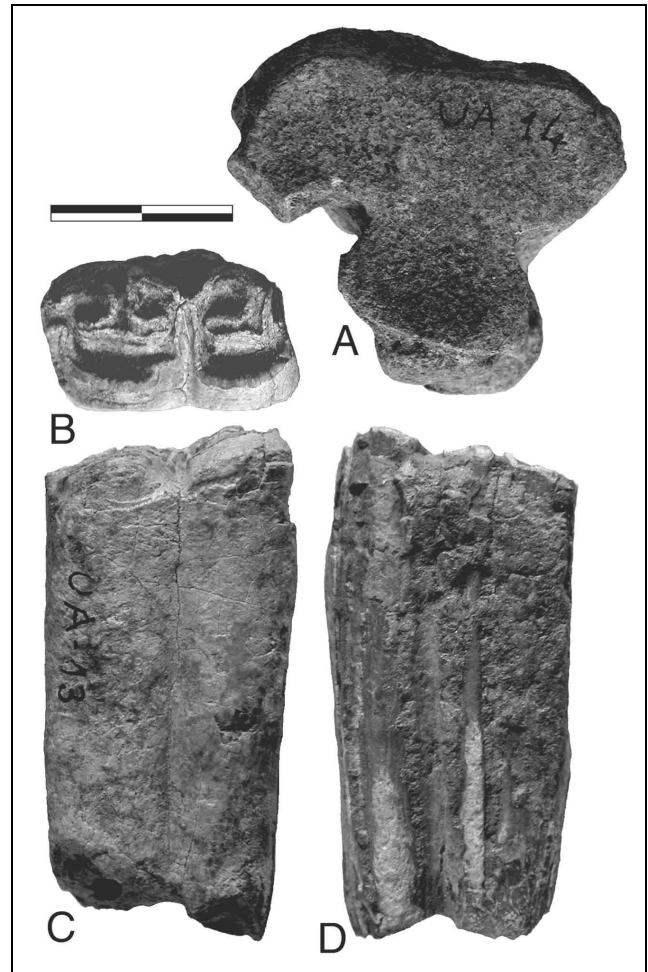

Fig. 4 — *Equus* cf. *E. grevyi*. A: UA-14, right magnum in proximal view; B-C: UA-13, right M$_2$ in occlusal (B), buccal (C) and lingual (D) views. Bar scale in centimetres.

in the lower series it has smaller labio-lingual diameters and smaller values in the postflexidic indices (FI). This difference in the FI is prominent on the lower P$_4$ and M$_2$, where the maximum values for 'Ubeidiya are 48.0 and 34.6, respectively, and for the specimens from Buia are 62.8 and 65.4, respectively (Table 3). These morphometrical data suggest that the Buia specimens are not referable to *Equus tabeti*, and their anatomy and measurements are close to *Equus grevyi*.

<div style="text-align: center">

Order **Artiodactyla** Owen, 1848
Suborder Suina Gray, 1821

</div>

		P3/				P4/				M1/				M2/				M3/		
		L ap ext	L ap int	W prot	W met	L ap ext	L ap int	W prot	W met	L ap ext	L ap int	W prot	W met	L ap ext	L ap int	W prot	W met	L ap ext	L ap int	W tr
DAN-150	Rt	48,8	38,9	47,3	47,1	49,6	40,2	48,6	46,8	54,8	47,8	56,7	54,4	63,9	47,7	50,0	46,1	56,1	55,9	46,4
DAN-150	Lt					50,5	38,0	45,3	48,8	57,8	48,3	58,9	53,4	64,0	48,4	55,4	40,6	51,3	50,3	46,4
ER-1190		49,4	46,4	51,5	48,8															
ER-328						54,5	41,1	63,6	56,5	50,0	39,8	70,0	64,5	64,0	56,0	77,2	64,8	64,4	61,3	59,8
ER-1189						46,1	43,4	59,2	55,3									77,4	69,4	54,7
ER-329										71,0	48,2	57,1	33,8							
ER-1191														58,4	54,8	67,6	54,9			
ER-659																		68,2	65,6	61,2
OM-2184		46,0	46,4	51,9	47,0	55,2	51,2	51,2	44,6	50,5	52,5	58,0	55,1	73,2	60,2	51,6	45,7			
OM-2216		38,0	30,4	34,7	31,0	44,6	39,0	39,0	35,8	46,1	37,9	42,6	36,2	46,4	43,8	51,0	40,5	58,3	46,3	42,3

Tab. 2 — Measurements of the *Ceratotherium simum* teeth (DAN-150), compared Koobi Fora and extant specimens (data from Harris, 1983a).

upper teeth		
	UA-301	DAN-230
	P4/	M1/
oc ap	30,0	27,1
oc tr	30,8	31,4
ptc	10,5	12,5
PI	35,0	46,1

lower teeth			
	UA-185	UA-254	DAN-140	UA-13
	P/2	P/2	P/4	M/2
oc ap	34,9	33,9	31,2	28,3
oc tr	20,0	16,8	19,6	18,5
l pf	14,8	17,3	14,9	10,5
FI	42,4	49,6	62,8	65,4

Tab. 3   - Measurements of the upper and lower cheek teeth of *Equus* cf. *E. grevyi* from Buia
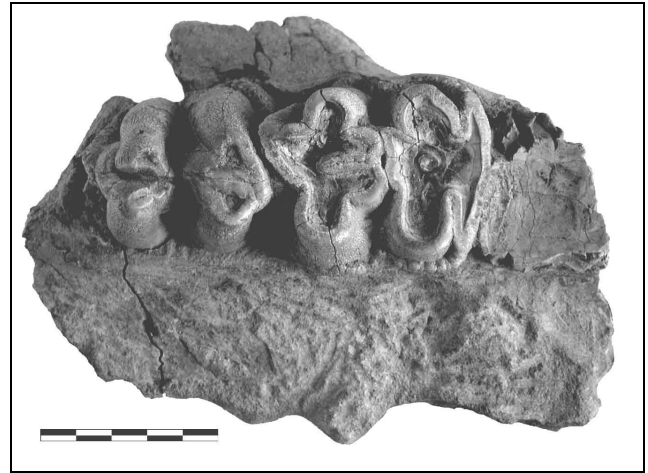

Fig. 5   - *Hippopotamus gorgops.* UA-223, right maxillary fragment with M^1 (deeply worn) M^2 and M^3, in occlusal view. Scale bar in centimetres.
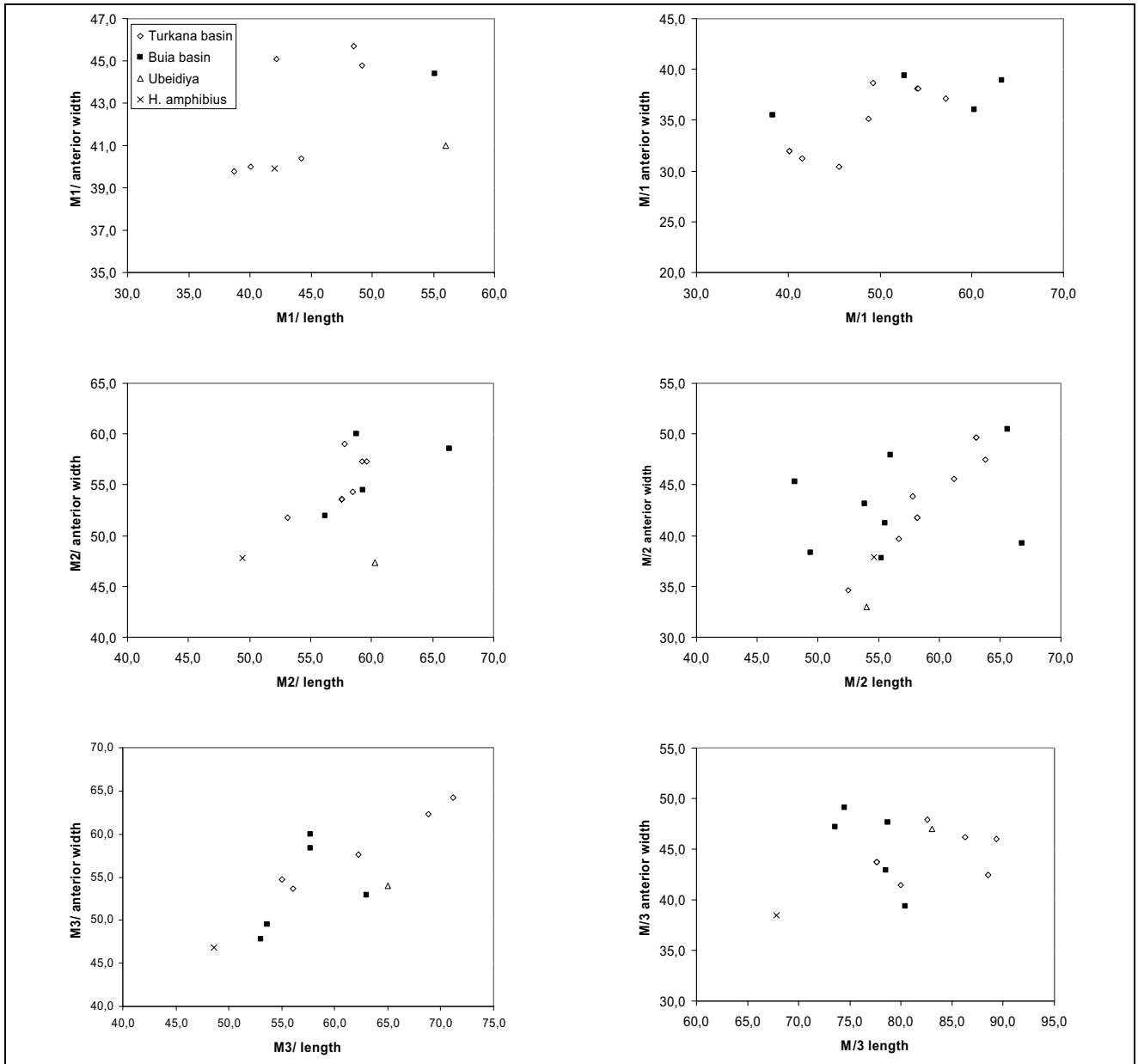

Fig. 6   - Bivariate plots of *Hippopotamus* upper (left column) and lower (right column) molars dimensions (see Tables 4 and 5 for data source).

Family Hippopotamidae Gray, 1821
Genus *Hippopotamus* Linnaeus, 1758

Hippopotamus gorgops Dietrich, 1926
(advanced form)

Material

Four upper canines (DAN-115, DAN-162, UA-22, UA-163), 3 I¹ (DAN-50, DAN-200, UA-5-7), 2 I² (DAN-50, DAN-161), 1 palate with right M¹-M³ and left M²-M³ (UA-223), 1 left palate fragment with M²-M³ (UA-54), 1 left palate with M¹-M³ (DAN-78), 1 P³ (DAN-115), 1 M¹ (DAN-219), 2 M² (DAN-91, DAN-218), 3 M³ (DAN-222, DAN-193, DAN-53), 2 mandibular fragments with I₁-C (UA-92, UA-184), 3 I₁ (DAN-20, UA-24, UA-263), 4 I₂ (DAN-116, DAN-117, UA-92, UA-345), 4 lower canines (DAN-15, DAN-154, DAN-166, UA-1), 3 mandibular fragments with M₁-M₃ (DAN-1, DAN-11, DAN-119, DAN-120, UA-112), 3 mandibular fragment with M₁-M₂ (DAN-175, MHB-6, UA-145), 2 mandibular fragments with M₂-M₃ (DAN-227, MHB-7), 1 mandibular fragment with P₃-M₁ (UA-452), 4 P₄ (DAN-16, DAN-173, UA-159, UA-282), 3 M₁ (DAN-113, DAN-159, UA-230), 4 M₃ (DAN-54, DAN-192, DAN-248, UA-100), 2 radius-ulna fragments (UA-85, UA-86, UA-87), 5 talus (DAN-48, DAN-93, UA-42, UA-232, UA-350), 4 calcanei (DAN-146, UA-40, UA-155, UA-239), and many other postcranial fragments (humerus, femurs, tibias, carpals, metapodials and phalanges).

Description

A large form of *Hippopotamus*, larger than the extant *H. amphibius*, has been documented at Buia (Fig. 5). It is the most abundant taxon in the area and has been ascribed to *Hippopotamus gorgops*. The collection is represented by dental and postcranial remains but unfortunately no complete skull has been documented to date.

Dentition – *Hippopotamus gorgops* from Buia shows robust and hypsodont teeth with thick enamel, and robust incisors and canines. Only one upper premolar is present in the collection (DAN-115). The upper molars are tetracuspid, and show a large cingulum on the mesial and distal sides, which is also present in the lingual and labial faces. The increase of size from M¹ to M² to M³ is very prominent (Figs. 5, 6; Table 4). The lower premolars are unicuspid with developed distal cingulum. The morphology of the lower molars is similar to that of the upper ones, but the linguo-labial dimension is proportionately smaller, the lingual and labial cingulum is less developed, and the third molar (M₃) has a large talonid (Table 5).

The metrical comparison of the dental specimens from Buia to the good collection of *H. gorgops* from Koobi Fora and West Turkana (Harris 1991a) (Fig. 6), shows that in the upper molar series, the Buia specimens have larger mesio-distal length for the first and the second molar and a shorter third molar. The measurements of the lower molar series from Buia are more similar to the *H. gorgops* collection from the Turkana Basin, than

	P1/		P2/		P3/		P4/		M1/			M2/			M3/		
	L	W	L	W	L	W	L	W	L	WAL	WPL	L	WAL	WPL	L	WAL	WPL
BUIA																	
UA-223 R.											46,5	66,4	58,6	57,7	53,6	49,5	46,2
UA-223 L.												66,9			53,0	47,8	45,7
UA-54 R.														60,0	60,8		59,6
DAN-78 L.											46,6	58,8	60,0	61,6	57,7	60,0	58,6
DAN-222 L.															63,0	52,9	46,1
DAN-219 R.									55,1	44,4	46,2						
DAN-118 L.												59,3	54,5	50,3			
DAN-91 L.												56,2	52,0	51,8			
DAN-193 L.													52,6				
DAN-53 R.															57,7	58,4	53,7
DAN-115 L.					37,9	26,4											
TURKANA BASIN																	
WT-19634 L. (1)	16,0	17,0	32,5	25,1	37,4	28,6	39,5	35,4	49,2	44,8	46,0	59,6	57,3	55,6	68,8	62,3	52,3
ER-305							38,6	37,4	38,7	39,8	41,7						
ER-1307R.							31,8	32,0	44,2	40,4	41,6	57,6	53,6	53,6	56,1	53,7	48,3
ER-1394 R					39,6	30,3	37,9	35,1	40,1	40,0	46,7	57,6	53,6	53,6	62,2	57,6	49,8
ER-1427 L							34,1	33,9	48,5		37,2	53,1	51,8	49,2			
ER-12884							33,4	34,8									
ER-637									42,2	45,1	47,4	57,8	59,0	57,4	55,0	54,7	
ER-1306 R									48,5	45,7	46,1	59,2	57,3	49,5			
ER-5518															71,2	64,2	53,7
ER-5514												58,5	54,3				
UBEIDIYA																	
H. behemoth					39,7	28,9	30,2	27,3	56,0	41,0	40,0	60,3	47,3	50,7	65,0	54,0	49,0
Living *Hippopotamus*																	
H. amphibius					35,5	27,6	28,8	32,2	42,0	39,9	41,9	49,4	47,8	46,8	48,6	46,8	41,5

Tab. 4 - Upper dentition of *Hippopotamus gorgops* from Buia, the Turkana Basin (Harris, 1991a), *H. behemoth* from 'Ubeidiya and extant *H. amphibius* (Faure, 1986).

