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 (Bua) 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.


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 Paleontology section) of the University of Florence, as well as other Italian and European institutions.

These activities led to the discovery of a new important paleoanthropological 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 & Napoleon 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).


**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.


**Measurements.** L: length; W: width; WALT: width at the anterior lobe; WPL: width at the posterior lobe; Trig: trigonid; oc: occlusal antero-posterior length; oc tr: occlusal transversal length; ptc: protocone length; Pt: Protoconal Index; I Pt: postprotocone length; FI: Postlacrimal Index; ap ex: length (anterior-posterior) on the external side; sp int: length (anterior-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 diaphysis; MAPD: antero-posterior diameter at the diaphysis; DTD: distal transverse diameter; DAPD: distal antero-posterior diameter. All measurements are given in millimeters.

**Systematic Paleontology**

Order Primates Linnaeus, 1758

Suborder Catarrhini (Simpson, 1945)

Family Hominidae Gray, 1825

Genus Homo Linnaeus, 1758

_Homo "erectus-like"

One mostly complete cranium (UA-31), one left P1 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-Hilaire, 1843

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); Cuevas Victoria, Spain (Gilbert et al. 1995) and Pirro Nord, Italy (Rook et al. in press).

Order Carnivora Bowdich, 1821
Suborder Fissipedia 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 hyaenid 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 hyaena 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 Ilere, 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)
Material

One mostly complete cranium with right P3-M1 and left P4-M1 (DAN-150), 3 incomplete lower molars (DAN-41, 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 germanoafrikanum 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-M1 and left P4-M1. 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).

Fig. 2 - Elephas recki (advanced form). A-B: DAN-243, right M1 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.

<table>
<thead>
<tr>
<th></th>
<th>DAN-150</th>
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<th>ER-329</th>
<th>ER-2320</th>
<th>OM-2184</th>
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<td>800.0</td>
<td>-635.0</td>
<td>-500.0</td>
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<td>633.0</td>
<td>756.0</td>
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<td>652.0</td>
<td>540.0</td>
<td>469.0</td>
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<td>400.0</td>
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<td>182.0</td>
<td>161.0</td>
<td>82.0</td>
<td>194.0</td>
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<td>120.0</td>
<td>115.0</td>
<td>112.0</td>
<td></td>
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<td>275.0</td>
<td>-208.0</td>
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<td>283.0</td>
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<td>106.0</td>
<td>69.0</td>
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<td>Width of the palate at M3</td>
<td>118.0</td>
<td>82.0</td>
<td>113.0</td>
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* until P3

Table 1 - Measurements of the Buia Ceratotherium simum DAN-150, compared to Koobi Fora and extant specimens (data from Harris 1983a).
Fig. 3 - Ceraterium sumum. 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 Eguus Linnaeus, 1758**

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

**Material**

One P₃ (UA-321), 1 M¹ (DAN-230), 1 right mandibular fragment with P₃ (DAN-140), 2 M₂ (DAN-133, UA-13), 2 P₂ (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 *Hippodon* (the genus was reported erroneously in the 1998 faunal list) and to attribute all the equid remains to the genus *Equis* (Fig. 4). They probably correspond to a species similar to the large zebra inhabitant of the semidesertic areas, *Equis grevyi*. The Buia dental remains include large molars with moderate protoconal indices in the upper series, and show stenoine 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 M₂ DAN-153, is not measurable (Table 3). In the upper series, as in the Koobi Fora specimens ascribed to *Equis cf. E. grevyi* (Eisenmann 1983), the P₃ UA-301 shows a developed caballine fold, and the protoconal indices (PI) is shorter in this specimen than in the M¹ 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 molar of the collection (M₂ UA-13, Fig.4). Their measurements fall in the variability of those of *E. grevyi* from Koobi Fora.

These specimens have also been compared to *Equis tabeti* from Koobi Fora (Eisenmann 1983) and *U. ubediya* (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 postflexid indices (FI). This difference in the FI is prominent on the lower P₄ and M₂, where the maximum values for *U. ubediya* 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 *Equis tabeti*, and their anatomy and measurements are close to *Equis grevyi*.

