



The early Pleistocene vertebrate fauna of Mulhuli-Amo (Buia area, Danakil Depression, Eritrea)

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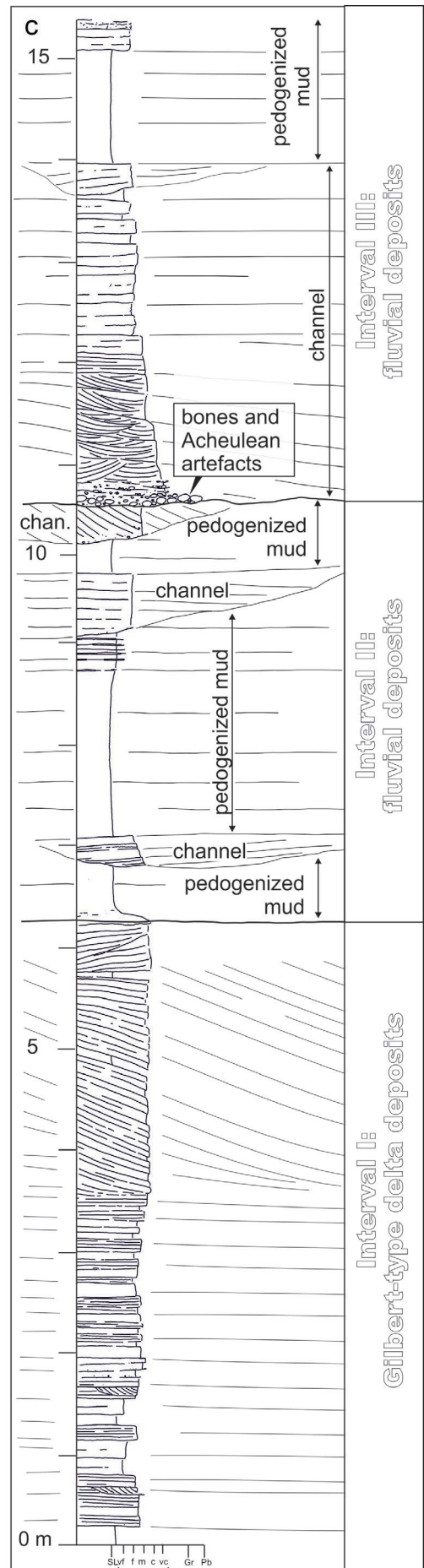
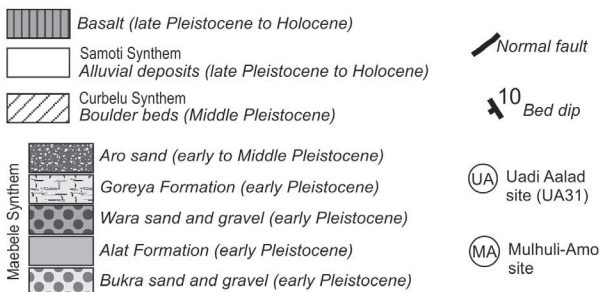
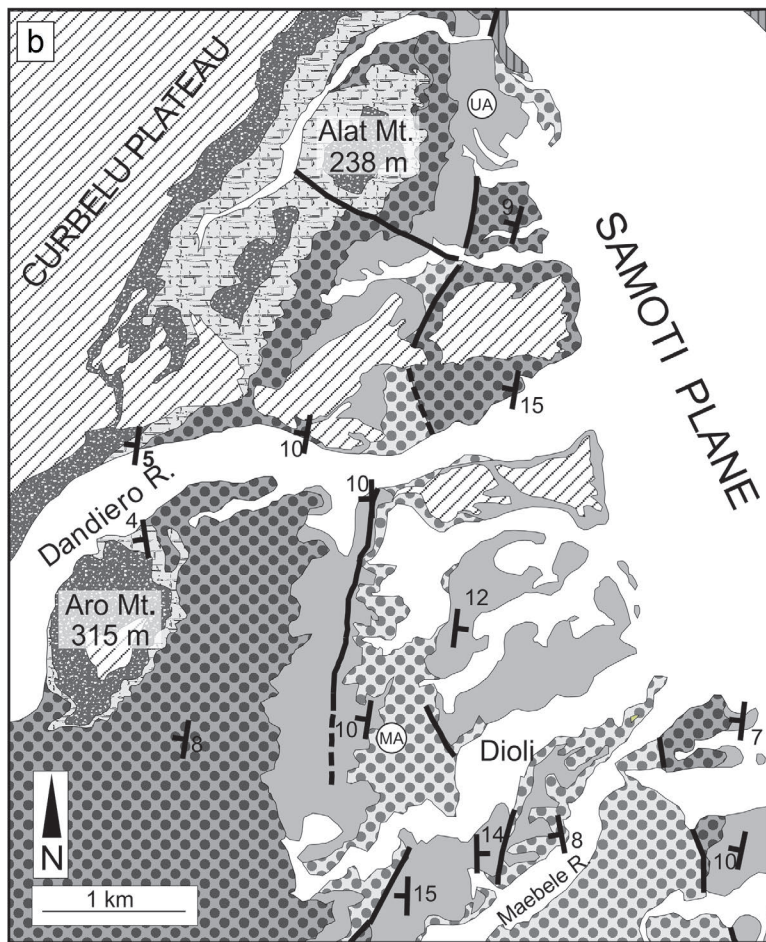
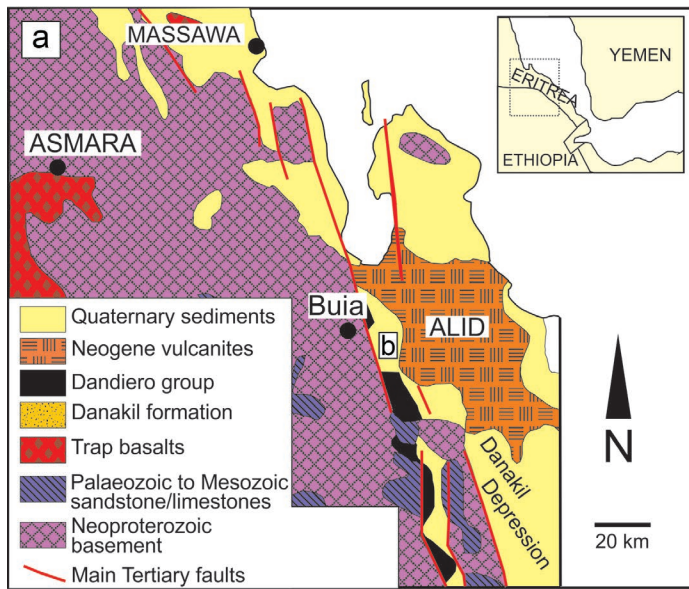
ABSTRACT - *Mulhuli-Amo is an early Pleistocene locality of the Buia area in the Dandiero Basin (Danakil Depression, Eritrea) already known for the presence of Homo remains and stone tools. Recent surface surveys lead to the retrieval of a rich vertebrate fauna that is here described for the first time in order to contribute to the palaeoenvironmental background to the Homo layers of the basin. The following 14 taxa (two fishes, four reptiles, one bird, and nine mammals) were identified: Clarias (Clarias) sp., ?Cichlidae indet., Crocodylus sp., Pelusios sinuatus, Varanus niloticus, Python gr. P. sebae, Ardeotis kori, Palaeoloxodon cf. P. recki, Ceratotherium simum, Equus cf. E. quagga, Hippopotamus gorgops, Kolpochoerus majus, Bos cf. B. buiaensis, and Kobus cf. K. ellipsiprymnus. With the exception of a fish and the bird that were identified at Mulhuli-Amo for the first time, the whole fauna is fully congruent with the taxa already described for the neighbouring locality of Uadi Aalad and confirms, in agreement with all the other proxies, an early Pleistocene age and the former presence of moist grassed habitats adjacent to persistent water.*