	P/1		P/2		P/3		P/4		M/1			M/2			M/3			M/1-M/3
	L	W	L	W	L	W	L	W	L	WAL	WPL	L	WAL	WPL	L	WAL	WPL	L
BUIA																		
DAN-1 R.									38,3	35,5		56,0	47,9	48,2	78,7	47,6	43,0	174,3
UA-112 R.									40,1		40,9	55,5	41,2	45,8	69,4			165,8
UA-43 L.												55,2	37,8	43,8				
DAN-175 L.									60,3	36,0	39,1	66,8	39,2	40,5				
DAN-227 L.												49,4	38,3	40,9		39,5	40,2	
DAN-54 R.																43,3	42,7	
DAN-192 R.															80,4	39,4	35,8	
DAN-111-119-120 R.									52,7	39,4		65,6	50,5	48,2	74,5	49,1	50,1	196,0
DAN-159 L.									50,5									
UA-230 R.										34,7	35,8							
UA-282 L.								29,8										
DAN-16 R.							41,6	29,0										
DAN-248 L.															78,5	42,9	40,7	
DAN-113 R.									63,3	38,9	37,0							
UA-100 L.															74,0			
UA-145 R.									66,1				41,5					
UA-452 L.					36,7	26,9		26,0	53,7									
UA-159 R.							40,0	23,2										
DAN-173 R.							42,8	27,1										
MHB-6 R.									46,4			53,9	43,1	45,5				
MHB-7 R.												48,1	45,3	47,5	73,6	47,2	41,7	
TURKANA BASIN																		
ER-2405	32,6	22,0																
ER-1427			37,6	23,3	36,8	26,9	43,4	31,7	54,1	38,1	41,4	63,0	49,7	42,2				
WT-19982			41,1	23,7	42,3	27,2	42,6	33,3	49,2	38,7	40,8	63,8	47,5	45,0	82,6	47,9	44,6	
ER-1421					37,5	23,8	37,2	26,9										
ER-1425 R							40,3	30,0										
ER-1514							41,0	32,9										
ER-2405							33,5	26,6	40,1	32,0	34,6	58,2	41,8	44,2	77,6	43,7	41,7	
ER-5527							44,3	33,3										
ER-785									57,2	37,1								
ER-1207 R									45,5	30,4	31,2							
ER-1394 R									41,5	31,2	36,8	56,7	39,7	43,7	88,5	42,5	41,9	185,6
ER-1427 R									54,2	38,1	41,4	63,0	49,7	42,2				
ER-2044									48,7	35,1	38,9	61,2	45,6	47,7				
ER-2405 R									40,1	32,0	34,6	58,2	41,8	44,2	77,6	43,7	41,7	172,5
ER-1307												52,5	34,6	36,3	57,0			
ER-5510												57,8	43,9	44,8				
ER-1409															89,3	46,0	42,4	
ER-5513															80,0	41,5	42,1	
ER-5527 L															86,3	46,2	46,1	
UBEIDIYA																		
H. behemoth			34,0	19,5	42,5	25,2	41,0	28,5				54,0	33,0	35,0	83,0	47,0	41,0	
Living *Hippopotamus*																		
H. amphibius			32,4	18,7	36,3	22,4	35,1	27,3				54,6	37,9	39,6	67,8	38,5	37,4	

Tab. 5 - Lower dentition of *Hippopotamus gorgops* from Buia, the Turkana Basin (Harris, 1991a), *H. behemoth* from 'Ubeidiya and extant *H. amphibius* (Faure, 1986).

are the upper ones from the same basin. These metrical data have also been compared to those of the sample from 'Ubeidiya, ascribed in Faure (1986) to the species *Hippopotamus behemoth*, which is interpreted as an endemic form from the Early Pleistocene of the Levantine Region. The specimens from Buia match the variability of this form from Israel. It seems as if the samples from Buia and 'Ubeidiya correspond to an advanced form of *Hippopotamus gorgops*.

Genus *Hexaprotodon* Falconer & Cautley, 1836

Hexaprotodon sp.

Material. One un-restored cranium (DAN-213), 1 un-restored neurocranium (DAN-205), 1 left talus (MHB-5), 1 right magnum (DAN-246), and several other teeth fragments and postcranial elements.
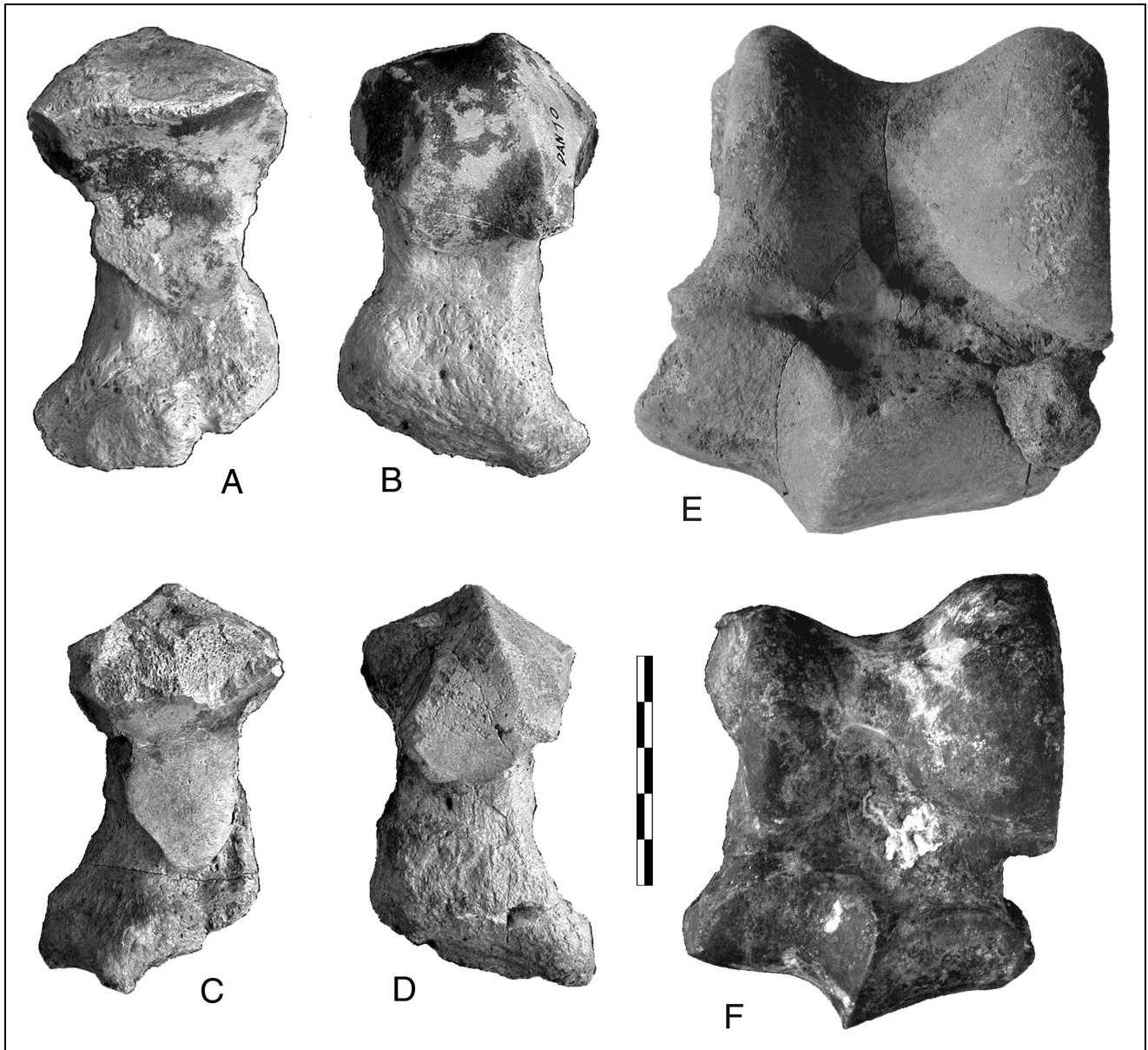
Fig. 7   - Comparative view of *Hippopotamus gorgops* (A-B, E) and *Hexaprotodon* sp. (C-D, F) postcrania. A-B: DAN-10, right magnum in
           distal (A) and proximal (B) views; C-D: DAN-246, right magnum in distal (C) and proximal (D) views; E: UA-232, left talus in
           posterior view; F: MHB-5, left talus in posterior view. Scale bar in centimetres.

Description

A small-sized brachydont hippo is present in the Buia assemblage together with *Hippopotamus gorgops*. It was cited as *Hexaprotodon karumensis* in Abbate (1998) because of its anatomical similarities with this species. A mostly complete cranium of this small hippo has been found recently (DAN-213), but it is still in the restoration process and cannot be included in this study. The anatomy of the cranium, the dental proportions and the anatomy of the other specimens ascribed to this species suggest a different species than *H. karumensis*. We have to await the restoration of this mostly complete cranium before we can assign a species name to the Buia *Hexaprotodon* species.

This is the first record of this genus from the Early Pleistocene of the Afar region, where the genus is reported to have disappeared after 2.5 Ma (Boisserie 2002).

The comparison of the postcranial elements of *Hippopotamus gorgops* and *Hexaprotodon* sp. from Buia shows clear functional differences between the two species: 1) in *H. gorgops* the articular facet for the third metacarpal on the distal face of the magnum, is relatively shorter antero-posteriorly, and wider transversely, than in *Hexaprotodon* sp. This means that the antero-posterior movement of the manus was wider in *Hexaprotodon* than in *H. gorgops* (Fig. 7); 2) in *Hexaprotodon* sp. the talus is relatively slender and more gracile,

while in *Hippopotamus gorgops* it is proportionately shorter and more robust, corresponding to a very massive species. This characteristic is remarkable in the difference of the length and transversal diameter of the talus (Fig. 7).

Family Suidae Gray, 1821

Three species of suids have been identified at Buia, two pertaining to the genus *Kolpochoerus* (*K. olduvaiensis* and *K. majus*) and one to the genus *Metridiochoerus* (*M.* aff. *M. modestus*).

Genus *Kolpochoerus* Van Hoepen and Van Hoepen, 1932

Kolpochoerus is belived to be the ancestor of the extant *Hylochoerus*, the forest hog. It is a sexually dimorphic suid of moderate to large size. It has low crowned and well rooted molars and inflated mandibles beneath the cheek teeth (Harris 1983b). Both species of *Kolpochoerus* recorded in the African Early Pleistocene, *K. olduvaiensis* and *K. majus*, are well represented at Buia.

Unfortunately, the best specimens of *Kolpochoerus*, the almost complete cranium DAN-142 and the muzzle UA-20 are still not restored and cannot be included in this study. UA-20 has been cited above because of the hyena gnaw marks found in the nasals and the palate of this specimen.

Kolpochoerus olduvaiensis (Leakey, 1942)

Material

One upper C (UA-154), 1 M^1 (DAN-221), 2 M^3 (UA-36, UA-167), 1 complete mandible with both branches (MHB-1), 1 mandible with most of complete left branch (UA-242), 1 right mandibular fragment with M_3 (DAN-199), 1 left mandibular fragment with P_4 (DAN-132), 1 P_4 (DAN-233), 1 M_1 (DAN-51), 9 M_3 (DAN-138, DAN-82, DAN-135, DAN-139, DAN-189, DAN-249, UA-116, UA-232, UA-329).

Description

Upper teeth – The canine (UA-154) has a greater mesio-distal diameter than the dorso-ventral one, and it has a longitudinal groove in the postero-dorsal face. The M^1 (DAN-221) is a worn typical tetracuspid molar, with labial cuspids (paracone and metacone) larger and higher than lingual ones (protocone and hypocone). It also shows a developed cingulum in the mesial and distal faces. Only one M^3 fragment is present (UA-36).

Lower teeth – Two more or less complete mandibles (UA-242 and MHB-1) (Fig. 8) are present in the sample. The mandibular body shows a triangular section. Preserved teeth include the canine, and the cheek dental series P_3-M_3. The premolars (P_3 and P_4) are subtriangular unicuspid pieces. The first and second molars (M_1 and M_2) are tetracuspid pieces with lingual cuspids (metaconid and entoconid) bigger and higher than the labial ones (protoconid and entoconid). In the specimen UA-242 the M_1 and M_2 labio-lingual diameter is greater than the mesio-distal one. DAN-51 exhibits small mesial and distal cingula. The lower third molar (M_3) is the best preserved specimen, it has tetracuspid trigonid (proto-, meta-, hypo- and entoconid) normally shorter than the talonid, which is very elongated and can have until four or five pair of cuspids (Fig. 9c-d). It is worth to note the occurrence of one important asymmetry in the specimen MHB-1, where the right M_3 is larger than the left one (61.1 and 56.1 mm, respectively), because it has

Fig. 8 - *Kolpochoerus olduvaiensis.* A-B: UA-242, right mandible in occlusal (A) and buccal (B) views. Bar scale in centimetres.
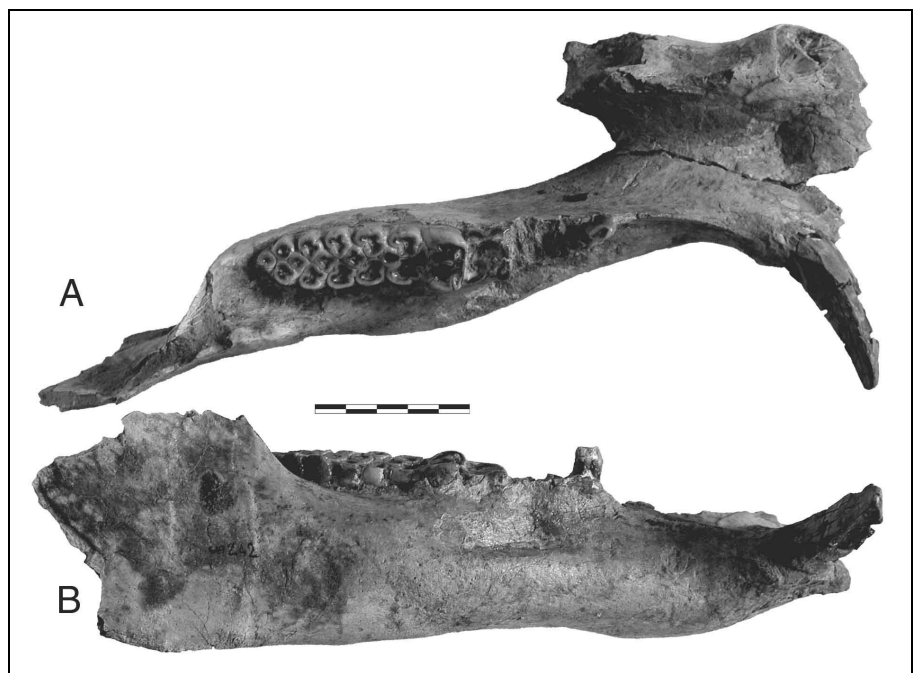
larger talonid with one more pair of cuspids. This asymmetry possibly is related to a high endogamy in the populations of *Kolpochoerus* in the area.

Kolpochoerus olduvaiensis is an advanced form of the type species *Kolpochoerus limnetes*, which increased the size and length of the third molars from the primitive *Potamochoerus* anatomy.

Kolpochoerus majus (Hopwood, 1934)

Material

One palate fragment with the left C (UA-303), 1 germinal upper C (UA-457), 3 M² (DAN-133, UA-223, UA-437), 1 mandibular symphysis (DAN-187) 1 incomplete mandible with left and right branches (DAN-141), 1 right hemimandibular fragment with M₁-M₂ (DAN-194), 1 left hemimandibular fragment with M₃ (DAN-174), 1 mandibular symphysis (UA-378), 3 M₃ (DAN-143, UA-44, UA-464).

