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

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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

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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 ?I^2 and one left I_1 (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) document 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.

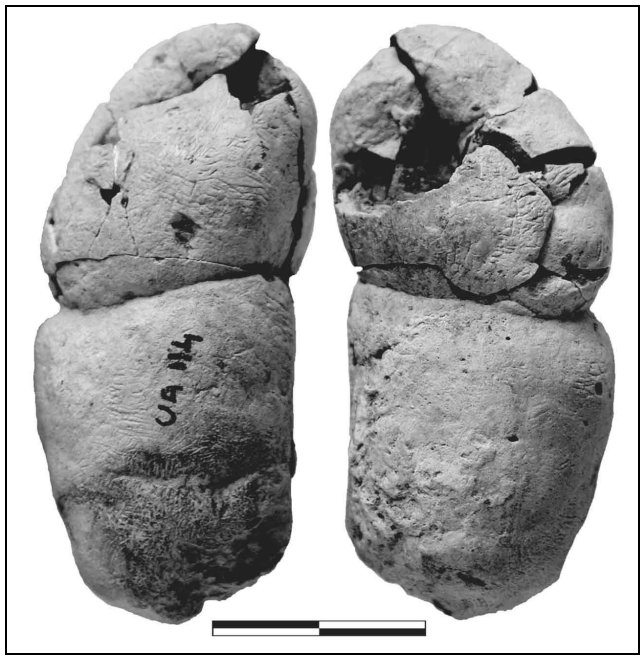

Fig. 1 - cf. *Crocuta crocuta*. UA-114, Coprolite. Bar scale in centimetres.

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

Ceratotherium simum (Burchell, 1817)

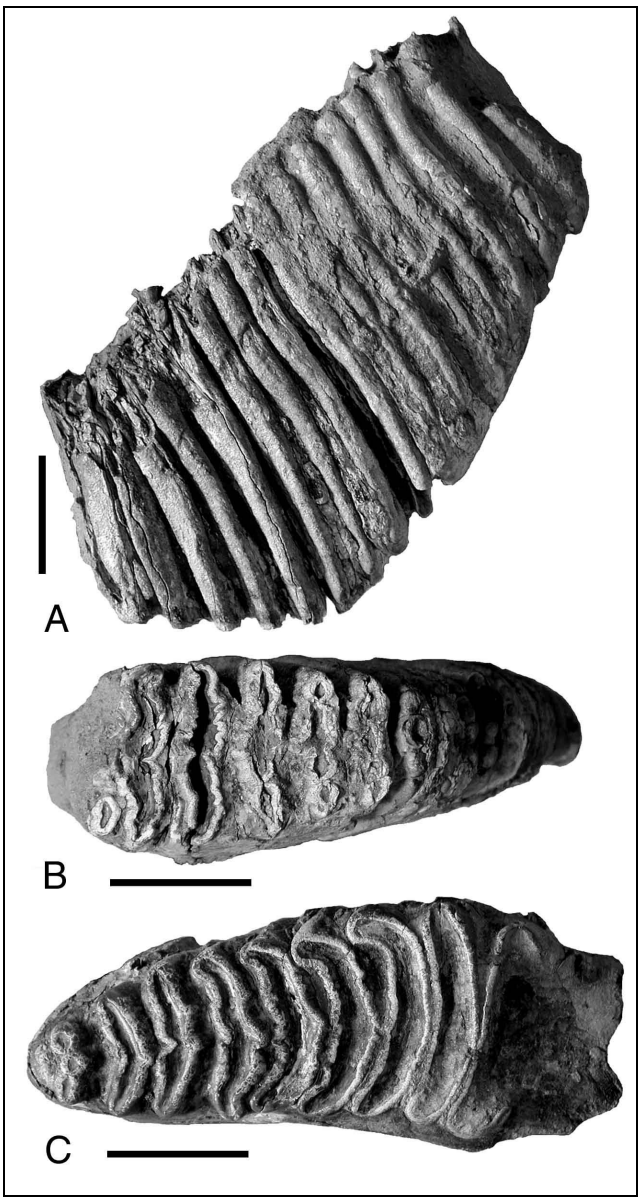

Fig. 2 - *Elephas recki* (advanced form). A-B: DAN-243, right M^3 in lateral (A, occlusal surface at bottom) and occlusal (B, anterior to the left) views; C: UA-41, right M_3 in occlusal view (anterior to the right). Bar scale represents 10 cm.