**Order Artiodactyla Owen, 1848**

**Suborder Suina Gray, 1821**

<table>
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<th>P₃</th>
<th>L ap ext</th>
<th>L ap int</th>
<th>W prot</th>
<th>W met</th>
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<td>42.3</td>
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Tab. 2 - Measurements of the *Ceratotherium simum* teeth (DAN-150), compared Koobi Fora and extant specimens (data from Harris, 1983a).
Tab. 3 - Measurements of the upper and lower cheek teeth of Equus cf. E. grevyi from Buia

Fig. 5 - *Hippopotamus gorops*. UA-223, right maxillary fragment with M' (deeply worn) M' and M", 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**

**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 M3 is very prominent (Figs. 5, 6; Table 4). The lower premolars are unicusp 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/ | WAL | WPL | M2/ | WAL | WPL | M3/ | 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 | 37,4 | 53,0 | 47,8 | 45,7 |
| UA-54 R. | 60,0 | 60,8 | 59,6 | 58,0 | 57,6 |
| DAN-78 L. | 46,6 | 58,6 | 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. |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| DAN-53 R. |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| 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 | 49,6 |
| 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 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| ER-5514 |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |     |
| 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).
are the upper ones from the same basin. These metrical data have also been compared to those of the sample from ‘Ubediya, 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 ‘Ubediya 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.
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 *Metridochoerus* (*M. aff. M. modestus*).

**Genus Kolpochoerus Van Hoepen and Van Hoepen, 1932**

*Kolpochoerus* is believed 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 M1 (DAN-221), 2 M1 (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 frag-


**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 M1 (DAN-221) is a worn typical tetracuspids molar, with labial cuspsids (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 M3 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 P1-M3. The premolars (P3 and P4) are subtriangular unicuspids pieces. The first and second molars (M1 and M2) are tetracuspids pieces with lingual cuspsids (metaconid and entoconid) bigger and higher than the labial ones (protoconid and entoconid). In the specimen UA-242 the M1 and M2 labio-lingual diameter is greater than the mesio-distal one. DAN-51 exhibits small mesial and distal cingula. The lower third molar (M3) is the best preserved specimen, it has tetracuspids trigonid (proto-, meta-, hypo- and entoconid) normally smaller than the talonid, which is very elongated and can have until four or five pair of cuspsids (Fig. 9c-d). It is worth to note the occurrence of one important asymmetry in the specimen MHB-1, where the right M3 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 *Kolpocherus* in the area.

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

**Kolpocherus majus** (Hopwood, 1934)

**Material**

One palate fragment with the left C (UA-353), 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 M1 (DAN-143, UA-44, UA-464).

**Description**

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

**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. olduvaensis*. M1 and M2 are evolutionarily advanced compared to *K. olduvaensis*. These molars are tetracuspid, larger, higher crowned and proportionally more elongated than in *K. olduvaensis* and show developed mesial and distal cingula. The third molar is shorter than in *K. olduvaensis*, have developed tetracuspid trigonid and short talonid with few pairs of cusps. In cross-section the enamel is generally more complicated than that of *K. olduvaensis*.

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

**Discussion on the genus Kolpocherus**

Besides DAN-142 and UA-20, the Buia *Kolpocherus* 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-
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-182), 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).

Kolpochoeris majus is a more conservative species than the lineage K. limnetes-olduwaiensis, 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 distalward expansion of the lower three 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. aferensis 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. de beamzeli) 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 hyasudricus. Kolpochoerus debeamzeli gave rise to K. cookei, a small and hypsodont species which is only found in Hadar, and to K. aferensis, which gave origin to K. majus and to K. limnetes-K. olдуwaiensis (Brunet & White 2000). Kolpochoerus olдуwaiensis 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. olдуwaiensis from Olduvai Bed IV, Tanzania (0.78 Ma) and K. majus at Bodo, Middle Awash, Ethiopia (0.6 Ma) (White 1995). Kolpochoerus olдуwaiensis 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. etronensis (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; Shafnouni et al. 2002).

Genus Metridiochoerus Hopwood, 1926

Metridiochoerus is believed to be ancestral to the living wart hog, Phacochoerus aethiopicus (Harris & White 1979). Metridiochoerus are sexually dimorphic pigs of small to large size. They are characterized 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 Pr-M2 (DAN-218), 1 mandibular fragment with M3 and roots of M3 (UA-449), 4 M3 (UA-367, DAN-197, DAN-222).
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 *Phacocherus*. 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. junae* Leakey, 1965

**Material**

A left maxillary fragment (UA-251) with M3-M6 and the roots of P4, one very worn right M1 or M6 (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. junai*, 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 junae* 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 brachyodont 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 (*Gazella*, *Spiroceros*, *Potoroco*, 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.