RIASSUNTO - [I vertebrati del Pleistocene inferiore di Mulhuli-Amo (area di Buia, Depressione Danacala, Eritrea)] - *Il Progetto Buia nasce nel 1994 come un progetto di ricognizione geologica finalizzato allo studio della geologia regionale di un'area circa 20 Km a sud di Buia nella Danacalia settentrionale (Eritrea) ma, già a partire dalle prime missioni, il rinvenimento di resti umani associati a strumenti litici e ad una ricca fauna di vertebrati ha ampliato notevolmente le prospettive di ricerca. I primi resti umani sono stati identificati nel 1995 in un livello della località Uadi Aalad attribuito al Subcrono Jaramillo e datato a circa 1.0 Ma. Successivamente, a partire dal dicembre 2000, ulteriori resti umani sono stati ritrovati a Mulhuli-Amo, una località lontana circa 5 Km dalla prima, già conosciuta per un eccezionale accumulo di strumenti litici e di resti di vertebrati. In questo lavoro viene descritta per la prima volta in modo unitario la fauna vertebrata non umana rinvenuta in superficie a Mulhuli-Amo. Complessivamente, sono stati identificati i seguenti 14 taxa: Clarias (Clarias) sp., ?Cichlidae indet., Crocodylus sp., Pelusios sinuatus, Varanus niloticus, Python gr. P. sebae, Ardeotis kori, Palaeoloxodon cf. P. recki, Ceratotherium simum, Equus cf. E. quagga, Hippopotamus gorgops, Kolpochoerus majus, Bos cf. B. buiaensis, Kobus cf. K. ellipsiprymnus. L'associazione faunistica è pienamente congruente con quella di Uadi Aalad e, nonostante sia meno diversificata di questa, presenta alcuni elementi di novità (?Cichlidae indet., Ardeotis kori). Alcuni mammiferi (Palaeoloxodon cf. P. recki, E. cf. E. quagga, H. gorgops, K. majus, B. cf. B. buiaensis) confermano l'attribuzione della fauna al Pleistocene inferiore finale. Da un punto di vista ambientale, l'associazione faunistica suggerisce la presenza di raccolte permanenti d'acqua circondate da praterie umide, in netto contrasto con gli ambienti attuali estremamente aridi.*

INTRODUCTION

Started in late 1994 as research focused mainly on geological survey and regional geology, thanks to collaboration between the Asmara Department of Mines (Eritrea) and the University of Florence (Italy), the Buia Project soon allowed the recovery of abundant early Pleistocene vertebrates associated to archaeological artifacts in an area located about 20 km south of the village of Buia (Northern Danakil Depression). In late 1995, a human cranium and other dental and post-cranial

remains (Abbate et al., 1998) were retrieved at Uadi Aalad (= Wadi Aalad) in a layer dated through different approaches and falling within the Jaramillo Subchron, at approximately 1.0 Ma (see Geological Setting below and Fig. 1). Exactly 15 years later, other cranial and dental human remains were found at Mulhuli-Amo, a different locality chronologically equivalent to Uadi Aalad, but nearly 5 km south of it (Fig. 1; Coppa et al., 2012, 2014). The area of Mulhuli-Amo was already known as A006 site for an exceptional concentration of stone tools on which Martini et al. (2004) briefly reported and for a number



of fossil remains exposed on the surface and known by the researchers, but never described as a comprehensive faunal assemblage (Delfino et al., 2004; Martínez-Navarro et al., 2004). Zanolli et al. (2014), while describing in detail the morphology of the human molar from Mulhuli-Amo (MA 93), not only listed the other human remains, but already cited also a few non-human vertebrates from the site. Here we report for the first time on the whole non-*Homo* vertebrate fauna from Mulhuli-Amo, in order to provide, along with the previously described fauna from Uadi Aalad (Ferretti et al., 2003; Delfino et al., 2004; Martínez-Navarro et al., 2004, 2010; Rook et al., 2010, 2013), a comprehensive faunal and therefore palaeoenvironmental background to the *Homo* layers of the Dandiero Basin. In accordance with field procedures employed in other African Plio-Pleistocene study areas, collected fossils were found by surface survey and not from systematic excavation (Gilbert, 2008). The spatial distribution of the fossils and the stone tools will be the subject of another work.

GEOLOGICAL SETTING

The Dandiero Basin forms the northern part of the Danakil Depression (Fig. 1a) and is filled with ca. 450-500 m thick alluvial to lacustrine Pleistocene deposits. Neoproterozoic rocks form the southern and western shoulders of the basin, whereas to the north it is bounded by the Alid volcanic complex and to the east by the fluvio-aolian sand of the Samoti plain. The basin fill consists of three main unconformity-bounded units (Abbate et al., 2004; Ghinassi et al., 2009; Papini et al., 2014): Maebele Synthem, Curbelu Synthem, and Samoti Synthem. The Maebele Synthem contains six lithostratigraphic units (Fig. 1b): fluvial Bukra sand and gravels, fluvio-deltaic Aalat formation, fluvial Wara sand and gravel, lacustrine Goreya formation, fluvio-deltaic Aro sand, and alluvial Addai fanglomerate. On the basis of palaeomagnetism, mammal biochronology, and radiometric dating (Abbate et al., 1998; Ferretti et al., 2003; Albanelli & Napoleone, 2004; Bigazzi et al., 2004; Delfino et al., 2004; Martínez-Navarro et al., 2004, 2010; Rook et al., 2013), the lower boundary of the Aalat formation has been ascribed to the base of the Jaramillo Subchron (1.07 Ma), whereas the upper boundary of the Jaramillo Subchron (0.99 Ma) occurs just below the transition between the Aalat formation and Wara sand and gravel. Deposits of the Maebele Synthem are characterized by a palaeo-transport direction towards the north (Abbate et al., 2004; Ghinassi et al., 2009, 2013, 2015; Rook et al., 2010; Papini et al., 2014). The Curbelu Synthem is made of alluvial fan gravels accumulated during the Late Pleistocene, whereas the Samoti Synthem consists of gravelly fluvial deposits interfingering with eolian sand deposited during Late Pleistocene-Holocene time span (Abbate et al., 2004).