Description

Upper teeth – The canines (Fig. 9a-b) are larger than in *K. olduvaiensis* (Table 6). Two M² (DAN-133 and UA-437) have been identified, which are morphologically similar to *K. olduvaiensis*, but are larger and more hypsodont than in *K. olduvaiensis*.

Lower teeth – No canines are present in the collection. The cheek teeth have P₃-M₃, which is shown in the specimens DAN-141 and DAN-174. The premolars have one main cusp and are larger and higher than in *K. olduvaiensis*. M₁ and M₂ are evolutionarily advanced compared to *K. olduvaiensis*. These molars are tetracuspid, larger, higher crowned and proportionally more elongated than in *K. olduvaiensis* and show developed mesial and distal cingula. The third molar is shorter than in *K. olduvaiensis*, have developed tetracuspid trigonid and short talonid with few pairs of cuspids. In cross-section the enamel is generally more complicated than that of *K. olduvaiensis*.

K. majus has a more conservative teeth anatomy than *K. olduvaiensis*, with less elongate M₃, and proportionately more developed M₁ and M₂ (Table 7).

Discussion on the genus *Kolpochoerus*

Besides DAN-142 and UA-20, the Buia *Kolpochoerus* sample includes specimens that may be referable to as many as two species, including: 1 occipital and temporal bone fragment (UA-441), 1 left hemimandib-
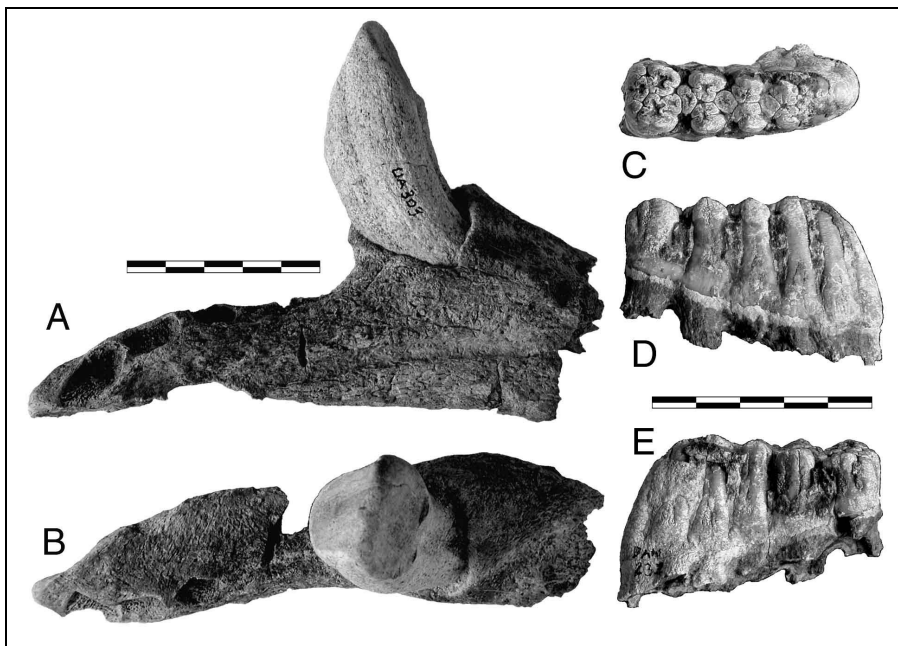

Fig. 9 - *Kolpochoerus majus.* A-B: UA-303, left maxillary fragment with C and incisors alveoli in occlusal (A) and buccal (B) views. *Kolpochoerus olduvaiensis.* C-E: DAN-232, right M₃ in occlusal (C), lingual (D) and buccal (E) views. Bar scales in centimetres.

	C		M1/		M2/		M3/			
	L	W	L	W	L	W	L	W	L trig	L tal
K. Olduvaiensis										
UA-36								24,60		
DAN-221			23,70	17,20						
UA-154	31,00	15,60								
K. Majus										
UA-437					34,80	15,40				
DAN-133					29,50	22,00				
UA-303	29,30	27,00								
UA-457	21,20	22,00				24,00				

Tab. 6 - Upper teeth of *Kolpochoerus olduvaiensis* and *K. majus* from Buia.

	C		P/2		P/3		P/4		M/1		M/2		M/3			
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L trig	L tal
K. Olduvaiensis																
UA-242 R.	23,90	17,80			10,60	7,20	14,20	12,70	10,50	15,40	16,40	17,90	67,00	19,70	25,20	41,80
DAN-138 L.													65,40	20,80	28,60	36,80
DAN-82 L.													61,30	20,00	30,10	31,20
UA-116 L.														19,90		42,10
DAN-139 L.														19,20		30,50
DAN-199 R.													57,50	17,60	28,70	28,80
DAN-132 L.							15,00	12,60								
DAN-51 L.									23,20	16,10						
UA-329 R.														22,50		
UA-232 R.													51,10	18,00	23,80	27,30
DAN-249 L.														17,90		37,50
DAN-233 R.							13,90	10,80								
MHB-1 L.		17,90									20,60	20,10	56,10	20,70	27,90	28,20
MHB-1 R.	18,60	16,11			11,50	5,30	13,30	10,90	17,40		22,60	20,60	61,10	20,90	28,50	32,60
K. Majus																
DAN-143 L.													45,20	22,90	28,20	17,00
UA-44 L.														21,80	25,90	
DAN-174 L.					14,00	10,60	19,50	11,80	18,70	16,80	26,40	18,60		21,70	27,00	
DAN-194 R.									16,70	16,90	27,20	21,10				
DAN-141 L.						9,90	16,90	12,60	21,10	14,30	26,10	18,00	40,10	21,00	24,60	15,10
DAN-141 R.									22,50	13,80	26,90	19,30	42,70	20,90	26,10	16,60
UA-464 R.														21,50		12,80

Tab. 7 - Lower teeth of *Kolpochoerus olduvaiensis* and *K. majus* from Buia.

ular fragment with no teeth (UA-37), 1 molar fragment (DAN-52), 1 atlas fragment (DAN-114), 1 humerus distal end (DAN-236), 1 femur distal end (UA-180), 1 tibia distal end (UA-312), 5 talus (DAN-12, DAN-59, DAN-149, DAN-181, UA-278), 1 proximal phalanx (DAN-60), 1 medial phalanx (UA-59).

Kolpochoerus majus is a more conservative species than the lineage *K. limnetes-olduvaiensis*, and preserves a primitive cheek teeth anatomy closer to the ancient forms related to *Potamochoerus* (Harris & White 1979).

These African suids are basically characterized by the development of the zygomatic arch and the distal-ward expansion of the lower third molars, with several pillar-pairs. The enamel is also very thick. The genus *Kolpochoerus* has been interpreted as an evolved African form which was derived from an Asian immigrant during the Middle Pliocene (Harris & White 1979; Harris 1983b; Pickford 1994). The oldest recognized species of the genus was *K. afarensis* from Hadar (Cooke 1978), but a new study of the Early and Middle Pliocene suid material from Ethiopia and Chad has determined the occurrence of a primitive species (*K. deheinzelini*) which gave origin to the *Kolpochoerus* lineage in the African continent (Brunet & White 2000). It would appear to be derived from the Late Miocene Asian species *Propotamochoerus hysudricus*. *Kolpochoerus deheinzelini* gave rise to *K. cookei*, a small and hypsodont species which is only found in Hadar, and to *K. afarensis*, which gave origin to *K. majus* and to *K. limnetes-K. olduvaiensis* (Brunet & White 2000). *Kolpochoerus olduvaiensis* and *K. majus* are common in most of the Early Pleistocene African assemblages including the site of Daka

(Ethiopia), which is similar in its age to Buia (Asfaw et al. 2002). The last representatives of the *Kolpochoerus* lineage in Africa are *K. olduvaiensis* from Olduvai Bed IV, Tanzania (0.78 Ma) and *K. majus* at Bodo, Middle Awash, Ethiopia (0.6 Ma) (White 1995). *Kolpochoerus olduvaiensis* extended its geographic range into the Levant, it is found in 'Ubeidiya, Israel (~1.4-1.5 Ma) (Geraads et al. 1986), and in Evron Quarry, also in Israel (~0.8-1.0 Ma), cited as *K. evronensis* (Tchernov et al. 1994). In North Africa, this genus is well known and cited as *K. phacochoeroides* in several sites, including Ain Hanech and Ahl al Oughlam (Geraads 1993; Sha-nouni et al. 2002).

Genus *Metridiochoerus* Hopwood, 1926

Metridiochoerus is believed to be ancestral to the living warthog, *Phacochoerus aethiopicus* (Harris & White 1979). Metridiochoeres are sexually dimorphic pigs of small to large size. They are characterised by the reduction of the premolar series and the increase in length, hypsodonty and root fusion of the molars, especially in the maxillary and mandibular M3s. Except in the least progressive examples, fusion of the crown elements of the cheek teeth begins shortly after wear commences (Harris & White 1979).

Metridiochoerus aff. *M. modestus* (Van Hoepen and Van Hoepen, 1932)

Material

One mandibular fragment with P4-M2 (DAN-218), 1 mandibular fragment with M3 and roots of M2 (UA-449), 4 M3 (UA-367, DAN-197, DAN-220).
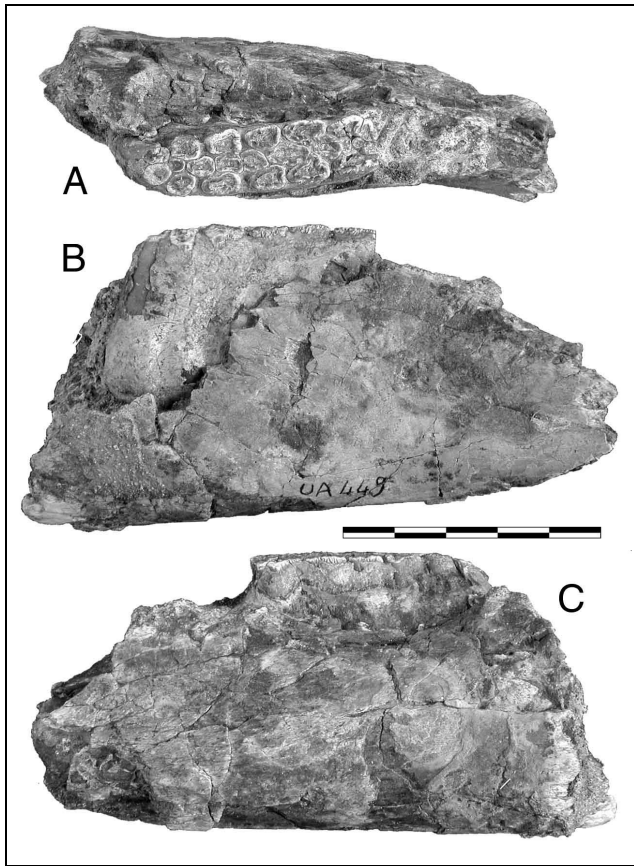
Fig. 10   - *Metridiochoerus* aff. *M. modestus*. A-C: UA 449, left mandibular fragment with M₃ in occlusal (A), lingual (B) and buccal (C) views. Bar scale in centimetres.

Description

Only five dental specimens from the total Buia fossil collection can be referred to a small sized species of the genus *Metridiochoerus*, *Metridiochoerus* aff. *M. modestus* (Table 8).

The specimen DAN-218 is a very old individual and no anatomical characteristics can be described. The other specimens, UA-449 (Fig. 10), UA-367, DAN-197 and DAN-220, are all lower third molars (M₃). They present enamel in the labial and lingual surfaces, but also in the mesial and distal ones. In the trigonid, the first pair of lobules (protoconid and metaconid) are separated from the second pair (hypoconid and entoconid) by two pair of central tubercules. The trigonid is also separated from the talonid by two central tubercules. The talonid terminates in small impaired lingual and labial pillars as in *M. modestus* (Harris & White 1979). Also the enamel corrugation is marked.

We believe that the specimens from Buia correspond to a form of *Metridiochoerus* aff. *M. modestus*, the small size species of *Metridiochoerus*. The Buia sample would represent one of the last occurrences of this species in the Early Pleistocene.

White & Harris (1979) recognize four species within the genus *Metridiochoerus*. *M. andrewsi* is the oldest, and arrived in Africa from Asia in the Middle Pliocene. It gave origin to two different lineages, 1) the *M. hopwoodi-M. compactus* lineage, characterised by a progressive increase of body size, and 2) to the small sized *M. modestus*, which is believed to be a plausible ancestor of *Phacochoerus*. The genus *Metridiochoerus* is also reported from north Africa, at the late Early Pleistocene site of Ternifine in Algeria.

Suborder Ruminantia Scopoli, 1777
Family Giraffidae Gray, 1821
Genus *Giraffa* Brisson, 1756

Giraffa cf. *G. jumae* Leakey, 1965

Material

A left maxillary fragment (UA-251) with M²-M³ and the roots of P², one very worn right M¹ or M² (DAN-198), two right talus (DAN-17 and DAN-70), and few other fragmentary specimens.

Description

A giraffid is recorded in the Buia sites. Only few specimens are ascribed to *Giraffa* cf. *G. jumai*, which has similar size to the extant species *Giraffa camelopardalis*, and it is well known in the Early and Middle Pleistocene from eastern Africa. The measurements of the molars from the specimens UA-251 and DAN-198 (Table 9) fall within the range of variability of *Giraffa jumae* from Koobi Fora (Harris 1991b), while the two talus specimens (Fig. 11) are larger than those of *Giraffa pygmaea* from Koobi Fora (Harris 1991b).

Family Bovidae Gray, 1821
Subfamily Bovinae Gray, 1821
Tribe Tragelaphini Jerdon, 1874

Members of the tribe Tragelaphini are medium to large antelopes with clockwise spiral horn-cores (on the right side). They are mostly browsers, having brachydont teeth without goat fold on the lower molars (Harris 1991c). This tribe was endemic to the African continent during the Plio-Pleistocene, as it is now. The Eurasian antelopes with spiral horn-cores (*Gazellospira, Spirocerus, Pontoceros*, and others) are sometimes included in the Tragelaphini, but all of them have well marked "Caprini" fold in the lower molars which is never present in this African tribe.

	P/4		M/1		M/2		M/3		
	L	W	L	W	L	W	L	W	L trig
UA-449							45,1	13,5	17,5
DAN-218	10,9	8,6	12,7	12,2	15,6	14,1			
DAN-197							12,9		
DAN-220 R.							42,2	14,4	18,4
UA-367 L								13,7	17,7
M. modestus	8,6	6,4	14,5	9,9	17,4	13,2	47,6	15,5	

Tab. 8   - Lower teeth of *Metridiochoerus* aff. *M. modestus* from Buia, and mean of extant *M. modestus*.