Material

One mostly complete cranium with right P^3-M^3 and left P^4-M^3 (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 P^3-M^3 and left P^4-M^3. 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).

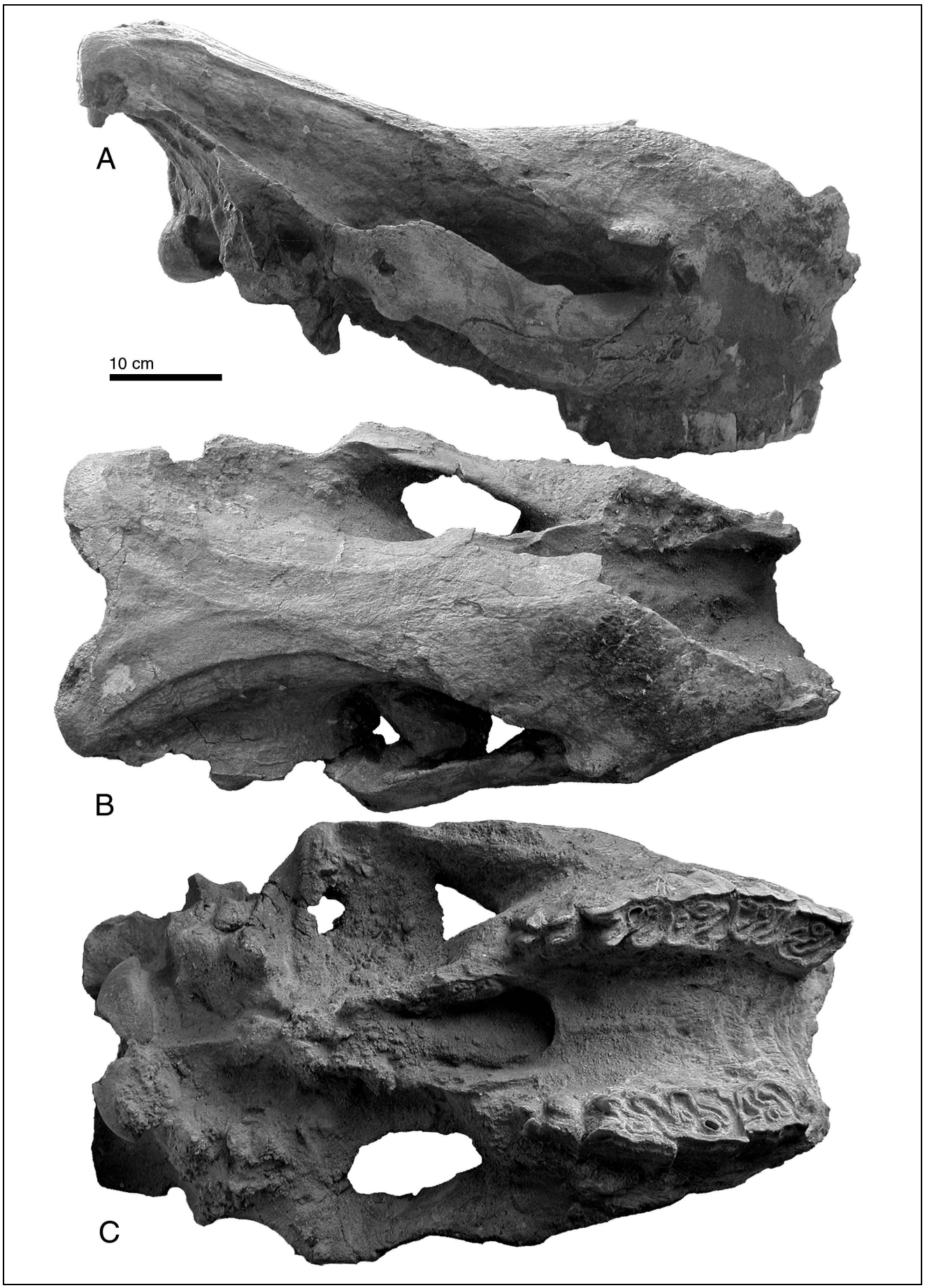

Fig. 3 - *Ceratotherium simum*. DAN-150, cranium in lateral (A), dorsal (B) and ventral (C) views. Bar scale represents 10 centimeters.

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

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

Equus cf. ***E. grevyi*** Oustalet, 1882