The Mulhuli-Amo section is located at about 5 km from the fossiliferous “*Homo*” site (Fig. 1b), which in 1995 provided one-million-year-old *Homo* cranial

and postcranial material (Abbate et al., 1998, 2004; Macchiarelli et al., 2004; Bondioli et al., 2006; Ghinassi et al., 2009). Recent stratigraphic and structural studies allow to ascribe these two sites to the same stratigraphic horizon (Sani et al., 2017), which is dated at the top of Jaramillo Subchron.

The studied sedimentary succession exposed in the Mulhuli-Amo site is about 15 m thick and consists of three main intervals (Fig. 1c). The first interval (6 m thick) is made of fine silty sand grading upward into medium coarse sand. Silty sands form sub-horizontal, tabular beds characterized by a diffuse ripple-cross lamination and plane-parallel stratification. Rare massive silty layers with scattered freshwater gastropod shells (*Melanooides tuberculata* [Müller, 1774]) are intercalated between these tabular beds. Medium coarse sands are made of clinostratified beds ranging from massive to plane-parallel stratified. Inclined beds dip 15°-20° toward North. The uppermost part of this interval is made of plane-parallel stratified coarse sands showing a sub-horizontal attitude. Deposits forming the lower interval are ascribed to a sandy Gilbert-type delta prograding toward north. Beds with different inclination are ascribed, from bottom up, to bottomset, foreset and topset deposits respectively.

The second interval (about 4 m thick) is made of tabular, sub-horizontal muddy beds with isolated, erosive-based lensoid bodies. Muddy deposits are mainly massive and contain abundant pedogenic carbonate concretions as well as discontinuous, 1-3 cm thick, sandy layers. At the base of the second interval a 10-15 cm thick sandy layer with abundant freshwater gastropod shells (*Melanooides tuberculata*) is present. Such a layer is overlain by muddy deposits bearing isolated *Melanooides* shells. Lensoid bodies are up to 130 cm thick and 6-8 m wide. Their base is commonly floored by very coarse sand with a variable amount of pebble-sized gravels. Internal architecture shows large-scale inclined beds, which are mainly ripple cross-laminated. Lensoid bodies show a fining-upward trend and are commonly capped by pedogenized sandy-silt deposits. Sediments of the second interval were accumulated in a floodplain setting. Muddy and sandy deposits are ascribed to floodbasin and fluvial channel sub-environments respectively. The fining upward trend of the channelised bodies highlights progressive channel deactivation, which culminates in channel abandonment and establishment of pedogenic processes.

The third interval (about 5 m thick) is made of medium-coarse sand grading upward into silty sand. Medium-coarse sand form amalgamated lensoid bodies up to 2 m thick and 15-20 m wide. Lensoid bodies are erosive based and consist of large-scale inclined bedsets, which are commonly cross- to plane-parallel stratified. The basal portion of these bodies is made of massive very coarse sand with pebbles and gravel-sized mudclasts. Lateral amalgamation of these pebbly sands formed a continuous layer, which provided most of the studied stone tools and mammal bones. The silty sand deposits primarily consist of massive horizontal beds bearing abundant pedogenic carbonate concretions. Deposits of

Fig. 1 - (color online) The geological setting of Mulhuli-Amo. a) Location and schematic geological map of the Danakil Depression. b) Schematic geological map of the Dandiero Basin. c) The sedimentary succession exposed at Mulhuli-Amo is about 15 m thick and consists of three main intervals.

the third interval were formed in fluvial setting. Sandy and silty deposits are ascribed to channel and floodbasin depositional environment. The fossil-bearing deposits at the base of sandy channels are interpreted as channel lag, where variable hydrodynamic conditions concentrate the larger clasts, which are commonly represented by large vertebrate bones and stone tools.

Institutional abbreviations

PCHPC: Peter C.H. Pritchard Collection hosted at the Chelonian Research Institute (Oviedo, FL, USA); MA: Mulhuli-Amo collection hosted at the Northern Red Sea Regional Museum of Massawa; UA: Uadi Aalad collection hosted at the Eritrean National Museum of Asmara.

SYSTEMATIC PALAEOLOGY

Subdivision TELEOSTEI sensu Patterson & Rosen, 1977

Order SILURIFORMES Hay, 1929

Family CLARIIDAE Bonaparte, 1845

Genus *Clarias* Scopoli, 1777

Subgenus *Clarias* (*Clarias*) Teugels, 1986

Clarias (*Clarias*) sp.
(Fig. 2a-e)

Material - MA 1118: partially complete vertebral centrum; MA 1119: partially complete mesethmoid; MA 1122: partially complete vertebral centrum; MA 1292: partially complete vertebral centrum; MA 1293: partially complete parietosupraoccipital; MA P 0001: partially complete right frontal; MA P 0002: partially complete mesethmoid; MA P 0003: partially complete abdominal vertebra; MA P 0004: about 20 fragmentary neurocranial bones of problematic anatomical interpretation.

Description - All the available specimens consist of robust isolated bones collected during the surface exploration of the fossiliferous site. The dermal neurocranial bones are flattened and exhibit the granular ornamentation pattern observed in certain species of the genus *Clarias* (in the sense of Teugels, 1986) and in *Heterobranchus*. The mesethmoid (Fig. 2a-b) has a poorly developed median notch along its anterior margin and the bases of its lateral anterior projections are perpendicular to the main axis of the bone; the median depression typical of *Heterobranchus* and a few species of *Clarias* appears to be absent (see Otero & Gayet, 2001). The frontal (Fig. 2c) is very thick and shows the posterior part of the depressed area surrounding the anterior fontanel. The specimen MA 1293 (Fig. 2d) consists of a large-based and almost triangular posterior process of a parietosupraoccipital bearing a well-developed medioventral crest along its inner surface (see Adriaens & Verraes, 1998). The vertebral centra (Fig. 2e) are discoid, anteroposteriorly compressed, and somewhat dorsoventrally flattened; lateral and ventral fossae of a variety of sizes are present along the lateral and ventral surfaces of the centra. The abdominal vertebrae possess well-developed parapophyses emerging ventrolaterally.