Fig. 11 - *Giraffa* cf. *G. jumae*. A-D: DAN-70, right talus in lateral (A), medial (B), dorsal (C) and ventral (D) views. Bar scale in centimetres.
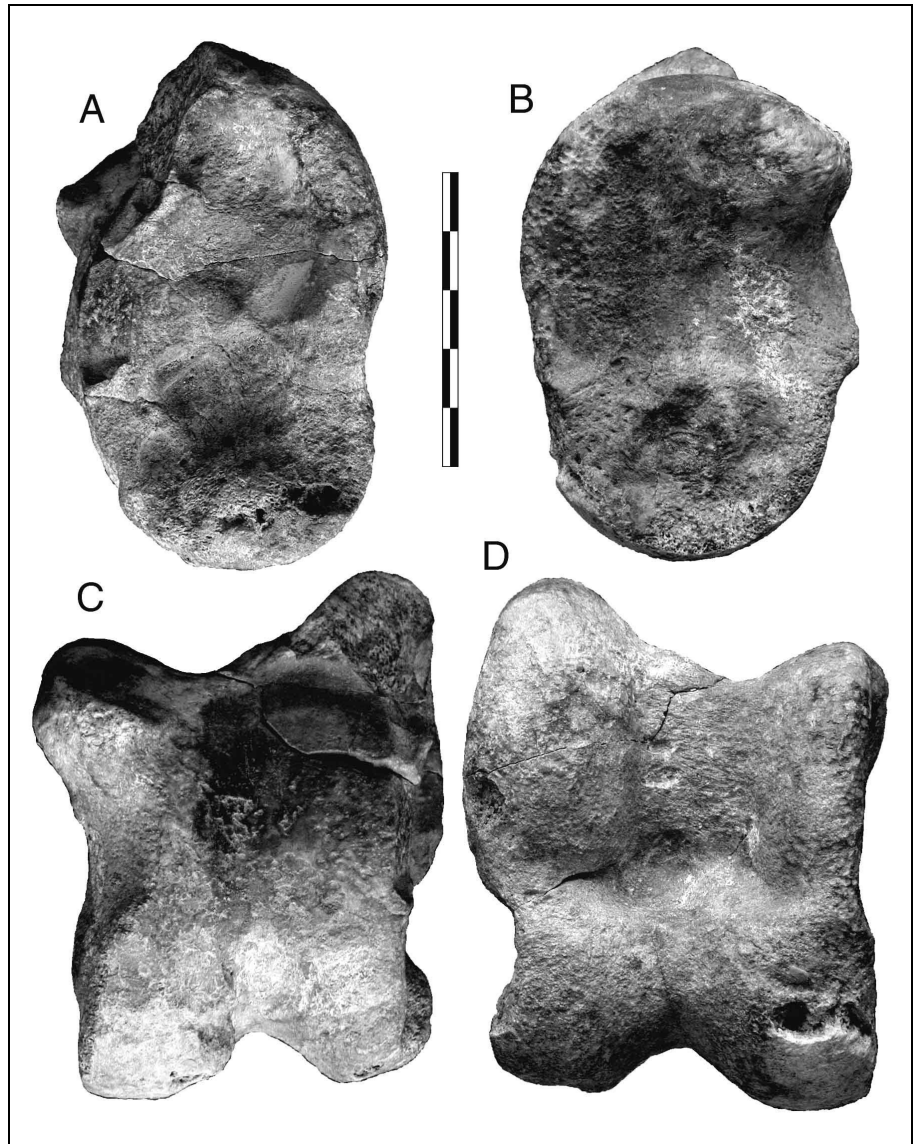
	M2/			M3/		
	L	WAL	WPL	L	WAL	WPL
UA-251	33,50			41,90	27,00	21,00
DAN-198	32,60					

Tab. 9 - Upper teeth of *Giraffa* cf. *G. jumae* from Buia

	M2/		
	L	WAL	WPL
UA-274 L.	18,7	14,8	13,4
Tragelaphus spekei			
OM-1895 L.	15,1	17,0	14,7
OM-5200 L.	18,0	14,0	13,3
Tragelaphus scriptus			
OM-935 L.	14,9	11,3	11,3
OM-926 L.	13,7	11,0	11,1

Tab. 10 - *Tragelaphus* cf. *T. spekei*, M2/ measurements compared to extant specimens

Genus *Tragelaphus* Blainville, 1816

Tragelaphus cf. *T. spekei* Sclater, 1863

Material

One M^2 (UA-274), 1 left mandible with P_3-P_4 and roots of M_1-M_2 (UA-245), 1 complete radius-ulna (MHB-2), 1 tibia distal end (MHB-3).

Description

Upper dentition – Only one specimen of a small-medium size tragelaphine has been found, UA-274 (Fig. 12d-g), a left M^2. It is a brachydont tooth, with wide lobules at the base that decrease rapidly to the apex of the crown. The lingual face has no internal pillar. The labial face shows a flattened paracone and metacone, and the three styles (parastyle, mesostyle and metastyle) are present. The measurements of this specimen are similar to those of the male of *Tragelaphus spekei* (OM-5200), from the National Museum of Kenya (Table 10).
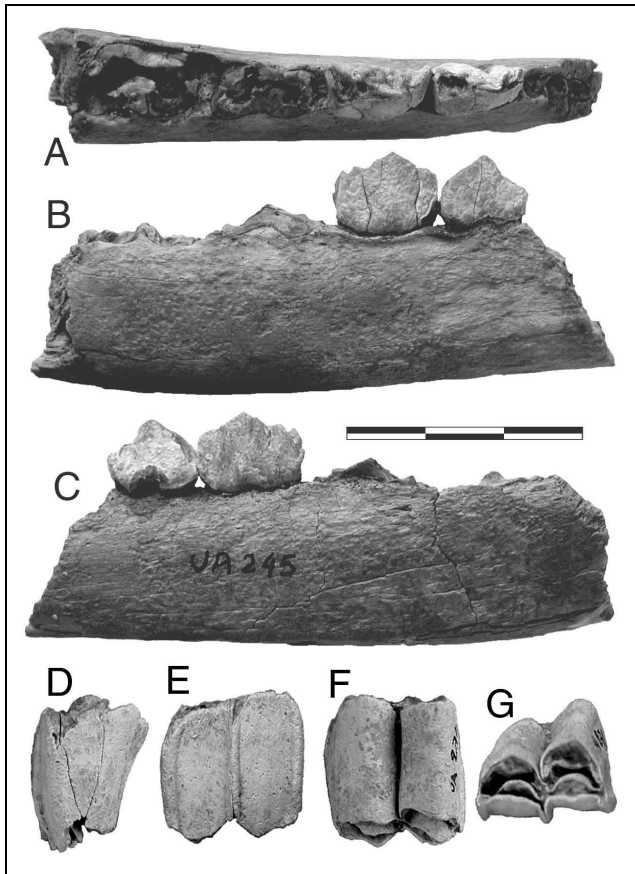
Fig. 12 - *Tragelaphus* cf. *T. spekei*. A-C: UA 245, right mandibular
corpus with P_2-P_3 in occlusal (A), buccal (B) and lingual
(C) views; D-G: UA 274, left M^2 in distal (D), buccal (E),
lingual (F) and occlusal (G) views. Bar scale in centi-
metres.

Lower dentition – Only one specimen has been
determined, the right hemimandible UA-245 (Fig. 12a-
c). It preserves the P_3 and P_4, and the roots of the M_1
and M_2. The morphology of the premolars is typically
Tragelaphus, with low crowns and no paraconid and
metaconid junction. Unfortunately we cannot say any-
thing about the molars (in Table 11, measurements of
the M_1 and M_2 for UA-245 are alveolus measurements,
and would be a little bit smaller than the real ones). As
for the upper specimen, the anatomy and measurements
of UA-245, are more similar to the specimens of *Tra-
gelaphus spekei*, than to *Tragelaphus scriptus* (Pallas,
1766), in the collections of the National Museum of
Kenya (Table 11).

	P/3		P/4		M/1			M/2		
	L	W	L	W	L	WAL	WPL	L	WAL	WPL
UA-245 L.	11,5	6,6	14,0	7,1	13,1	6,2	6,5	15,9	8,9	9,4
Tragelaphus spekei										
OM-1895 L.	11,1	8,0	12,2	8,5	13,2	10,7	10,4	15,9	12,3	12,2
OM-5200 L.	12,3	7,0	14,2	7,6	14,8	8,7	8,9	17,5	9,4	9,9
Tragelaphus scriptus										
OM-935 L.	10,8	5,2	11,9	5,8	11,6	6,6	7,3	14,3	7,4	8,2
OM-926 L.	11,4	6,0	11,4	6,6	12,3	7,1	7,4	14,0	8,0	8,3

Tab. 11 - *Tragelaphus* cf. *T. spekei*, lower dentition measurements
compared to extant specimens

	L	PTD	PAPD	MTD	MAPD	DTD	DAPD
MHB-2	201,6	35,3	20,1	24,3	15,9	34,0	23,5
Tragelaphus spekei							
OM-1895 R.	202,0	33,4	19,0	21,2	14,4	33,5	29,3
OM-5200 R.	227,5	37,2	21,3	25,6	15,7	38,9	24,0
Tragelaphus scriptus							
OM-935 L.	201,0	34,6	19,0	24,7	15,1	34,1	19,2

Tab. 12 - *Tragelaphus* cf. *T. spekei*, radius measurements compared
to extant specimens

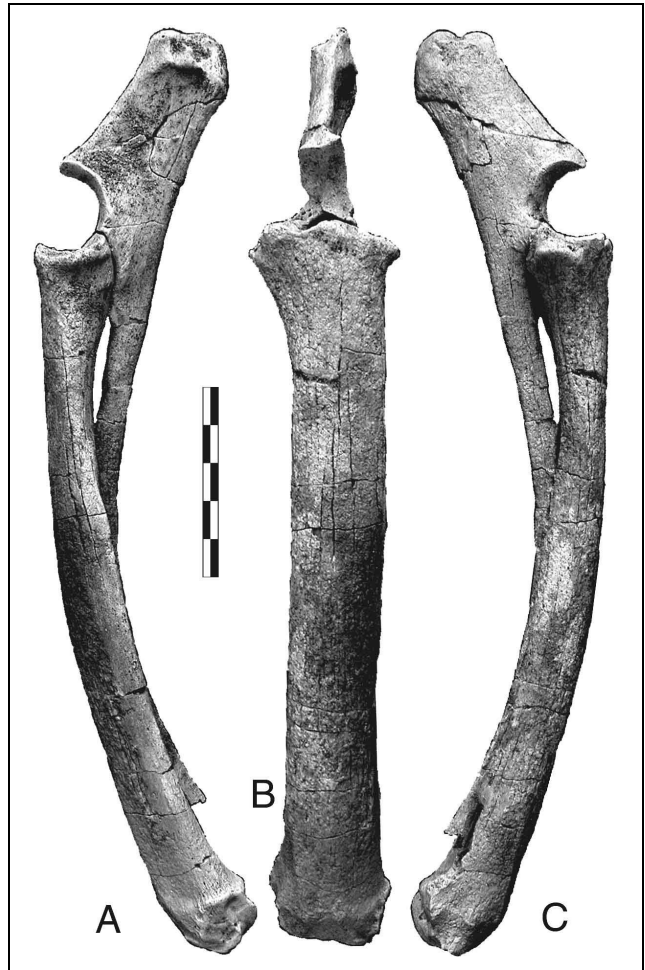

Fig. 13 - *Tragelaphus* cf. *T. spekei*. A-C: MHB-2, right radio-ulna
lateral (A), dorsal (B) and medial (C) views. Bar scale in
centimetres.

Postcranial skeleton – Only one complete right
radius-ulna (MHB-2) can be referred to *Tragelaphus*
cf. *T. spekei* (Fig. 13). It is a specimen slender and
gracile, and its measurements are closer to *T. spekei* than
T. scriptus (Table 12).

We conclude that the species of *Tragelaphus*
found in the Early Pleistocene of the Buia area is *Tra-
gelaphus* cf. *T.spekei*, the sitatunga, an antelope adapted
to water environments with a very long distal phalanges
used for swimming and walking on mudflats.

Fig. 14 - *Pelorovis oldowayensis.* A-C: UA-451, left horn-core fragment in dorsal (A), ventral (B) and medial (C) views. Bar scale in centimetres.
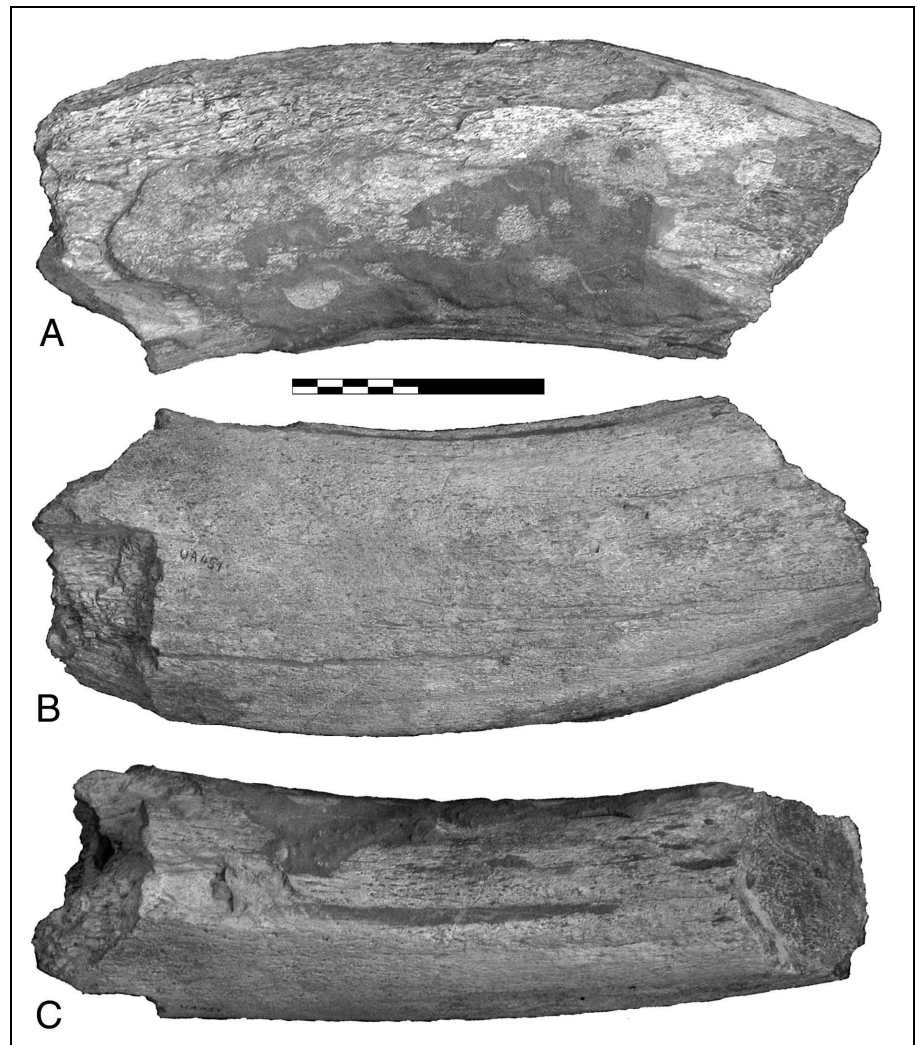
Subfamily Bovinae Gray, 1821
Tribe Bovini Gray, 1821
Genus *Pelorovis* Reck, 1928

Pelorovis oldowayensis Reck, 1928

Material

Three right horn-core fragments of the same individual (UA-138, UA-142 and UA-144), 1 apical left horn-core fragment (UA-143), 1 left horn-core fragment (UA-451), 1 horn-core fragment (UA-150) 1 left maxillary fragment with M^1-M^2 (UA-450), 1 M^1 (DAN-63) 1 left M^3 (UA-168), 2 upper molar fragment (UA-8, UA-134), 1 left mandibular fragment with DP$_3$ and fragmented DP$_4$ (DAN-83), 1 left scapular fragment (UA-360), 1 right scapular fragment (UA-359), 1 right radius-ulna (UA-361), 1 distal end right radius-ulna (DAN-235), 2 left talus (DAN-127, DAN-237), 2 right talus (UA-65, DAN-85), 1 left calcaneum fragment (UA-380), 1 right naviculocuboideum (UA-311), 1 distal fragment of Mc (UA-46), 1 distal end left Mt (UA-459), 1 distal fragment of Mt (UA-165), 3 medial phalanges (UA-106, DAN-196).