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 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*.

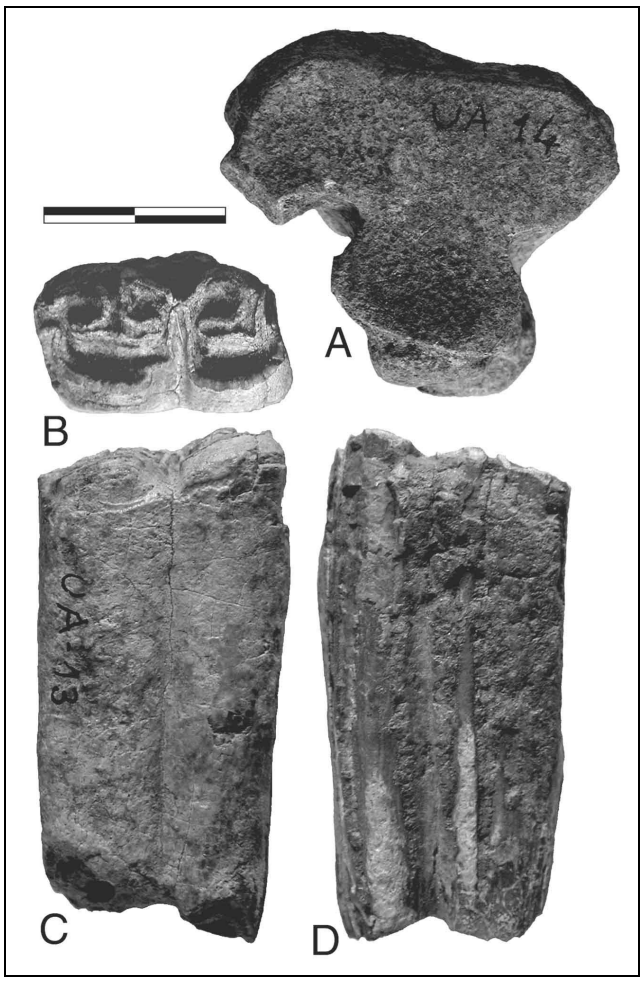

Fig. 4 - *Equus* cf. *E. grevyi*. A: UA-14, right magnum in proximal view; B-C: UA-13, right M_2 in occlusal (B), buccal (C) and lingual (D) views. Bar scale in centimetres.

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

		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

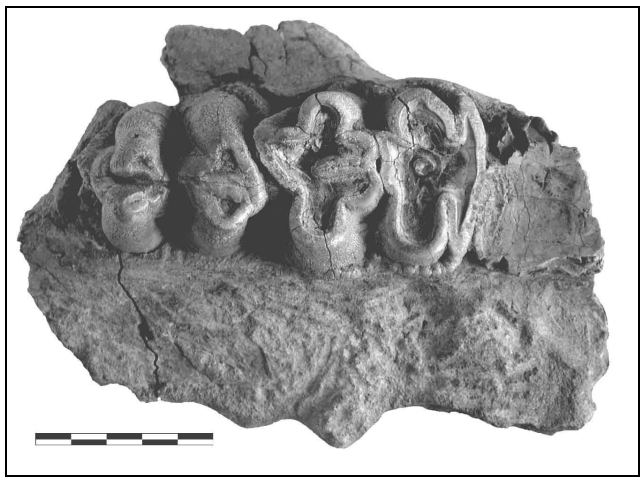

Fig. 5 - *Hippopotamus gorgops.* UA-223, right maxillary fragment with M^1 (deeply worn) M^2 and M^3, in occlusal view. Scale bar in centimetres.