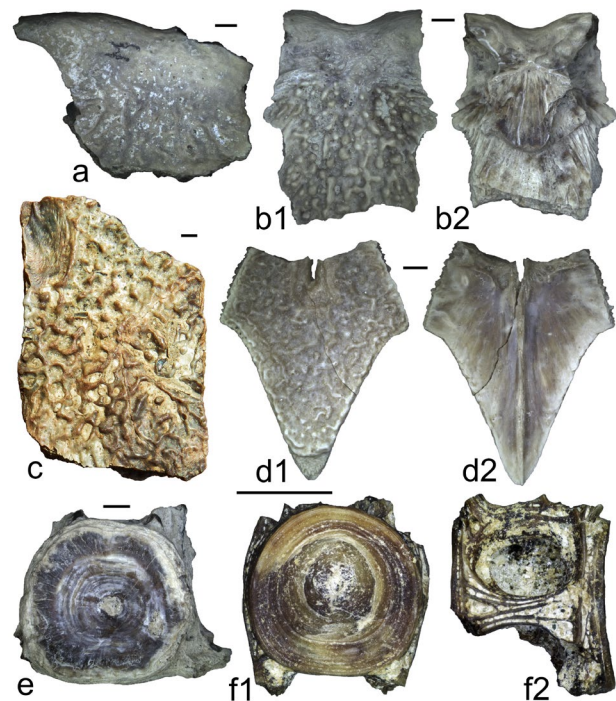


Fig. 2 - (color online) Fishes from Mulhuli-Amo. a) *Clarias* (*Clarias*) sp., MA P 0002, mesethmoid, dorsal view; b) *Clarias* (*Clarias*) sp., MA 1119, mesethmoid, dorsal (b1) and ventral (b2) views; c) *Clarias* (*Clarias*) sp., MA P 0001, partially complete right frontal, dorsal view; d) *Clarias* (*Clarias*) sp., MA 1293, posterior process of the parietosupraoccipital, dorsal (d1) and ventral (d2) views; e) *Clarias* (*Clarias*) sp., MA P 0003, abdominal vertebra, anterior view; f) ?Cichlidae gen. et sp. indet., MA 993, caudal vertebra in anterior (f1) and lateral (f2) views. Scale bars equal 2 mm.

Remarks - The morphology and ornamentation pattern of the neurocranial bones and the very short and dorsoventrally depressed vertebral centra strongly support their assignment to the catfish family Clariidae (e.g., Otero & Gayet, 2001; Otero et al., 2009). Within this family, the flattened and very robust cranial bones characterised by a dense sculpturing of their external surface are exclusive of the genus *Heterobranchus* and the African subgenera of the genus *Clarias* (in the sense of Teugels, 1986), *C. (Clarias)*, *C. (Claroides)*, and *C. (Anguilloclarias)*. The absence of a median depression in the mesethmoid and large base of the posterior process of the parietosupraoccipital clearly exclude the possibility of an attribution to the genus *Heterobranchus* (see Otero & Gayet, 2001). The overall morphology of the posterior process of the parietosupraoccipital is consistent with that of the species of the African subgenus *C. (Clarias)* (Otero & Gayet, 2001) to which these specimens are tentatively referred. An indeterminate species of the subgenus *C. (Clarias)* has been recently reported from the almost coeval deposits of the Uadi Aalad site (Rook et al., 2013).

Order PERCIFORMES Bleeker, 1859
Family ?CICHLIDAE Bonaparte, 1835

Gen. et sp. indet.
(Fig. 2f)

Material - MA 993: a single partially complete and poorly preserved vertebral centrum.

Description and remarks - The specimen is identified herein as a probable cichlid vertebral centrum based on its rounded anterior facet, absent central notochordal foramen, large lateral fossae, and bases of the neural and haemal arches fused to the centrum (see Stewart & Murray, 2013, 2017). Moreover, the bone has the open, strut-like texture typical of cichlids and other perciforms.

Class REPTILIA Laurenti, 1768
Order CROCODYLIA Gmelin, 1789
Family CROCODYLIDAE Cuvier, 1807

Genus *Crocodylus* Laurenti, 1768

Crocodylus sp.
(Fig. 3)

Material - MA 829: partial skull and lower jaw.

Description - In its current state of preservation, the partially preserved skull and lower jaw MA 829, is characterised by being fragmented into many pieces with most of the surface covered by a variably thick concretion. The concretion is very thin or nearly absent in the prefrontal area or on the squamosal dorsal surface, but fills the supratemporal fossae and the otic notches. Even

if there are no sutures fully visible, a few characters can be preliminary described as follows. The preorbital ridges and median boss on the rostrum are not developed. The orbits have distinctly raised edges. The squamosal dorsal area is slightly raised into a modest squamosal horn, but lacks of triangular projections above the otic notch. The skull table is deeply concave and, in dorsal view, its lateral edges diverge from the sagittal plane of about 10°.

Remarks - Since the referral of the crocodylian remains from Uadi Aalad to *Crocodylus niloticus* Laurenti, 1768 (Delfino et al., 2004), the taxonomy of African crocodiles has become rather complex because of the resurrection of an extant species and description of two extinct species. The populations of *Crocodylus niloticus* from western Africa were referred on a molecular basis by Hekkala et al. (2011) to the species *Crocodylus suchus* Geoffroy Saint-Hilaire, 1807, which was also present in eastern Africa in the past. Moreover, Brochu et al. (2010) described the species *Crocodylus anthropophagus* from the early Pleistocene of Olduvai Gorge (Tanzania) and Brochu & Storrs (2012) described *Crocodylus thorbjarnarsoni* from the Plio-Pleistocene of Lake Turkana Basin (Kenya).

The morphology of the squamosals allows to exclude the referral of the material from Mulhuli-Amo to *C. anthropophagus* and the absence of a median boss to exclude the geologically older *Crocodylus checchiai* Maccagno, 1947 (Brochu & Storrs, 2012). However, due to the poor preservation and preparation of the fossil material from Mulhuli-Amo and considering on one hand that the comparative osteology of *C. niloticus* and *C. suchus* is still unknown and on the other hand that the skull table of MA 829 is only slightly less trapezoidal than that of *C. thorbjarnarsoni*, it is preferred to preliminarily identify the material here described only at genus level.