The large Olduvai buffalo is well recorded from the Buia sites. A more or less complete cranium, with both horn-cores, was recovered from the site A094 in November 2003, but it is still un-prepared so that its morphology cannot be described.

Description

Horn-cores - Apart the cranium mentioned above, the largest preserved *Pelorovis* horn-core fragment in the Buia collection is the specimen UA-451 (Fig. 14). It is a stout fragment, dorso-ventrally flattened, with oval cross-section, that has internal and external grooves, and corresponds to the middle part of the horn core. Its measurements (TD and DVD of the basal preserved area) 128.5 and 100.0 mm, respectively. This anatomy is typical of *Pelorovis*.

Upper dentition - Two M^1, 1 M^2 and 1 M^3 are identified in the collection (Table 13). These molars have thick enamel and robust internal pillars. The M^1

	M1/			M2/			M3/		
	L	WAL	WPL	L	WAL	WPL	L	WAL	WPL
UA-168							36,70	29,80	28,40
DAN-63	26,20	28,40	28,70						
UA-450	25,60			31,40					

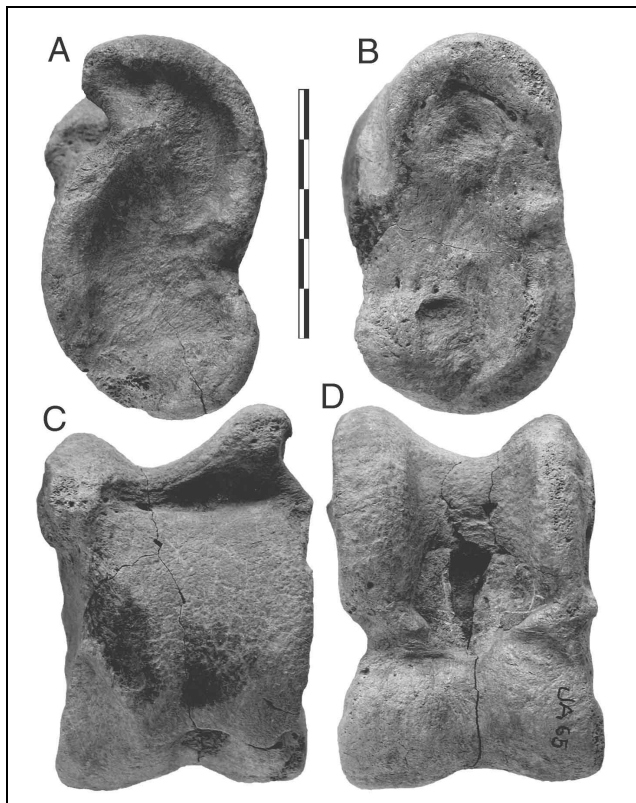Tab. 13 - Upper teeth of *Pelorovis oldowayensis* from Buia.

Fig. 15   - *Pelorovis oldowayensis*. A-D: UA-65, right talus in lateral (A), medial (B), dorsal (C) and ventral (D) views. Bar scale in centimetres.

developed. The parastyle, mesostyle and metastyle are also pronounced. The fossettes are not complicated.

The Late Pliocene species *Pelorovis turkanensis* (Harris 1991c) is characterised by the presence of a marked enamel fold in the postero-lingual area of the hypocone lobule. This fold is present in the Buia specimens, but it is less marked than in *P. turkanensis* from Koobi Fora. This character probably means that the Buia specimens were more evolved forms, similar to those of the Early Pleistocene from Olduvai, *Pelorovis oldowayensis*.

Lower dentition – No lower adult dentition specimens have been recorded, at the moment, in the Buia sites. Only the mandibular fragment (DAN-83) with fragmentary and poorly preserved DP_3 and DP_4 is known in the collection.

Postcranial skeleton – The postcranial specimens (Fig. 15) fall within the anatomical and metrical variability of *Pelorovis* (Table 14).

Discussion about the genus *Pelorovis*

The genus *Pelorovis* evolved from the Early Pliocene African genus *Simatherium* (Vrba 1987), and is the large Late Pliocene and Pleistocene buffalo of Africa. It is a common bovine in the African savannahs until the extinction of its last representative species, *Pelorovis antiquus*, in the Late Pleistocene. *Pelorovis oldowayensis* has been described from Olduvai, and the holotype (field numbers 1516, 1517, and 1518; Reck 1928) was published from the locality RK, but Dietrich (1933) suggested that it came from the Bed IV. On the contrary, Gentry & Gentry (1978) published that all the remains of this species from Olduvai are confined to middle and upper Bed II and Bed III.

Pelorovis oldowayensis is an evolved form that dispersed to the north. It was unknown outside of Africa until the first record in 'Ubeidiya (Geraads 1986). Later, other records of *Pelorovis* in the Levant have been cited. *P.* cf. *P. oldowayensis*, at the Early Pleistocene deposits of the An Fafud desert in the north of Saudi Arabia (Thomas et al. 1998). The same species is reported at Gesher Benot Ya'aqov, in Israel (Martínez-Navarro et al. 2000), a site dated at the Early-Middle Pleistocene transition (Goren-Inbar et al. 2000), where it is represented by a cranium and several teeth and postcranial elements. A similar form was also recorded in the North African site of Ain Hanech (Algeria), described as *Bos bubaloides* (Arambourg 1979). Actually, *Pelorovis* has never been found in other areas of Eurasia outside the Levant, but its arrival into this region of western Asia, together with other open habitat African ruminants, suggests that African savannah faunas extended into Eurasian middle latitudes during Early Pleistocene times.

DAN-63 represents an old individual. It has cementum on the labial face, and the parastyle, paracone, mesostyle, metacone and metastyle are well developed. On the lingual face, protocone and hypocone are also developed. The enamel of the fossettes is not complicated, and the specimen shows an enamel island between them. The M^2 UA-450 is poorly preserved. The M^3 UA-168 has thick enamel and thick cementum over most of the external surface, especially on the labial face. The paracone and metacone are robust and well-

RADIUS							
	L	PTD	PAPD	MTD	MAPD	DTD	DAPD
UA-361	365,00	95,50		57,00	38,00	78,00	50,90

TALUS				
	ML	EL	PTD	DTD
DAN-85	75,10	80,80	51,30	53,40
DAN-127	73,70	82,40	54,10	52,40
UA-65	79,50	84,10	59,50	56,00
DA-237	78,40	82,00	2,09	54,80

2nd PHALANX					
	L	PTD	PAPD	DTD	DAPD
UA-106	50,00	37,10	35,00	29,20	34,40
UA-195	56,70	36,50	39,50	31,20	32,70
UA-7				27,70	29,30
DAN-196	55,00	38,20	38,80	30,00	

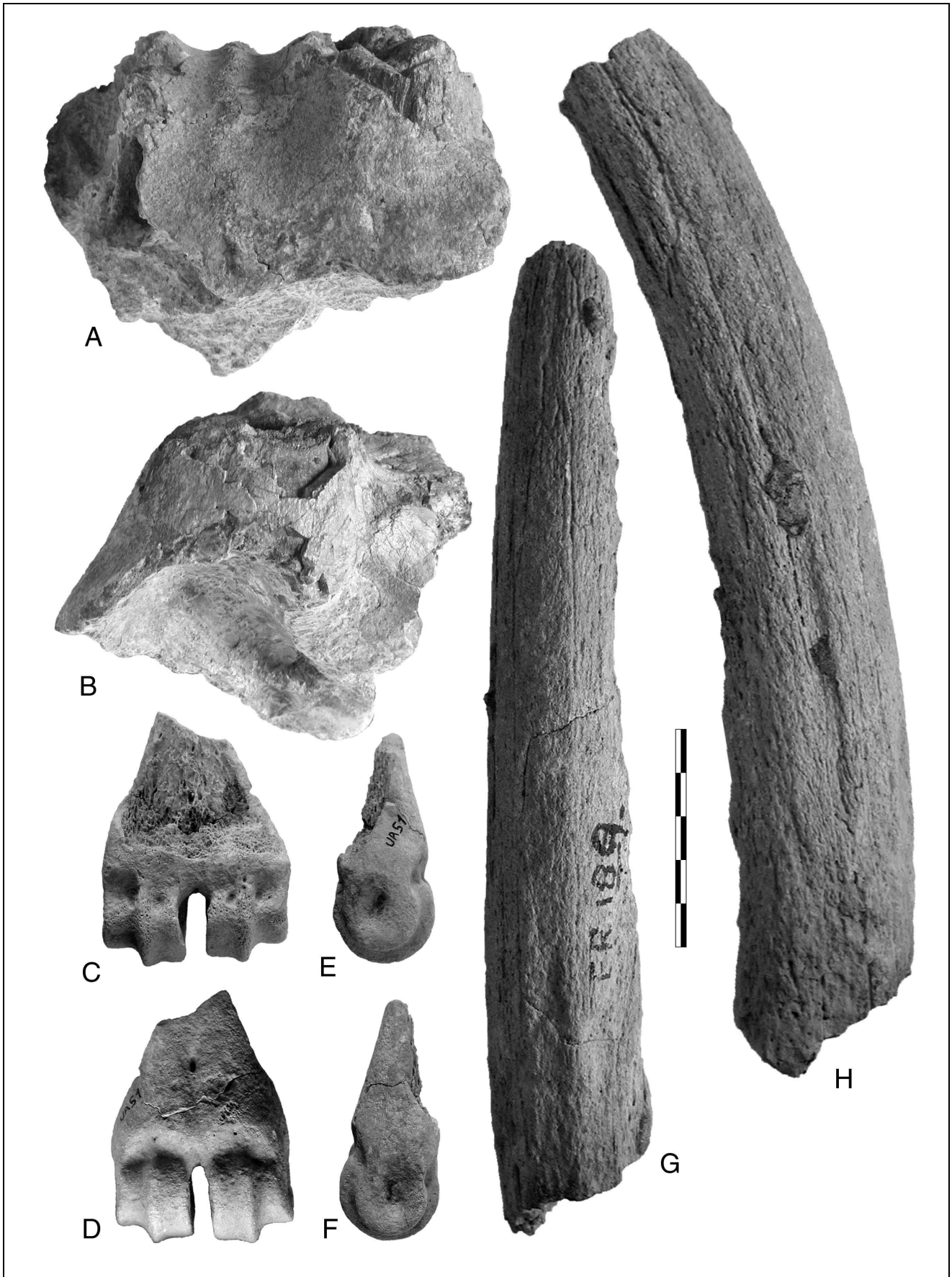Tab. 14   - Postcranial specimens of *Pelorovis oldowayensis* from Buia.

Fig. 16 - *Hippotragus gigas*. A-B: DAN-182, calvarium fragment in frontal (A) and lateral (B) views; C-F: UA-51, right metacarpus in ventral (C), lateral (E), dorsal (D) and medial (F) views; G-H: UA-433, left horn core in anterior (G) and medial (H) views. Bar scale in centimetres.
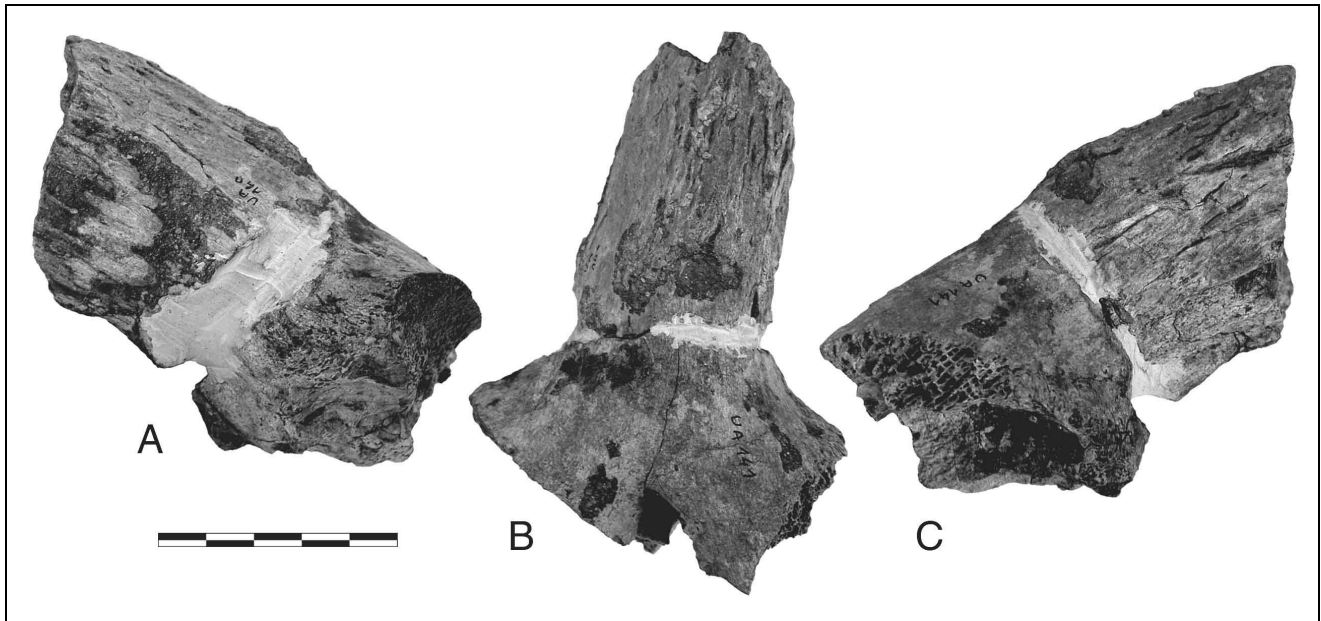
Fig. 17   - *Kobus* cf. *K. ellipsiprymnus*. A-C: UA-140-141, left horn core fragment in medial (A), anterior (B) and lateral (C) views. Bar scale in centimetres.

Subfamily Hippotraginae Retzius & Lovén, 1845
Tribe Hippotragini Retzius & Lovén, 1845
Genus *Hippotragus* Sundevall, 1846

Hippotragus gigas Leakey, 1965

Material

One cranium fragment (DAN-182), 2 horn-core fragments (UA-433 and DAN-215), 1 medial phalanx (UA-377), 1 distal end of a metacarpal (UA-51), and 1 distal phalanx (UA-376).

Biparietal Transv. Diam.	86,50
Supraorbital foramens Transv. Diam.	63,00
External Transv. Diam. at the base of the Horn-cores	117,80
Tansv. Diam. Left horn-core	47,40
Antero-Posterior Diam. Left horn-core	53,20

Tab. 15   - Measurements of the *Hippotragus* gigas cranial fragment DAN-182

	Preserved Length	Transverse Diameter (base)	Antero-posterior Diameter (base)
UA-60	227,00	46,30	55,70
UA-30	95,50	37,00	40,00
UA-141+UA-140	50,70	45,70	57,00
UA-136	297,00	43,60	54,50
UA-137	255,00	41,00	50,70
UA-276	90,00	34,70	37,90
DAN-99	490,00	51,00	64,30
UA-436	105,00	42,70	50,10
DAN-148	466,00	41,90	56,60
DAN-148	115,00	43,90	51,30
DAN-207	145,00	45,70	55,20

Tab. 16   - Horn-core fragments measurements of *Kobus* cf. *K. ellipsiprymnus* from Buia.

Description

The cranial fragment DAN-182 (Table 15) preserves both frontals, joined by the inter-frontal suture (Fig. 16). The left orbital cavity is mostly complete, and is situated just below the horn-core pedicel, which is totally pneumatic in the base. The frontal sinus is developed but not as in the Alcelaphini. The fronto-parietal suture is situated 30 mm behind the posterior face of the horn-cores, and is T-shaped to the inter-frontal one. The braincase roof is flattened, but its uppermost point is situated on the interfrontal suture. The lateral edge of the roof is marked by a crest which starts at the central posterior face of the horn-core. The base of the horn-core is oval with no keels.