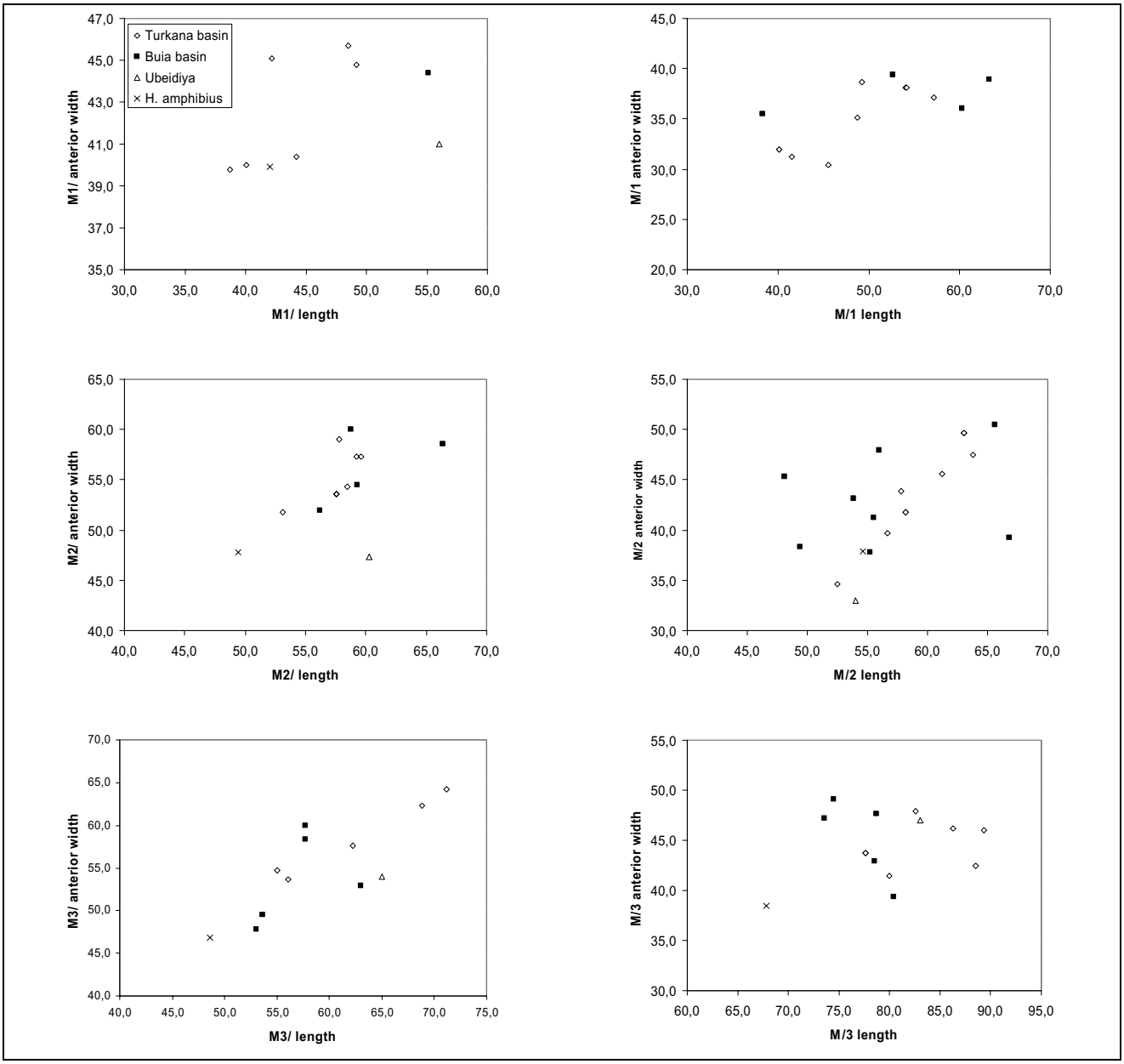

Fig. 6 - Bivariate plots of *Hippopotamus* upper (left column) and lower (right column) molars dimensions (see Tables 4 and 5 for data source).