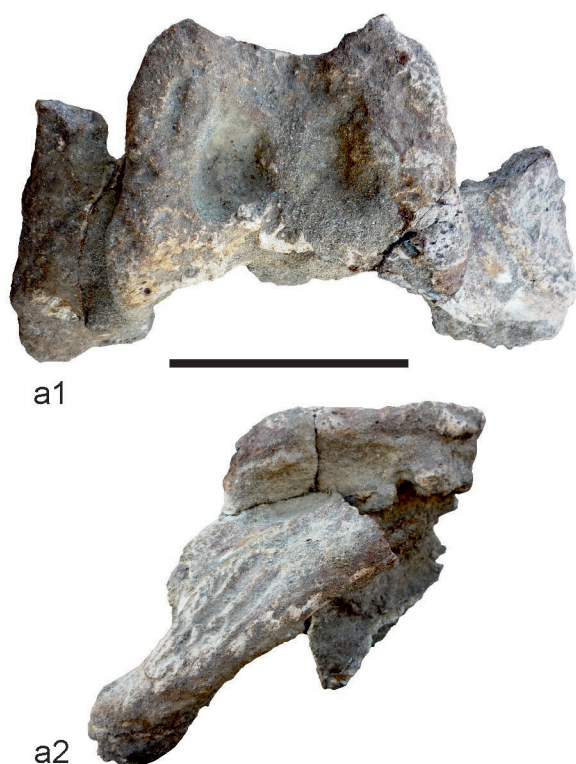


Fig. 3 - (color online) *Crocodylus* sp. MA 829 from Mulhuli-Amo. a) Posterior portion of the skull in dorsal (a1) and right lateral (a2) views. Scale bar equals 10 cm.

Order TESTUDINES Batsch, 1788
Family PELOMEDUSIDAE Cope, 1868

Genus *Pelusios* Wagler, 1830

Pelusios sinuatus (Smith, 1838)
(Fig. 4)

Material - MA 204: a partial shell and the associated pelvic girdle; MA 506: left xiphiplastron.

Description - The partial shell and fragmentary pelvic girdle catalogued under the accession number MA 204 appear to belong to a single individual. Besides about 20 major unidentifiable fragments, the shell preserves the following elements: five neurals, 11 costals, 17 peripherals, right and left epiplastra, entoplastron, fragmentary hyoplastra, and mesoplastra, right and left xiphiplastra. A few shell elements are joined together, but most of them are isolated and their surface is highly altered or is covered by concretion. Nevertheless the following morphological features allow to better characterize the chelonian from Mulhuli-Amo: the three largest neurals are hexagonal (Fig. 4a), the fourth is irregularly hexagonal (Fig. 4b1) and the fifth is nearly rounded; with one exception (Fig. 4b), the neurals are dorsally flat; the costal elements (Fig.



Fig. 4 - (color online) *Pelusios sinuatus* (Smith, 1838) MA 204 from Mulhuli-Amo. a) Anterior neural in dorsal view; b) posterior neural in dorsal (b1) and lateral (b2) views; c) costal in dorsal (c1), ventral (c2) and lateral (c3) views; d) right epiplastron in ventral view; e) left epiplastron partially hidden by the entoplastron (both in ventral view); f) xiphiplastra in dorsal (f1) and ventral (f2) views. In f1, the scars for the sutural attachment with the pubis and ischium are marked by a black line. Scale bars equal 10 mm.

4c) are significantly bent indicating that the carapace was flattened or concave between the vertebrals; the last costal bears on the visceral surface the trace of its former relationship with the vertebral column indicating that the last costals met on the midline, posterior to the last neural;

the pleuro-marginal sulci are located on the peripheral bones, far from the costo-peripheral suture; the peripheral elements involved in the bridge are L-shaped (with an inner angle of about 90°) and have a modest external keel; the epiplastra (Fig. 4d-e) do not develop a marked

epiplastral lip; the general shape of the entoplastron (Fig. 4e) is congruent with that previously found at Uadi Aalad (UA 466, see fig. 4 in Delfino et al., 2004) but no scute sulci are visible because of preservational reasons; a hinge and not a suture separates the hyoplastra and the mesoplastra; xiphiplastra host a clear sutural scar for the suture with the pubis and the ischium (Fig. 4f1); the tip of the xiphiplastra are modestly bent downward; the anal notch is well developed, but there is not a significant notch on the lateral side of the xiphiplastra (Fig. 4f). Moreover, it is worth noting that the pads of the epiplastra and xiphiplastra are only modestly developed, but the thickness of some elements is remarkable (up to 15 mm in the case of the neurals).

The fragmentary left xiphiplastron MA 506 (not figured) is 45 mm wide and 49 mm long. It preserves part of the suture with the right xiphiplastron (for about 10 mm). The external surface does not host any sulcus but the visceral one shows the scar for the pelvic girdle. The posterior tip is distinctly bent downward.

Remarks - The above described characters are fully congruent with a pleurodiran terrapin (pubis and ischium sutured with the xiphiplastra; presence of mesoplastra) and with the morphology of *P. sinuatus*, the Serrated Hinged Terrapin, in particular. Worth mentioning is that costals are distinctly bent in some extant specimens of *P. sinuatus* (as PCHPC 5469) that have the area covered by the vertebrae not only flattened, but even slightly concave (but with a median convexity), a character very well expressed in this species (Auffenberg, 1981; Ernst & Barbour, 1989). The presence of a “bump” on one of the small, posterior neurals is congruent with the fact that, according to Broadley & Boycott (2009) adults of *P. sinuatus* have keeled posterior vertebrae (the carapace is strongly keeled in juveniles and subadults). Last but not least, the size of the preserved elements (and somehow also their thickness) indicates that the shell was originally very large (length of about 30 cm); *P. sinuatus* is currently the largest species of the genus with a carapace length up to 55 cm (Broadley & Boycott, 2009). The remains from Mulhuli-Amo significantly improve the knowledge of the morphology of the Serrated Hinged Terrapin previously reported as *Pelusios* cf. *P. sinuatus* first on the basis of a single entoplastron (UA 374; Delfino et al., 2004) and then on several shell fragments (Rook et al., 2013) from Uadi Aalad.

Order SQUAMATA Oppel, 1811
Family VARANIDAE Gray, 1827

Genus *Varanus* Merrem, 1820

Varanus niloticus (Linnaeus, 1766)
(Fig. 5a)

Material - MA 397: caudal vertebra; MA3 1092: fragment of caudal vertebra; MA3 1099: caudal vertebra; MA3 1144: cloacal vertebra.