<table>
<thead>
<tr>
<th></th>
<th>P4/4</th>
<th>M1/1</th>
<th>M2/2</th>
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<tr>
<td></td>
<td>L W</td>
<td>L W</td>
<td>L W</td>
<td>L W</td>
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<tr>
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<td>10.9</td>
<td>8.6</td>
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<td>DAN-218</td>
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<td>8.6</td>
<td>12.7</td>
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<td>DAN-197</td>
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<td>12.7</td>
<td>12.2</td>
</tr>
<tr>
<td>DAN-220</td>
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<td>8.6</td>
<td>12.7</td>
<td>12.2</td>
</tr>
<tr>
<td>UA-367</td>
<td>10.9</td>
<td>8.6</td>
<td>12.7</td>
<td>12.2</td>
</tr>
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</table>

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

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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.
Fig. 11 - *Giraffa cf. G. jamae*. A-D: DAN-70, right tibia in lateral (A), medial (B), dorsal (C) and ventral (D) views. Bar scale in centimetres.

<table>
<thead>
<tr>
<th>Tab. 9</th>
<th>Upper teeth of <em>Giraffa cf. G. jamae</em> from Buia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M2/</td>
</tr>
<tr>
<td>UA-251</td>
<td></td>
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<td>DAN-198</td>
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<table>
<thead>
<tr>
<th>Tab. 10</th>
<th><em>Tragelaphus cf. T. spekei</em>, M2/ measurements compared to extant specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M2/</td>
</tr>
<tr>
<td></td>
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</table>

**Genus Tragelaphus** Blainville, 1816  

**Tragelaphus cf. T. spekei** Sclater, 1863

**Material**
One M2 (UA-274), 1 left mandible with $P_1$, $P_2$, 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 M2. 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).
Lower dentition – Only one specimen has been determined, the right hemimandible UA-245 (Fig. 12a-c). It preserves the P3 and P4, and the roots of the M1 and M2. The morphology of the premolars is typically Tragelaphus, with low crowns and no paraconid and metaconid junction. Unfortunately we cannot say anything about the molars (in Table 11, measurements of the M1 and M2 for UA-245 are alveolus measurements, and would be a little smaller than the real ones). As for the upper specimen, the anatomy and measurements of UA-245, are more similar to the specimens of Tragelaphus spekei, than to Tragelaphus scriptus (Pallas, 1766), in the collections of the National Museum of Kenya (Table 11).

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 Tragelaphus cf. T. spekei, the sitatunga, an antelope adapted to water environments with a very long distal phalanges used for swimming and walking on mudflats.
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-152) 1 left maxillary fragment with M1-M2 (UA-452), 1 M1 (DAN-63) 1 left M2 (UA-168), 2 upper molar fragment (UA-8, UA-134), 1 left mandibular fragment with DP2 and fragmented DP3 (DAN-83), 1 left scapular fragment (UA-360), 1 right scapular fragment (UA-359), 1 right radius-ulna (UA-341), 1 distal end right radius-ulna (DAN-235), 2 left talus (DAN-127, DAN-277), 2 right talus (UA-65, DAN-85), 1 left calcaneum fragment (UA-382), 1 right naviculocuboidum (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 M1, 1 M2 and 1 M3 are identified in the collection (Table 13). These molars have thick enamel and robust internal pillars. The M1

| Tab. 13 | Upper teeth of *Pelorovis oldowayensis* from Buia. |
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 M² UA-450 is poorly preserved. The M³ 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-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 DP₃ and DP₄ 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.
Fig. 16 - *Hippotherium 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.
Subfamily Hippotraginae Retzius & Lovén, 1845
Tribe Hippotragini Retzius & Lovén, 1845
Genus *Hippotragus* Sundevall, 1846

*Hippotragus gigas* Leakey, 1965

**Material**

One cranial 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).

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

<table>
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<tr>
<th></th>
<th>Preserved Length</th>
<th>Transverse Diameter (base)</th>
<th>Antero-posterior Diameter (base)</th>
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<td>227.00</td>
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<td>UA-30</td>
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<td>40.00</td>
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<td>UA-141+UA-140</td>
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<td>57.00</td>
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<td>490.00</td>
<td>51.00</td>
<td>64.30</td>
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<tr>
<td>UA-436</td>
<td>105.00</td>
<td>42.70</td>
<td>50.10</td>
</tr>
<tr>
<td>DAN-148</td>
<td>406.00</td>
<td>41.90</td>
<td>56.60</td>
</tr>
<tr>
<td>DAN-148</td>
<td>115.00</td>
<td>43.90</td>
<td>51.90</td>
</tr>
<tr>
<td>DAN-207</td>
<td>145.00</td>
<td>45.70</td>
<td>55.20</td>
</tr>
</tbody>
</table>