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 chronology; 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*.

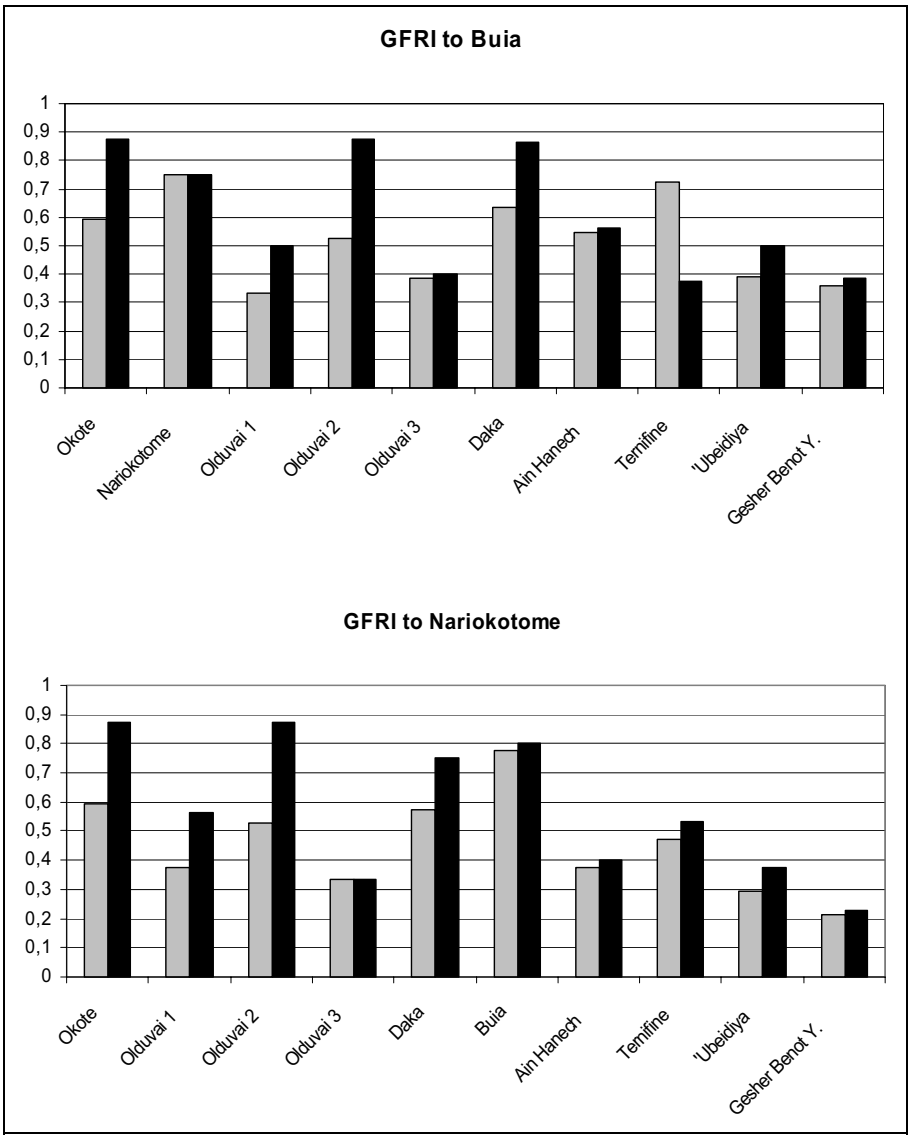

Fig. 21 - Genus Faunal Resemblance Index (GFRI) plots comparing the set of localities to Buia (top) and to Nariokotome (Bottom). Gray bars Dice's GFRI, Black bars Simpson's GFRI (see text for explanation and discussion).

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.

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			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.

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