Description - All specimens are represented by procoelous, large, and robust vertebrae. They are provided with a slightly dorsoventrally compressed centrum, that

reaches 20 mm in length in the largest specimen (MA3 1099; Fig. 5a). The cotyle is wide, sub-trapezoidal in shape in anterior view, and distinctly oriented in anteroventral direction. The posterior condyle is wide and displays a precondylar constriction in ventral view. The pedestals for the chevron bones are visible on the ventral surface of the centrum in the caudal vertebrae. Transverse processes are almost always broken off, but they were as long as the centrum by their bases. Only MA3 1144 preserves the right one. When preserved, zygapophyses are either circular or subelliptical and dorsally tilted of 45°. The neural canal is narrow in anterior view and subcircular in shape. No autotomy plane is present in the caudal vertebrae.

Remarks - A large posterior condyle preceded by a precondylar constriction is considered a derived feature of varanoid vertebrae by Estes (1983). In terms of morphology, the vertebrae from Mulhuli-Amo are fully comparable with those of *V. niloticus*, still living in Eritrea nowadays (but not in the Buia area). In particular, they resemble *V. niloticus* rather than *Varanus exanthematicus* (Bosc, 1792) (the other varanid currently living in Eritrea; Largen & Spawls, 2010) in the larger size and in the anterior cotyle being more ventrally oriented (Bailon & Rage, 1994). Moreover, these specimens have a morphology congruent with the trunk vertebra previously reported from Uadi Aalad and attributed to *V. niloticus* by Delfino et al. (2004).

Family PYTHONIDAE Fitzinger, 1826

Genus *Python* Daudin, 1803

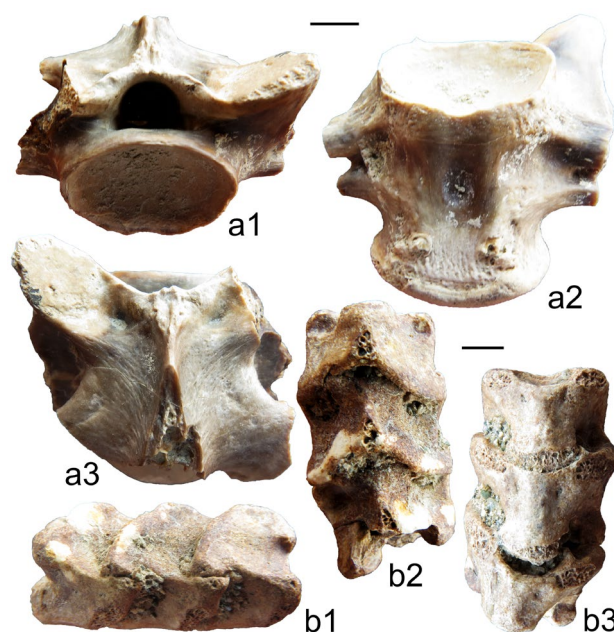


Fig. 5 - (color online) Squamates from Mulhuli-Amo. a) Caudal vertebra of *Varanus niloticus* (Linnaeus, 1766) MA3 1099 in anterior (a1), ventral (a2) and dorsal (a3) views; b) articulated trunk vertebrae of *Python* gr. *P. sebae* (Gmelin, 1789) MA 1089 in right lateral (b1), dorsal (b2) and ventral (b3) views. Scale bars equal 5 mm.

Python gr. *P. sebae* (Gmelin, 1789)
(Fig. 5b)

Material - MA 1089: three articulated trunk vertebrae.

Description - MA 1089 is composed by three procoelous and robust vertebrae, partially encrusted with sediment. Their maximum centrum length is, from the anteriormost one to the posteriormost one respectively, 9 mm, 10 mm, and 8 mm. The vertebral centrum is wider than long and it is provided with a hemal keel on the ventral surface. The keel is very low and wide; its posterior end is barely differentiated from the rest of the ventral surface. Paradiapophyses are eroded, but they were rather slender in origin. Prezygapophyseal processes seem not to be present. In anterior view, the neural canal has a sub-triangular cross-section. Zygosphene and zygantrum are present, but they are eroded or barely visible because of connection and sediments. No postzygapophyseal spines are visible. Zygapophyses are eroded or not visible, but they are only slightly tilted dorsally. The neural arch is robust and vaulted in posterior view; an angle is recognizable in the middle of each side of the vaulted posterior margin. Neural spines are eroded, but they start roughly at mid-length of the neural arch.

Remarks - Because of their wide and short aspect, these vertebrae can be attributed either to a boid or a pythonid snake (Szyndlar, 1984; note that in the latter work pythons were still considered as a subfamily in the Boidae). Boids are currently represented in Eritrea by an erycine, *Eryx colubrinus* (Linnaeus, 1758), whereas Eritrean pythonids include only *Python sebae* (Largen & Spawls, 2010). The rather large size of the herein-described vertebrae is more consistent with a pythonid rather than with an erycine boid. Among the current African pythonid species, MA 1089 differs from *Python regius* (Shaw, 1802) in the lower keel, the more slender paradiapophyses, the more posteriorly located neural spine and the more vaulted neural arch (Bailon & Rage, 1994; Rage & Bailon, 2011). This morphology, on the other hand, recalls the members of the *P. sebae* group, namely *P. sebae* and *Python natalensis* Duméril & Bibron, 1844 (Broadley, 1999). The osteology of the southwestern African species *Python anchietae* Bocage, 1887 is not known, and therefore a comparison with the fossil from Mulhuli-Amo is not possible. Moreover, MA 1089 cannot be assigned to the extinct species *Python maurus* Rage, 1976, known from the middle Miocene of Morocco, because of the slender paradiapophyses (Rage, 1976; Rage & Bailon, 2011). Given that, we here refer this specimen to *Python* gr. *P. sebae*, pending a comparative osteological analysis that allows to discriminate between the two species of the group.