The horn-core fragments UA-433 and DAN-125, are stout and have a sub oval section with a posterior keel, marked in the DAN-125 specimen. They have a longitudinal curvature with no torsion. UA-433 has a preserved length of 250 mm, and basal transverse and antero-posterior diameters of 39.70 mm and 41.00 mm respectively; DAN-125 has a preserved length of 103 mm, and basal transverse and antero-posterior diameters of 37.20 mm 47.30 mm, respectively.

Hippotragus gigas is a large Hippotragini described from Olduvai, widely distributed in Africa, and common in Early Pleistocene African sites (Gentry & Gentry 1978).

Subfamily Reduncinae Lydekker & Blaine, 1914
Tribe Reduncini Lydekker & Blaine, 1914
Genus *Kobus* Smith, 1840

Kobus cf. **K. ellipsiprymnus** (Ogilby, 1833)

The most abundant antelope from Buia is a water-buck similar to the extant *Kobus ellipsiprymnus*. The representatives of the genus *Kobus* are large size hypsodont Reduncini that live in grasslands near permanent water.

Material

Two non-measurable cranial fragments (UA-140+UA-141, DAN-207), horn-core fragments (UA-30, UA-60, UA-136, UA-137, UA-276, UA-135a, UA-143b, UA-436, DAN-99, DAN-148), 1 left maxillary fragment with M^1-M^3 (DAN-152), 1 M^2+M^3 (DAN-209), 1 upper molar fragment (DAN-216), 1 M_2 (DAN-87), 1 M_3 (UA-255), 1 Mc distal end (DAN-88), 4 Mt distal ends (UA-32, UA-58, UA-261, UA-275), 1 Metapodial distal end (DAN-130), 2 talus (UA-52, DAN-71), 1 naviculocuboideum (UA-256), 3 proximal phalanges (UA-17, UA-50, DAN-126), 2 medial phalanges (UA-265, DAN-190). There are also other postcranial specimens probably belonging to this taxon.

Description

Cranium – The cranial fragment UA-140+141 (Fig. 17) is heavily built and lacks a pneumatised frontal bone. It has a similar anatomy to the extant male individuals of *Kobus ellipsiprymnus* housed at the National Museum of Eritrea. Horn-cores are long, with the base curving backwards and the apex curving upward, forward and inward, mediolaterally compressed with subtriangular sections at the base and flattened postero-internal faces (Table 16). The specimens exhibit well-marked transverse ridges (Fig. 18c-d).

Dentition – The cheek teeth are hypsodont. Upper molars show the three styles, paracone, and metacone marked in the labial face, and pronounced lobules (protocone and hypocone), with presence of an internal pillar on the lingual face. The fossettes are simple (Fig. 18a-b). Lower molars have marked goat folds, a prominent external pillar, and three marked internal stylids with the metaconid and entoconid being pronounced. The measurements (Table 17) fall within the variability range of this large reduncine antelope (Harris 1991c).

Postcranial skeleton – The postcranial elements fall within the variability of *Kobus ellipsiprymnus*.

The extant waterbuck species *Kobus ellipsiprymnus*, probably evolved from *K. sigmoidalis,* is a common large Reduncini in late Early Pleistocene Eastern African fossil assemblages (Gentry & Gentry 1978; Gentry 1985; Harris et al. 1988; Harris 1991c).

<div style="text-align:center">

Subfamily Antilopinae, Gray 1821
Tribe Antilopini Gray, 1821
Genus *Gazella* Blainville, 1816

Gazella sp.

</div>

Material

One P^4 (UA-269), 1 M^3 (DAN-211), 1 left mandibular fragment with alveolus P_2-P_3 (DAN-229), 1 Talus (UA-281), 1 radius proximal end (DAN-64), 1 Metacarpal distal end (DAN-195), and 1 proximal phalanx (UA-368).

Description

The upper cheek teeth are hypsodont, the P^4 has the styles well marked on the labial face and the postero-lingual region has a small cingular pillar (Table 18). The M^3 shows a small internal pillar and has no marked styles in the labial face (Fig. 19e-h). The measurements of the postcranial elements (Fig. 19a-d, i-m) are provided in Table 19.

These data do not allow a specific referral for the Buia *Gazella*. The genus *Gazella* is recorded in Africa
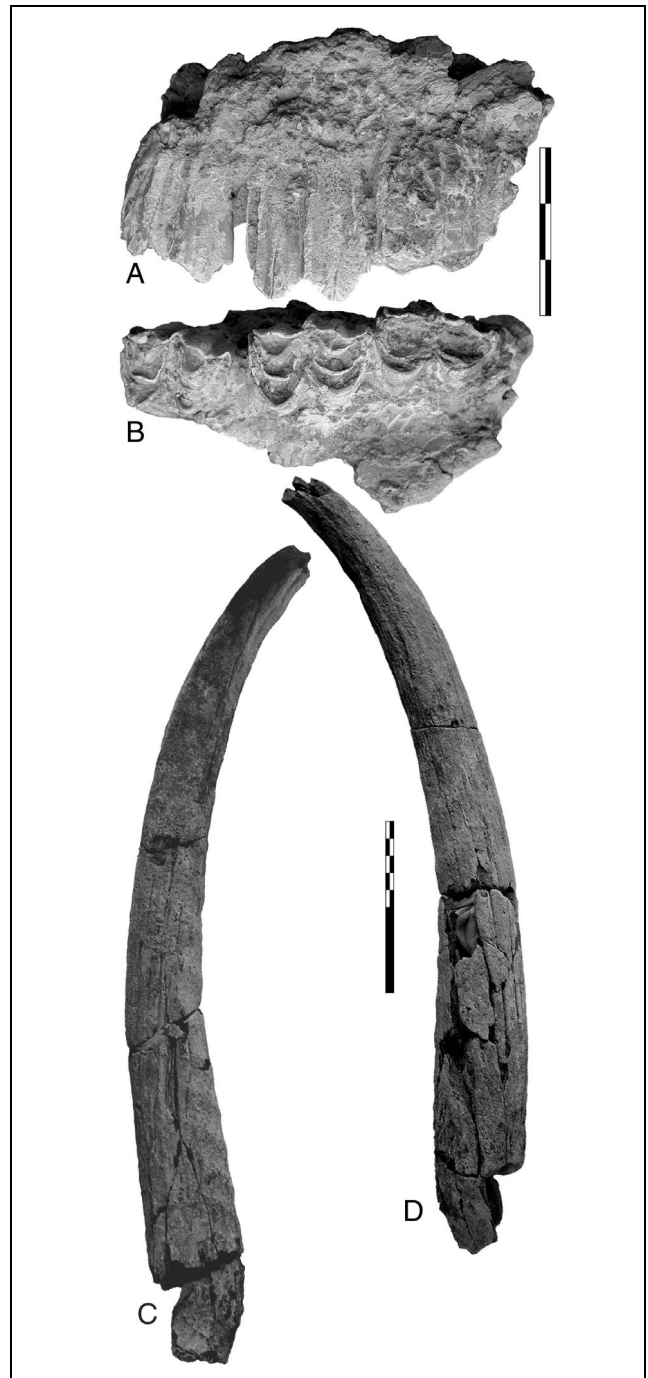

Fig. 18 - *Kobus* cf. *K. ellipsiprymnus*. A-B: DAN-152, left maxillary fragment with M^1-M^2 in buccal (A) and occlusal (B) views; C-D: DAN-148, left horn core in medial (C) and lateral (D) views. Bar scales in centimetres.

| | M1/ | | | M2/ | | | M3/ | | |
	L	WAL	WPL	L	WAL	WPL	L	WAL	WPL
DAN-152	18,00	19,10	19,00	21,00	22,90		24,00		
DAN-209				22,70	22,70	21,30	28,00	21,70	17,70

| | | | | M/2 | | | M/3 | | |
				L	WAL	WPL	L	WAL	WPL
DAN-87				23,00	13,90	13,50			
UA-255							32,70	13,50	12,70

Tab. 17 - Upper and lower dentition measurements of *Kobus* cf. *K. ellipsiprymnus* from Buia.

| | P4 | | M3 | | |
	L	W	L	WAL	WPL
UA-269 L.	8,40	10,40			
DAN-211 L.			14,20	11,00	9,90

Tab. 18 - Upper teeth specimens of *Gazella* sp. from Buia.

	EL	IL	PTD	PAPD	MTD	MAPD	DTD	DAPD
Talus								
UA-281	28,00	25,00	16,20				16,40	
Mc								
DAN-195							24,50	19,10
1st phalanx								
UA-368			10,90	15,50	9,60	10,50		

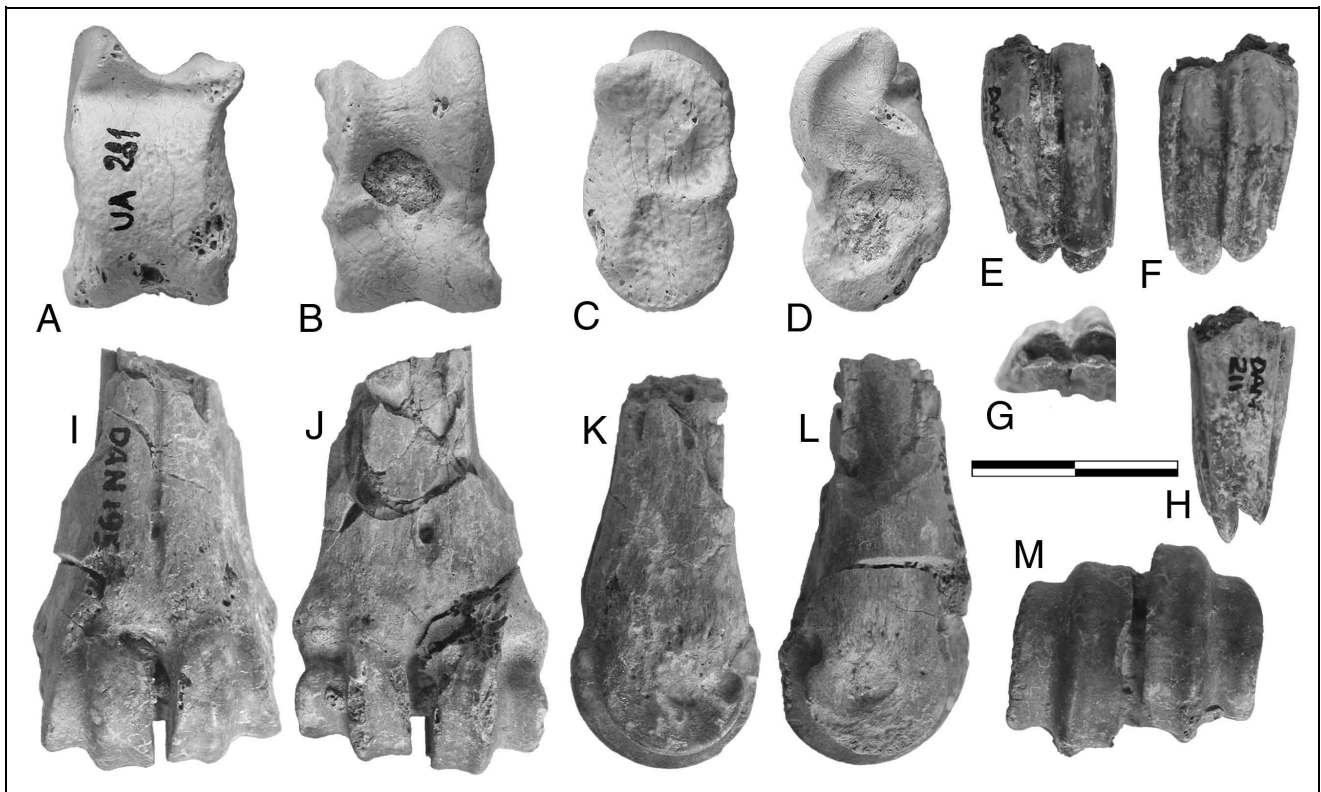Tab. 19 - Measurements of postcranial specimens of *Gazella* sp. from Buia.

Fig. 19 - *Gazella* sp. A-D: UA-281, right talus in dorsal (A), ventral (B), medial (C) and lateral (D) views; E-H, DAN-211, left M³ in lingual (E), buccal (F), occlusal (G) and mesial views; I-M: DAN-195, left fragmentary metacarpal in dorsal (I), ventral (J), lateral (K), medial (L) and distal views. Bar scale in centimetres.

from the Late Miocene (Thomas 1979) and persists until present.

Subfamily Caprinae Gray, 1821
Tribe Caprini Simpson, 1945
**Genus indet.**

Caprini gen. et sp. indet.

Material
One right mandibular fragment with M₂-M₃ (DAN-21), 1 M₁ (UA-273), 1 M₂(DAN-129), and 1 M² (DAN-62). There are also 3 distal humeri and 1 proximal phalanx fragments that probably correspond to this taxon.

Description
The tribe Caprini is represented at Buia by some dental specimens. These dental specimens corre-

Fig. 20 - Caprini indet.; A-D: DAN-62, left M² in distal (A), buccal (B), lingual (c) and occlusal (D) views. E-G: DAN-21, right mandibular corpus with M₂-M₃ in buccal (E), lingual (F) and occlusal (G) views. Bar scales in centimetres.
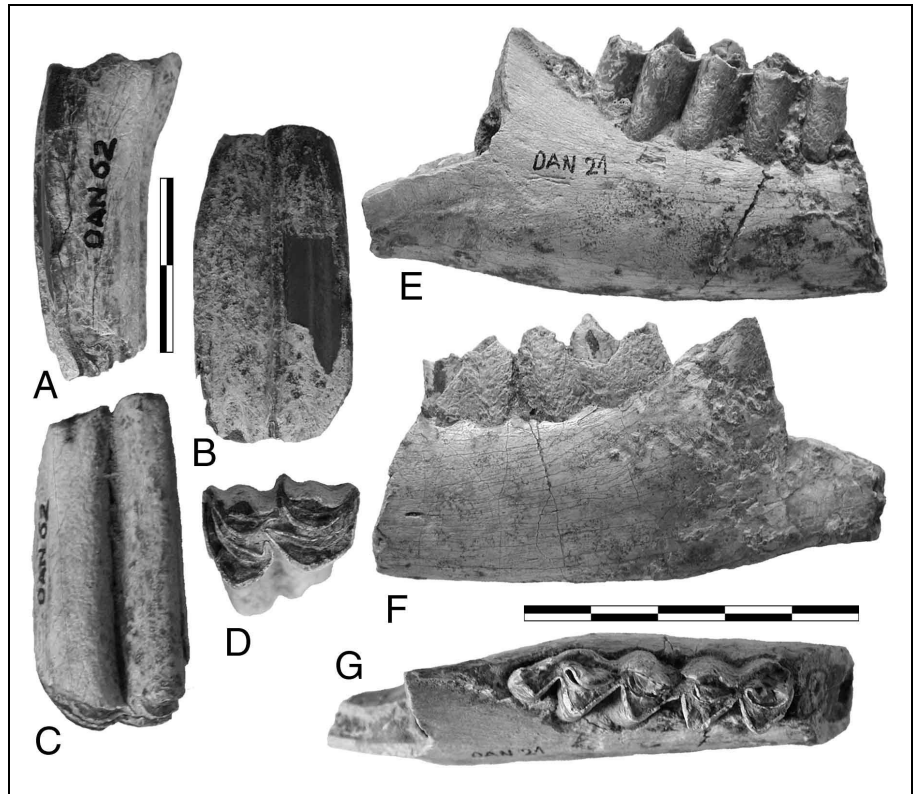
spond to a medium size caprine (Fig. 20; Table 20). They are very hypsodont. The upper molar (DAN-62), is an M² that shows prismatic structure with no pronounced para- and metastyles, more pronounced mesostyle and relatively pronounced pillars of paracone and metacone on the labial face. On the lingual face, the anterior lobule is more mesio-distally compressed than the posterior one, and this last one has a ridge on the postero-lingual area. The lower molars have no goat fold and no mesostylid, the pillars of the metaconid and entoconid are well marked in the lingual face, and the section of the labial lobules is very angular.