**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-145b, UA-436, DAN-99, DAN-148), 1 left maxillary fragment with M\(^1\)+M\(^2\) (DAN-152), 1 M\(^1\)+M\(^3\) (DAN-209), 1 upper molar fragment (DAN-216), 1 M\(_2\) (DAN-87), 1 M\(_3\) (UA-255), 1 M\(_4\) distal end (DAN-88), 4 M\(_4\) distal ends (UA-32, UA-38, UA-261, UA-273), 1 Metapodial distal end (DAN-132), 2 talus (UA-52, DAN-71), 1 naviculocuboid (UA-286), 3 proximal phalanges (UA-17, UA-50, DAN-126), 2 mediolateral phalanges (UA-265, DAN-190). There are also other postcraniial specimens probably belonging to this taxon.

Description

Cranium — The cranial fragment UA-140+141 (Fig. 17) is heavily built and lacks a pneumatized 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. 18a-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 reducine 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).

Subfamily Antilopinae, Gray 1821
Tribe Antilocpini Gray, 1821
Genus Gazella Blainville, 1816

Gazella sp.

Material
One P\(^4\) (UA-269), 1 M\(^4\) (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).

![Fig. 18 - Kobus sp. K. ellipsiprymnus. A-B: DAN-152, left maxillary fragment with M\(^1\)-M\(^3\) 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.](image-url)
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.

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Tab. 17 - Upper and lower dentition measurements of *Kobus* cl. *K. ellipsocephalus* from Buia.

<table>
<thead>
<tr>
<th></th>
<th>M1/WAL</th>
<th>M2/WPL</th>
<th>M3/WPL</th>
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<tbody>
<tr>
<td>DAN-152</td>
<td>19.00</td>
<td>19.10</td>
<td>19.30</td>
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<td>DAN-209</td>
<td>21.00</td>
<td>22.90</td>
<td>21.30</td>
</tr>
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<td>DAN-87</td>
<td>23.00</td>
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<td>13.50</td>
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<tr>
<td>UA-255</td>
<td>32.70</td>
<td>13.50</td>
<td>12.70</td>
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</table>

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

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<tr>
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<th>P4/W</th>
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</thead>
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<tr>
<td>UA-269 L.</td>
<td>8.40</td>
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<tr>
<td>DAN-211 L.</td>
<td>14.20</td>
<td>11.00</td>
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</table>

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

<table>
<thead>
<tr>
<th></th>
<th>EL</th>
<th>IL</th>
<th>PTD</th>
<th>PAPD</th>
<th>MTD</th>
<th>MAPD</th>
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<tr>
<td>Talus</td>
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<tr>
<td>UA-281</td>
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<td>16.20</td>
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<td>16.40</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mc</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>DAN-195</td>
<td>24.50</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st phalanx</td>
<td>10.90</td>
<td>15.50</td>
<td>9.80</td>
<td>10.50</td>
<td></td>
<td></td>
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</tbody>
</table>

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.

Material
One right mandibular fragment with M2-M3 (DAN-21), 1 M1 (UA-273), 1 M2 (DAN-129), and 1 M3 (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-
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 Natikotome 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.

<table>
<thead>
<tr>
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<td></td>
<td>12</td>
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</tr>
<tr>
<td>DAN-21</td>
<td>L</td>
<td>17.5</td>
<td>11.2</td>
<td>11.2</td>
</tr>
<tr>
<td></td>
<td>M3</td>
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<td></td>
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<tr>
<td></td>
<td>18.4</td>
<td>10.8</td>
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</tr>
<tr>
<td>DAN-129</td>
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<td></td>
<td>16.2</td>
<td>9.8</td>
<td>9.8</td>
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<tr>
<td>UA-273</td>
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</tbody>
</table>

Tab. 20 - Upper and lower teeth measurements of Caprini indet. from Buia.
We also use Simpson’s (1947, 1962) 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.

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
Early Pleistocene association of the Eastern African Rift, characterised by evolved last representative forms of Theropithecus cf. T. oswaldi, Elephas recki, Hippopotamus gorgops, Kolpochoerus oldowayensis, Kolpochoerus major, 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; Albanielli & Napoleon 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 fluvo-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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