Class AVES Linnaeus, 1758
Order OTIDIFORMES Wagler, 1830
Family OTIDIDAE Rafinesque, 1815

Genus *Ardeotis* Le Maout, 1853

Ardeotis kori (Burchell, 1822)
(Fig. 6)

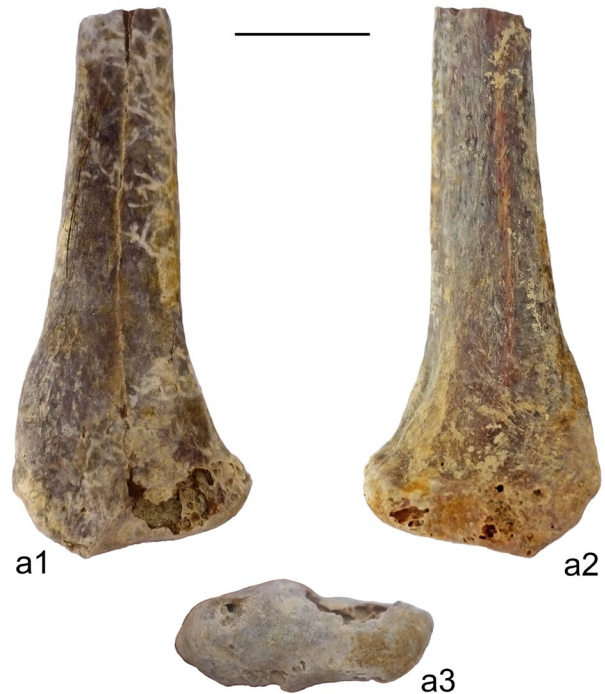


Fig. 6 - (color online) *Ardeotis kori* (Burchell, 1822) MA 4316 from Mulhuli-Amo. Right radius in dorsal (a1), ventral (a2), and distal (a3) views. Scale bar equals 1 cm.

Material - MA 4316: distal portion of right radius.

Description and remarks - The relatively large size of the distal portion of a right radius found at Mulhuli-Amo (distal width: 17.9 mm; distal depth: 8.1 mm) allows to exclude most of the African bird taxa, with the exception of large-sized Anatidae, Pelecanidae, large-sized Accipitridae, Ciconiidae, Gruidae, and Otididae. The Pelecanidae and the large-sized Accipitridae can be excluded because the distal radius of these species shows pneumatic foramina, absent in the Mulhuli-Amo bone. The Anatidae, particularly the genus *Cygnus*, show a deeper sulcus tendineus, a wider depression ligamentosa, and a dorsally-oriented distal point of the bone. The Ciconiidae and Gruidae show the distal end of the radius not flat in distal view, as in the Mulhuli-Amo specimen. This character is unique of Otididae among the large birds and the huge size of the Mulhuli-Amo specimen constricts the attribution to either *Neotis* or *Ardeotis*, the two largest taxa of the Family. The presence of a rounded insertion ligament on the medial side of the distal end in ventral view and the pointed end of the facies articularis radiocarpalis allow to attribute the bone to *Ardeotis*, in particular to *Ardeotis kori*, which is clearly larger than *Ardeotis arabs* (Linnaeus, 1758), the other species of the genus living in Africa.

Class MAMMALIA Linnaeus, 1758
Order PROBOSCIDEA Illiger, 1811
Family ELEPHANTIDAE Gray, 1821

Genus *Palaeoloxodon* Matsumoto, 1924

Palaeoloxodon cf. *P. recki* Dietrich, 1915
(Figs 7a, 8; Tab. 1)

Material - MA 184A/B: damaged cranium; MA 476: partial cranium; MA 503, MA 724, MA 784, MA 901: tooth fragments; MA 137, MA 908: tusk fragments; MA 514: thoracic vertebra; MA 802: intermediate phalanx of digit II.

Description - The crania, one almost complete (MA 184A/B) and the other with just the splanchnocranium preserved (MA 476), of two large individuals have been identified on the surface of the Mulhuli-Amo site. They are largely damaged and weathered. MA 184 lacks all teeth, except for one heavily fragmented molar. Various fragments of molar lamellae have been recovered all along the site as well as tusk fragments of both juvenile (MA 908) and adult individuals (MA 137). The dentine of the lamellae is uniformly black, while the enamel tends to be ivory white, with darker web-like stripes. The centrum of the thoracic vertebra (probably T-16/17) is quite compressed anteroposteriorly and possesses a well-developed spinal process.

Remarks - *Palaeoloxodon* is one of the most represented taxa in the Mulhuli-Amo site. Due the high

MA 514 - Thoracic vertebra	
Centrum anterior height	87.1
Centrum anterior width	122.9
Spine height	128.4
Foramen height	55.9
Foramen width	92.2
MA 802 - Intermediate phalanx of digit II	
Length	47.4
Proximal width	49.2
Distal width	36.0

Tab. 1 - Measurements (in mm) of Mulhuli-Amo *Palaeoloxodon* cf. *P. recki* specimens.

degree of fragmentation of the specimens and the absence of complete dental material, an attribution to the species level is difficult. However, the size of MA 802 and MA 514, combined with the morphology of the posteriorly inclined neural spine, excludes the attribution of the specimens to *Palaeoloxodon antiquus* Falconer & Cautley, 1847, one of the largest elephants to have ever lived, and



Fig. 7 - (color online) Mammals from Mulhuli-Amo. a) *Palaeoloxodon* cf. *P. recki* Dietrich, 1915, MA 514, thoracic vertebra (T-16/17) in anterior view. Scale bar equals 20 mm. b) *Equus* cf. *E. quagga* Boddaert, 1785, MA 800, left mandibular fragment with p2-p3 in occlusal (b1), lingual (b2), and labial (b3) views. Scale bar corresponds to 10 mm.



Fig. 8 - (color online) *Palaeoloxodon* cf. *P. recki* Dietrich, 1915 fragmentary cranium MA 184A/B on the surface of the Mulhuli-Amo site.

accounts for a generally smaller species. Moreover, the dimension of the MA 184 molar alveolus is compatible with *P. recki* found in the Dandiero Basin (Ferretti et al., 2003; Martínez-Navarro et al., 2004). *Palaeoloxodon recki* is a very common and well-known species of the Plio-Pleistocene record of East Africa and has been recorded in Kenya, Tanzania, Ethiopia, Chad, Uganda (Maglio, 1973; Beden, 1987; Kalb & Mebrate, 1993; Todd, 1997), and Djibouti (Chavaillon et al., 1990).

Order PERISSODACTYLA Owen, 1848
Family RHINOCEROTIDAE Gray, 1821

Genus *Ceratotherium* Gray, 1868

Ceratotherium simum (Burchell, 1817)
(not figured)

Material - MA 182: cranium.

Description - An almost complete cranium belonging to a Rhinocerotidae has been identified on the surface of the Mulhuli-Amo site. It lacks only the most rostral portion and preserves both tooth rows. It is sparsely covered by a thick layer of coarse sand, a condition that is commonly found in many of Mulhuli-Amo specimens. The recovery of the specimen has not yet been possible due to technical issues, thus precluding the preparation of the cranium for detailed analysis.

Remarks - The preliminary analysis of MA 182 shows that the general morphology of the cranium closely resembles the one of DAN 150 from Dioli. The cranium is markedly dolichocranial, with a prominent occipital crest that protrudes posteriorly. The size of the specimens fits that of *Ceratotherium simum*, the only species of white rhino that inhabited Africa after 3 Ma. Even if further analysis and restoration of the specimen are needed, on the basis of the resemblance of the Mulhuli-Amo specimen with the correlable Dioli sample, we are confident in the attribution of MA 182 to *C. simum*.