Goats have an Eurasian origin, but become relatively common in the eastern Early Pleistocene African assemblages, cited in the Turkana Basin at the Narikotome and Kaitio Members of the Nachukui Formation (Harris et al. 1988). The species *Capra primaeva* is also recorded in the Late Pliocene of North Africa at the site of Ain Brimba, Tunisia (Arambourg 1979).

Zoogeographic comparison of the Buia large mammal assemblage using Simpson's and Dice's *"Genus Faunal Resemblance Index"*

To compare the Buia large mammal fauna with other Plio-Pleistocene African and Near East faunal assemblages, we have performed an analysis of genus-rank faunal resemblance indices (GFRI). We selected a number of African and Near East faunas whose ages range between 2 and 0.5 Ma. Faunal lists from which this computation is based are derived from the available literature (Geraads 1981; Turner et al. 1999; Asfaw et al. 2002) in some cases updated by the authors (BMN and LR) personal observations (Table 21). We follow Fortelius et al. (1996) in calculating both Dice and Simpson GFRI's. Dice is the one most highly recommended by Archer & Maples (1987) and Maples & Archer (1988) and is calculated as: **2A / (2A + B + C)**, where **A** is the number of taxa present in both faunas, **B** the number of taxa present in fauna 1 but absent in fauna 2, and **C** the number of taxa present in fauna 2 but absent in fauna 1.

					M2/					
				L	WAL	WPL				
DAN-62				18,4	16,1	14,3				
	M1			M2			M3		
	L	WAL	WPL	L	WAL	WPL	L	WAL	WPL
DAN-21				17,5	11,2	11,2	25,7	12	11,5
DAN-129				18,4	10,8	10,5			
UA-273	16,2	9,8	9,8						

Tab. 20 - Upper and lower teeth measurements of Caprini indet. from Buia.

We also use Simpson's (1947, 1960) faunal resemblance index because it has a long tradition of use in paleontology and it corrects for differences in diversity of faunas being compared (Flynn 1986; Bernor & Pavlakis 1987; Bernor et al. 2001). Simpson's faunal resemblance index is calculated as: $A / (A + E)$ where E is the smaller of B or C. The latter adjusts for differences in sample sizes between pair-wise faunas being considered (as the case of the sample used here) and has a demonstrable robustness in paleontology (Bernor 1978).

Figure 21 includes two plots of GFRI. The first one provides pair-wise comparisons between Buia and the set of localities under consideration, the second one provides the pair-wise comparisons between Nariokotome and the other localities. In the first one it is to note how the Ethiopian site Daka (this fauna is the closest to Buia both in terms of geographic distance and chronol-ogy; Asfaw et al. 2002), Olduvai Bed 2, Nariokotome, and Okote show the highest resemblance values to Buia. 'Ubeidiya and Gesher Benot Ya'aqov (Israel; Martínez-Navarro et al. in prep; Goren-Inbar et al. 2000) as well as Ternifine (Geraads 1981) and Ain Hanech (Sahnouni et al. 2002) in both plots shows the lowest values. This is either due to a difference in age in some of them, and to the strong influence of "Eurasian" taxa occurring at those latter sites (e.g. deer, "Eurasian" proboscideans and carnivores). It is worth to note, however, that the GFRI values, although low (with respect to those shown by the East African sites), document a relatively high degree of similarity between the Near East faunas and Buia (note the Simpson's value of 0.500 for the Buia-'Ubeidiya pair-wise comparison). This is mainly due to the common occurrence of taxa such as *Theropithecus*, *Kolpochoerus*, *Hippopotamus*, *Gazella* and *Pelorovis*.

The same is evident also for the comparison Buia-Gesher Benot Ya'aqov. The latter site maintains a relatively significant degree of similarity with Buia (with a Simpson's value of 0.384) and generally speaking with a Pleistocene "African bioprovince" (cf. the GFRI to Nariokotome, low but above 0.2) thanks to the occurrence of taxa such as *Hippopotamus*, *Gazella* and *Pelorovis*.

The pair-wise comparison to Nariokotome is particularly informative. The highest similarity indices are found with Okote and Olduvai Bed 2 (closer in space and time to Nariokotome). A high, although slightly lower value, is also shown by Daka and Buia (both very close in time and space). Olduvai Beds 1 and 3, on the other hand, show low similarity values, but this could be due to the relative small sample from the two localities, while even lower values characterize Ain Hanech, Ternifine, 'Ubeidiya and Gesher Benot Ya'aqov. The latter is an expression of their major distance in space and/or time from Nariokotome.
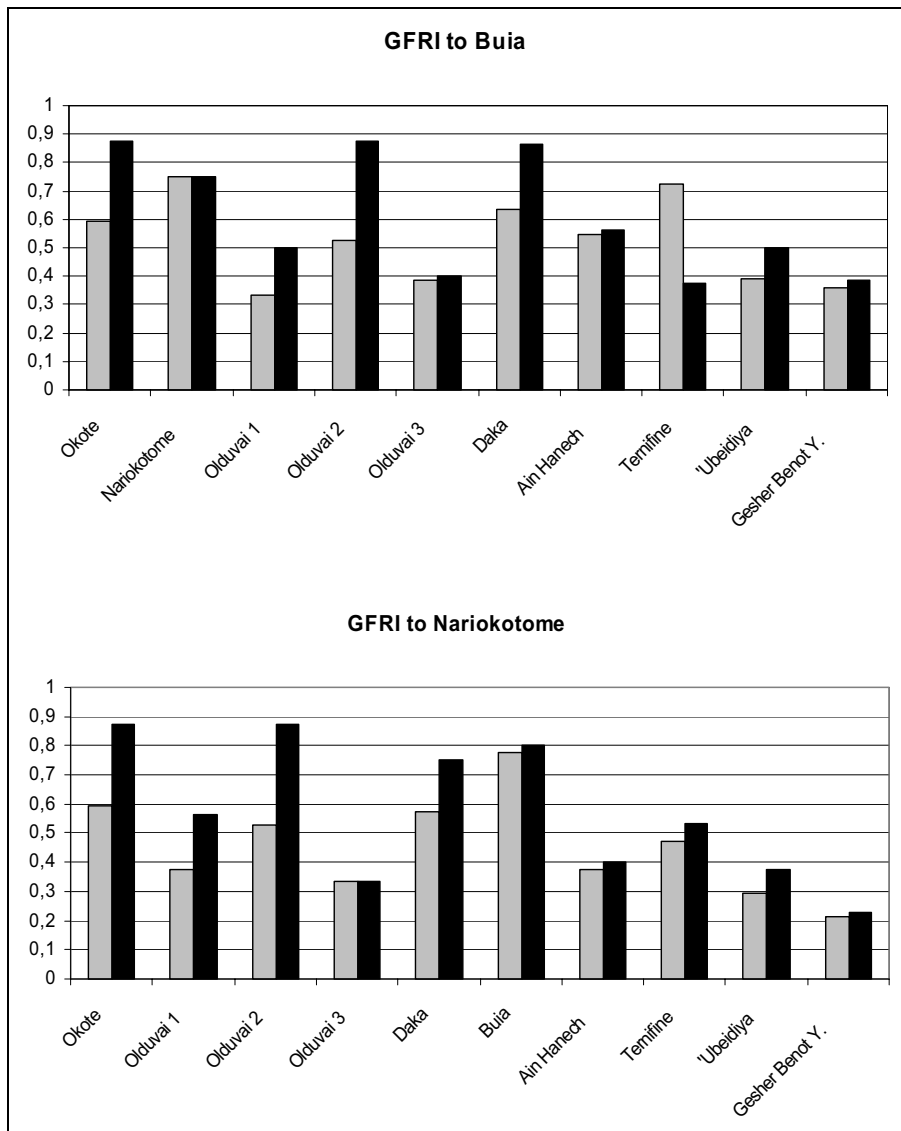

Fig. 21 - Genus Faunal Resemblance Index (GFRI) plots comparing the set of localities to Buia (top) and to Nariokotome (Bottom). Gray bars Dice's GFRI, Black bars Simpson's GFRI (see text for explanation and discussion).

Concluding remarks

The large mammal assemblage from Buia represents a late

	1	2	3	4	5	6	7	8	9	10	11
Paranthropus	X		X	X							
Homo	X	X	X	X		X	X	X	X	X	X
Theropithecus	X	X				X	X		X	X	
Parapapio			X	X							
Papio			X		X						
Cercocebus	X										
Macaca										X	
Cercopitecoides			X		X						
Colobus	X		X		X	X					
Atillax				X							
Crossarchus			X								
Herpestes			X							X	
Ichneumia			X								
Mungos			X		X						
Pseudocivetta			X	X							
Lutra			X	X						X	
Vormela										X	
Pannonictis										X	
Homotherium	X										
Dinofelis	X										
Megantereon	X									X	
Panthera	X		X	X		X					
Acinonyx				X							
Felis								X			
Lynx										X	
Pachycrocuta						X					
Crocuta	X	X	X	X			X	X	X	X	
Hyaena	X		X	X							
Canis			X							X	
Lycaon	X		X	X				X		X	
Vulpes									X	X	
Ursus										X	X
Loxodonta									X		
Elephas	X	X		X		X	X				
Mammuthus								X		X	
Stegodon											X
Palaeoloxodon											X
Hipparion	X			X		X		X			
Equus	X	X		X		X	X	X	X	X	X

	1	2	3	4	5	6	7	8	9	10	11
Ceratotherium	X	X		X		X	X	X	X		
Diceros	X	X		X							
Stephanorhinus										X	X
Kolpochoerus	X	X	X	X	X	X	X	X		X	
Metridiochoerus	X	X	X	X	X	X	X		X		
Sus										X	X
Hexaprotodon		X				X					
Hippopotamus	X	X		X		X	X	X	X	X	X
Sivatherium	X						X		X		
Giraffa	X			X		X	X	X	X		
Camelus			X						X	X	
Beatragus			X	X							
Alcelaphus		X					X				
Sigmoceros			X								
Connochaetes			X	X	X			X			
Damaliscus			X	X							
Megalotragus	X	X	X	X	X	X					
Parmalarius	X		X	X	X	X			X		
Hippotragus			X	X	X		X		X		
Brabovus			X								
Oryx								X	X	X	
Kobus	X	X	X	X	X	X	X		X		
Menelikia	X										
Redunca			X	X	X						
Gazella	X		X	X		X	X	X	X	X	X
Antidorcas	X		X	X	X						
Tragelaphus	X	X	X	X	X	X	X		X		
Taurotragus				X				X			
Syncerus		X	X	X							
Pelorovis	X			X	X	X	X	X	X	X	X
Bos								X			
Aephiceros	X	X	X	X		X					
Rabaticeras						X					
Bouria						X					
Nitidarcus						X					
Numidocapra						X					
Praemegaceros									X		
Megaloceros											X
Dama											X
Cervus											X

1) Okote member; 2) Nariokotome; 3) Olduvai Bed 1; 4) Olduvai bed 2; 5) Olduvai bed 3; 6) Daka; 7) Buia; 8) Hain Anech; 9) Ternifine; 10) 'Ubeidiya; 11) Gesher Benot Ya'aqov

Tab. 21   - Genus occurrences in the localities used fro the GFRI analysis.

Early Pleistocene association of the Eastern African Rift, characterised by evolved last representative forms of *Theropithecus* cf. *T. oswaldi*, *Elephas recki*, *Hippopotamus gorgops*, *Kolpochoerus olduvaiensis*, *Kolpochoerus majus*, *Metridiochoerus* aff. *M. modestus* and *Pelorovis oldowayensis*, and some others that persist until present like *Ceratotherium simum*, *Equus* cf. *E. grevyi Tragelaphus* cf. *T. spekei* or *Kobus* cf. *K. ellipsiprymnus*. The geological and sedimentological survey, paleomagnetism and fission track datings are in good agreement with data of mammal assemblage biochronology, attesting to the *Homo*-bearing level an age of approximately 1 Ma (Abbate et al. 2004; Albianelli & Napoleone 2004; Bigazzi et al. 2004).

The mammal assemblage is predominantly composed of taxa with a strong water dependence (hippos, water-buck, sitatunga, *Kolpochoerus*), associated with much less represented mammalian taxa typical of more open landscapes. The herpetofauna also is composed of predominantly water-dependent taxa since the crocodile and the pelomedusid chelonian remains are found strictly associated to all kind of aquatic environments and the African rock pythons are most abundant near low altitude rivers, lakes and swamps (Delfino et al. 2004). The paleoecological characteristics of the fauna fully agree with the kind of environment documented by the sedimentary deposits, which correspond to a fluvio-deltaic and lacustrine environments (Abbate et al. 2004).

The scarce presence of carnivores in the faunal assemblage can be explained as due to poor sampling in the Buia beds, but may also be related to human activity in the sites (Fiore et al. 2004), where most of the fossil large vertebrate bones are associated with abundant Acheulian lithic artefacts.

The analysis of "Faunal Resemblance Index" (GFRI) with some well known faunal assemblages of Africa and Near East revealed some interesting clues.

As expected, the Buia assemblage overall shows the highest resemblance with East Africa assemblages like Okote, Olduvai bed 2, and Daka. However, in respect to other East African assemblages, Buia has a relatively high similarity with some Near East faunas like 'Ubeidiya, and Ghesher Benot Ya'aqov.

REFERENCES

Abbate E., Albianelli A., Azzaroli A., Benvenuti M., Tesfamariam B., Bruni P., Cipriani N., Clarke R. J., Ficcarelli G. Macchiarelli R., Napoleone G., Papini M., Rook L., Sagri M., Tecle T. M., Torre D. & Villa I. (1998) - A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea. *Nature,* 393: 458-460, London.

Abbate E., Woldehaimanot B., Bruni P., Falorni P., Papini M., Sagri M., Girmay S. & Tecle T.M. (2004) - Geology of the *Homo*-bearing Dandiero Basin (Buia Region, Eritrean Danakil Depression). *Riv. It. Paleont. Strat.,* 110 (supplement): 5-34, Milano.

Albanelli A. & Napoleone G. (2004) - Magnetostratigraphy of the Homo-bearing Pleistocene Dandiero Basin (Danakil Depression, Eritrea), *Riv. It. Paleont. Strat.,* 110 (supplement): 35-44, Milano.

Arambourg C. (1979) - Vertebres Villafranchiens d'Afrique du Nord (Artiodactyles, Carnivores, Primates, Reptiles, Oiseaux). Singer-Polignac, Paris.

Archer A.W. & Maples C.G. (1987) - Monte Carlo simulation of selected binomial similarity coefficient (I): effect of number of variables. *Palaios,* 2: 609-617, Bloomington.

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, London.

Beden M. (1987) - Les Faunes Plio-Pleistocenes de la Vallé de l'Omo (Ethiopie), Tome 2: Les Eléphantidés (Mammalia, Proboscidea). *Cahiers de Paléontologie,* 126 pp. CNRS, Paris.

Belmaker M. (2002) - First Evidence of the presece of *Theropithecus* sp. in the Southern Levant. *Isr. J. Zool.,* 48 (2): 165, Jerusalem.

Bernor R.L. (1978) - *The Mammalian Systematics, Biostratigraphy and Biochronology of Maragheh and its importance for Understanding Late Miocene Hominoid Zoogeography and Evolution,* Ph.D. dissertation, University of California, Los Angeles.

Bernor R.L., Fortelius M. & Rook L. (2001) - Evolutionary Biogeography and Paleoecology of the "*Oreopithecus bambolii* Faunal Zone" (late Miocene, Tusco-Sardinian Province). *Boll. Soc. Paleont. It.,* 40(2): 139-148, Modena.

Bernor R.L. & & Pavlakis P. (1987) - Zoogeographic relationships of the Sahabi large mammal fauna (Early Pliocene, Libya). In: Boaz N.T., El-Arnauti A., Gaziry A.W., de Heinzelin J. & Boaz D.D. (eds) – Neogene Paleontology and Geology of Sahabi: 337-348. Alan Liss, New York.

Bigazzi G., Balestrieri M.L., Norelli P., Oddone M. & Tecle T.M. (2004) - Fission-Track Dating of a Tephra layer in The Alat Formation of the Dandiero Group (Danakil Depression, Eritrea). *Riv. It. Paleont. Strat.,* 110 (supplement): 45-49, Milano.

Boisserie J.-R. (2002) - *Nouveaux Hippopotamidae du Mio-Pliocène du Tchad et d'Ethiopie: implications phylogénétiques et paléoenvironnementales.* PhD thesis, Univerity of Poitiers, pp. 1-440.

Brunet M. & White T.D. (2000) - Deux nouvelles espèces de Suini (Mammalia, Suidae) du continent Africain (Éthiopie; Tchad). *C. R. Acad. Sci.,* 332: 51-57, Paris.

Chavaillon J., Berthelet A. Boisaubert J. L., Faure M., Guéren C. & Warsama. S. A. (1990) - Un *Elephas recki,* découvert en connexion anatomique dans le site de Haidalo, près de As Eyla (République de Djibouti). *C. R. Acad. Sci.,* 310: 441-446, Paris.

Cooke H. B. S. (1978) - Pliocene-Pleistocene Suidae from Hadar, Ethiopia. *Kirtlandia,* 29: 1-63, Cleveland.

Delfino M., Segid A., Yosief D., Shoshani J., Rook L. & Libsekal Y. (2004) - Fossil Reptiles from the Pleistocene *Homo*-bearing locality of Buia (Eritrea, Northern Danakil Depression). *Riv. It. Paleont. Strat.,* 110 (supplement): 51-60, Milano.

Delson E. (1993) - *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In: Jablonski N.G. (ed.) - *Theropithecus:* The rise and fall of a primate genus: 157-189. Cambridge University Press, Cambridge.

Dietrich W. (1933) - Zur Altesfrageder Oldowaylagerstatte. *Zentralblatt Miner., Geol. und Paleont.,* B 1933(5): 299-304, Stuttgart.

Eisenmann V. (1983) - Family Equide. In: Harris J.M. (ed.) - Koobi Fora Research Project. Vol 2: The Fossil Un-

gulates: Proboscidea, Perissodactyla, and Suidae: 156-214, Clarendon Press, Oxford.

Eisenmann V. (1986) - Les Equidés du Pléistocène d'Oubeidiyeh. In: Tchernov E. (ed.) - Les Mammifères du Pléistocène inférieur de la Vallée du Jordain a Oubeidiyeh. *Mém. Trav. Centre Rech Fr. Jerusalem*, 5: 191-212, Paris.

Faure M. (1986) - Les Hippopotamidés du Pléistocène ancien d'Oubeidyeh (Israël). In: Tchernov E. (ed.) – Les Mammifères du Pléistocène inférieur de la Vallée du Jordan a Oubeidiyeh. *Mém. Trav. Centre Rech Fr. Jerusalem*, 5: 107-142, Paris.

Ferretti M. P., Ficcarelli G., Libsekal Y., Tecle T. M. & Rook L. (2003) - Fossil elephants from Buia (northern Afar Depression, Eritrea) with remarks on the Systematics of *Elephas recki* (Proboscidea, Elephantidae). *J. Vert. Pal.*, 23(1): 244-257, Lawrence.

Fiore I., Bondioli L., Coppa A., Macchiarelli R., Russom R., Kashay A., Solomon T., Rook L. & Libsekal Y. (2004) - Taphonomic Analysis of the Late Early Pleistocene Bone Remains from Buia (Dandiero Basin, Danakil Depression, Eritrea): Evidence for Large Mammals and Reptiles Butchering. *Riv. It. Paleont. Strat.*, 110 (supplement): 89-97, Milano.

Flynn L. (1986) - Faunal provinces and the Simpson coefficient. *Contr. Geol., University of Wyoming Special Paper*, 3: 317-338, Laramie.

Fortelius M., Werdelin L., Andrews P., Bernor R.L., Gentry A., Humphrey L., Mittmann H.-W. & Viranta S. (1996) - Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the alter Miocene of Western Eurasia. In: Bernor R.L., Fahlbusch V. & Mittmann H.-W. (eds) – Evolution of Neogene Continental Biotopes in Europe and the Eastern Mediterranean: 137-156. Columbia University Press, New York.

Foster J.B. (1967) - The squared-lipped rhinoceros (*Ceratotherium simum cottoni* Lydekker) in Uganda. *East Afr. Wildl. Jour.*, 5: 167-170, Nairobi.

Gentry A. W. (1985) - The Bovidae of the Omo Group deposits, Ethipia. In: Coppens Y. & Howell F.C. (eds.) - Les faunes Plio-Pléistocènes de la basse Vallée de l'Omo (Éthiopie). *Cahiers Paléont.*, 1: 119-191, Paris.

Gentry A. W. & Gentry A. (1978) - Fossil Bovidae (Mammalia) of Olduvai Gorge, Tanzania. *Bull. Brit. Mus. (Nat. Hist.) (Geol.)*, 29: 289-446, London.

Geraads D. (1981) - Bovidae et Giraffidae (Artiodactyla, Mammalia) du Pléistocène de Ternifine (Algérie). *Bull. Mus. Nat. Hist. Nat., Paris*, 3(1): 47-86, Paris.

Geraads D. (1986) - Les ruminants du Pléistocène d'Oubeidiyeh (Israël). In: Tchernov E. (ed.) - Les Mammifères du Pléistocène inférieur de la Vallée du Jordan a Oubeidiyeh. *Mém. Trav. Centre Rech Fr. Jerusalem*, 5: 1143-181, Paris.

Geraads D. (1993) - *Kolpochoerus phacochoeroides* (Thomas, 1884) (Suidae, Mammalia) du Pliocène supérieur de Ahl al Oughlam (Casablanca, Maroc). *Géobios*, 26: 731-743, Lyon.

Geraads D., Guérin C. & Faure M. (1986) - Les suidés du Pléistocéne ancien d'Oubeidiyeh (Israël). In: Tchernov E. (ed.) - Les Mammifères du Pléistocène inférieur de la Vallée du Jordain a Oubeidiyeh. *Mém. Trav. Centre Rech Fr. Jerusalem*, 5: 193-105, Paris.

Gibert J., Ribot F., Gibert L., Leakey M. G., Arribas A. & Martínez-Navarro B. (1995) - Presence of the Cercopithecid genus *Theropithecus* in Cueva Victoria (Murcia, Spain). *J.Hum. Evol.*, 28: 487-493, London.

Goren-Inbar N., Feibel C.S., Verosub K.L., Melamed Y., Kislev M.E., Tchernov E. & Saragusti I. (2000) - Pleistocene milestones on the Out-of-Africa corridor at Gesher Benot Ya'aqov, Israel. *Science*, 289: 944-947, Washington D.C.

Groves C.P. (1972) - The White Rhinoceros *Ceratotherium simum*. *Mamm. Sp.*, 8: 1-6, Lawrence.

Guerin C. (1985) - Les rhinocéros et les chalicothères (Mammalia, Perissodactyla) des gisements de la Vallée de l'Omo en Ethiopie (collections françaises). *Cahiers Paléont., Trav. Paléont. Est-Africaine*. Tome 1, Perissodactyles, Artiodactyles (Bovidae): 67-95, Paris.

Harris J. M. (1983a) - Family Rhinocerothidae. In: Harris J.M. (ed.) - Koobi Fora Research Project. Vol 2: The Fossil Ungulates: Proboscidea, Perissodactyla, and Suidae: 139-155, Clarendon Press, Oxford.

Harris J. M. (1983b) - Family Suidae. In: Harris J.M. (ed.) - Koobi Fora Research Project. Vol 2: The Fossil Ungulates: Proboscidea, Perissodactyla, and Suidae: 215-302, Clarendon Press, Oxford.

Harris J. M. (1991a) - Family Hippopotamidae. In: Harris J.M. (ed.) - Koobi For a Research Project. Vol. 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments: 31-85, Clarendon Press, Oxford.

Harris J. M. (1991b) - Family Giraffidae. In: Harris J.M. (ed.) - Koobi For a Research Project. Vol. 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments: 93-138, Clarendon Press, Oxford.

Harris J. M. (1991c) - Family Bovidae. In: Harris J.M. (ed.) - Koobi For a Research Project. Vol. 3: The Fossil Ungulates: Geology, Fossil Artiodactyls, and Palaeoenvironments: 139-320, Clarendon Press, Oxford.

Harris J.M., Brown F. H., & Leakey M. G. (1988) - Stratigraphy and Paleontology of Pliocene and Pleistocene localities West of Lake Turkana. Contr. *Sci, Nat. Hist. Mus. Los Angeles County*, 399: 1-128, Los Angeles.

Harris J. M. & White T. D. (1979) - Evolution of the Plio-Pleistocene African Suidae. *Trans. Am. Phil. Soc*, 69(2): 1-128, Philadelphia.

Hilman-Smith A.K.K., Owen-Smith N., Anderson J.L., Hall-Martin A. & Selaladi J. (1986) - Age estimation of the White rhinoceros (*Ceratotherium simum*). *J. Zool.*, A, 210: 355-379, London.

Kalb J. E. & Mebrate A. (1993) - Fossil elephantoids from the hominid-bearing Awash Group, Middle Awash Valley, Afar Depression, Ethiopia. *Trans. Am. Phil. Soc.*, 83: 1-114, Philadelphia.

Macchiarelli R., Bondioli L., Chech M., Coppa A., Fiore I., Russom R., Vecchi F., Libsekal Y. & Rook L. (2004) - The late Early Pleistocene Human Remains from

Buia, Danakil Depression, Eritrea. *Riv. It. Paleont. Strat.*, 110 (supplement): 133-144, Milano.

Macchiarelli R., Bondioli L., Coppa A., Rook L., Libsekal Y. & Abbate E. (2002) - The one-million-year-old human remains from the Danakil (Afar) Depression of Eritrea. *Am. J. Phys. Antr.*, Suppl. 34: 104, Lawrence.

Maglio V. J. (1973) - Origin and evolution of the Elephantidae. *Trans. Am. Phil. Soc.*, 63:1-144, Philadelphia.

Maples C.G. & Archer A.W. (1988) - Monte Carlo simulation of selected binomial similarity coefficient (I): effect of sparse data. *Palaios*, 3: 95-103, Bloomington.

Martínez-Navarro B., Belmaker M. & Bar-Yosef O. (in prep.) - Systematic revision of the large Carnivores (Felids, Hyaenids, Canids and Ursids) and Bovids from the Early Pleistocene archaeological site of 'Ubeidiya, Israel.

Martínez-Navarro B., Rabinovich R. & Goren-Inbar N. (2000) - Preliminary study of the fossil Bovidae assemblage from the late Lower Pleistocene archaeological site of Gesher Benot Ya'aqov (northern Israel). Abstracts of 2000 Meeting of the INQUA-SEQS "The Plio-Pleistocene boundary and the Lower/Middle Pleistocene transition: Type areas and sections". Bari (Italy).

Martini F., Libsekal Y., Filippi O., Ghebre/her A., Kashay H., Kiros A., Martino G., Okubatsion D., Segid A., Solomon T., Teka Z., Yosief D. & Yamane S. (2004) - Characterization of Lithic Complexes from Buia (Dandiero Basin, Danakil Depression, Eritrea). *Riv. It. Paleont. Strat.*, 110 (supplement): 99-132, Milano.

McKenna M. & Bell S.K. (1998) - Classification of Mammals Above the Species Level. Columbia University Press, New York, 631pp.

Pickford M. (1994) - Fossil Suidae of the Albertine Rift, Uganda-Zaire. In: Senut B. & Pickford M. (eds.) - Geology and Paleobiology of the Albertine Rift Valley, Uganda-Zaire. Paleobiology, vol. II: 339-373, Cifeg, Orléans.

Rook L., Ficcarelli G., Torre D., Clarke R.J., Macchiarelli R., Tesfamariam B. & Liebeskal J. (1999) – The Early Middle Pleistocene *Homo* bearing succession of Buia (Eritrea). *Am. J. Phys. Anthrop.*, suppl. 28: 205, Lawrence.

Rook L., Kibreab A., Russom R., Tecle T.M. & Abbate E. (2002) - The Buia Project: a collaborative geo-paleontological and paleoanthropological research project in Eritrea. *J. Hum. Evol.*, 42(3): A29-A30, London.

Rook L., Martínez-Navarro B. & Howell F. C. (in press) - Occurrence of *Theropithecus* sp. in the Late Villafranchian of Southern Italy and implication for Early Pleistocene "out of Africa". *J. Hum. Evol.*, London.

Sahnouni M., Hadjouis D., Made J. v. d., Derradji A.e.K., Canals A., Medig M., Belahrech H., Harichane Z. & Rabhi M. (2002) – Further research at the Oldowan site of Ain Hanech, North-eastern Algeria. *J. Hum. Evol.*, 43: 925-937, London.

Simpson G.C. (1947) - Holoarctic mammalian faunas and continental relationships during the Cenozoic. *Bull. Soc. Geol. Am.*, 58: 613-688, Boulder.

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

Tchernov E., Horwitz L.K., Ronen A. & Lister A. (1994) - The faunal remains from Evron Quarry in relation to other Lower Paleolithic hominid sites in the Southern Levant. *Quat.Res.,* 42: 328-339, Seattle.

Thomas H. (1979) - Les Bovidés miocènes des rifts est-Africains: implications paléobiogéographiques. *Bull. Soc. Géol. Fr.*, 7th series, 21: 295-299, Paris.

Thomas H., Geraads D., Janjou D., Vaslet D., Memesh A., Billou D., Bocherens H., Dobigny G., Eisenmann V., Gayet M., Lapparent de Broin F. de, Petter G. & Halawani M. (1998) - First Pleistocene faunas from the Arabian Peninsula: An Nafud desert, Saudi Arabia. *C. R. Acad. Sci.*, 326: 145-152, Paris.

Todd N. E. (1997) - *Comparison of variation in cranial and dental morphology of* Elephas recki *and extant elephants: implication for phylogeny and macroevolution*. PhD dissertation, George Washington University, Washington D.C., 432 pp.

Turner A., Bishop L.C., Denys C. & McKee J.K. (1999) - Appendix. A locality-based listing of African Plio-Pleistocene mammals. In: Bromage T.G. & Schrenk F. (eds) - African Biogeography, Climate Change & Human Evolution: 369-399, Oxford University Press, New York.

Vrba E.S. (1987) - A revision of the Bovini (Bovidae) from a preliminary revised checklist of Bovidae from Makapansgat. *Paleont. Afr.*, 26: 33-46, Johannesburg.

Werdelin L. (1999) - *Pachycrocuta* (hyaenids) from the Pliocene of east Africa. *Paläont. Zeit.*, 73: 157-165, Stuttgart.