Family EQUIDAE Gray, 1821

Genus *Equus* Linnaeus, 1758

Equus cf. *E. quagga* Boddaert, 1785
(Fig. 7b; Tab. 2)

Material - MA 800: left mandibular fragment with p2-p3.

Description - The left hemimandible is highly fragmented and lacks the majority of the corpus. The hypsodont lower premolars have a pronounced rectangular shape, with the p2 very elongated mesiodistally and missing its mesial portion. Both teeth are immersed in cement, partially detached especially on the lingual wall. The shallow ectoflexid reaches a tight isthmus, but does not pass through it. The linguaflexid is shallow and rounded and the caballine fold is scarcely marked. The protoconid, hypoconid, and entoconid are well developed, forming a narrow and sinuous preflexid and postflexid. The metaconid and metastylid are small, tear-shaped.

Remarks - The two premolar preserved in the mandibular fragment show a stenonine morphology, with shallow ectoflexid and linguaflexid (Eisenmann & De Giuli, 1974; Eisenmann et al., 1988). The large species of zebra *Equus grevyi* Oustalet, 1882, also known as imperial zebra, is reported from the Uadi Aalad and shares a general zebrine morphology with MA 800. However, the individual from Mulhuli-Amo presents some differences if compared with *E. grevyi*. In particular, the caballine fold and the linguaflexid are consistently less developed. In addition, the inner cristid of the hypoconid has a simpler, less crenulated shape and overall the conids are more rounded than the ones of the imperial zebra. The latter condition, instead, is commonly found in Burchell's zebra *Equus quagga*. That is a slightly smaller zebrine species, very common throughout central and southern Africa, while it is extinct in East Africa at present. Metrically, MA 800 falls into the upper part of the dimensional range of *E. quagga*, *E. grevyi*, and the large-sized European *Equus stenonis* Cocchi, 1867 (Tab. 2).

Order ARTIODACTYLA Owen, 1848
Suborder SUINA Gray, 1821
Family HIPPOPOTAMIDAE Gray, 1821

Genus *Hippopotamus* Linnaeus, 1758

Hippopotamus gorgops Dietrich, 1926
(Fig. 9a-b; Tab. 3)

Material - MA 138: right mandibular fragment with m3 (Fig. 9a); MA 142: left P3; MA 155: left M3; MA 170: left maxillary fragment with M1-M2; MA 937: right maxillary fragment with M1-M3 (Fig. 9b); MA 938: left p4 and m1; MA 941: left p4; MA 409: lower canine; MA 496-7: two lower canines; MA 492, MA 494, MA 530, MA 593, MA 626, MA 759, MA 856, MA 940, MA 946: molar fragments.

	p2		p3	
	L	W	L	W
MA 800	37.1*	15.1*	29.0	16.4
<i>Equus grevyi</i>	33.6 (27.5 – 36.0)	15.4 (14.0 – 17.5)	29.2 (25.5 – 32.0)	16.4 (14.2 – 18.5)
<i>Equus burchelli</i>	28.3 (25.0 – 30.3)	13.3 (10.9 – 15.5)	24.4 (20.1 – 28.0)	14.4 (12.3 – 17.0)
<i>Equus quagga</i>	30.6 (28.0 – 33.0)	14.3 (12.0 – 16.5)	25.9 (23.0 – 30.0)	15.4 (14.0 – 17.5)
<i>Equus zebra</i>	29.5 (26.0 – 33.0)	14.3 (11.0 – 16.0)	25.8 (23.0 – 29.0)	15.5 (14.0 – 18.0)
<i>Equus africanus</i>	29.0 (25.3 – 31.0)	13.9 (11.1 – 16.0)	25.7 (24.5 – 27.5)	15.5 (12.0 – 17.2)
<i>Equus asinus</i>	25.3 (21.0 – 27.5)	12.5 (11.5 – 13.5)	23.3 (20.0 – 26.5)	14.4 (13.0 – 16.0)
<i>Equus hemionus</i>	29.1 (26.0 – 33.5)	14.1 (12.0 – 17.0)	25.5 (22.0 – 31.0)	15.7 (13.5 – 19.0)
<i>Equus kiang</i>	30.4 (27.5 – 34.0)	14.2 (13.5 – 15.5)	26.7 (24.5 – 29.0)	15.8 (13.9 – 18.0)
<i>Equus przewalskii</i>	32.6 (28.0 – 35.0)	15.0 (14.0 – 16.0)	28.5 (25.0 – 32.0)	17.1 (15.0 – 20.0)
<i>Equus caballus</i>	33.2 (27.3 – 39.0)	15.3 (12.5 – 17.5)	27.8 (22.0 – 33.0)	16.7 (13.5 – 20.0)
<i>Equus stenonis vireti</i>	36.7 (33.0 – 39.5)	15.9 (14.3 – 17.0)	31.6 (27.4 – 34.0)	17.3 (15.0 – 18.5)
<i>Equus stenonis cf. vireti</i>	37.0 (33.9 – 38.0)	15.8 (14.0 – 16.6)	30.9 (25.0 – 36.0)	16.9 (15.5 – 18.1)
<i>Equus stenonis senezensis</i>	33.6 (30.4 – 38.0)	14.8 (13.0 – 16.0)	29.3 (26.0 – 33.0)	15.9 (13.5 – 17.0)
<i>Equus mosbachensis</i>	37.4 (34.0 – 39.0)	16.5 (15.5 – 17.5)	32.4 (29.5 – 36.0)	17.9 (16.0 – 20.5)
<i>Equus tabeti</i>	31.1 (27.0 – 35.0)	14.0 (12.0 – 16.5)	27.2 (24.0 – 30.5)	14.9 (12.0 – 17.0)
<i>Equus mauritanicus</i>	34.1 (30.0 – 36.2)	15.4 (14.2 – 16.4)	30.4 (27.5 – 34.0)	16.8 (14.2 – 18.6)
<i>Equus sp. (Turkana)</i>	33.4 (32.0 – 35.7)	15.1 (14.0 – 16.0)	28.6 (26.0 – 33.5)	16.2 (14.0 – 18.5)
<i>Equus numidicus</i>	37.0*	16.0*	31.0	17.7

Tab. 2 - Measurements (in mm) of Mulhuli-Amo *Equus cf. E. quagga* specimen and of the comparative material used in the study. *, alveolar measurements; L, length; W, width; minimum and maximum values in parenthesis (Eisenmann, 1981).

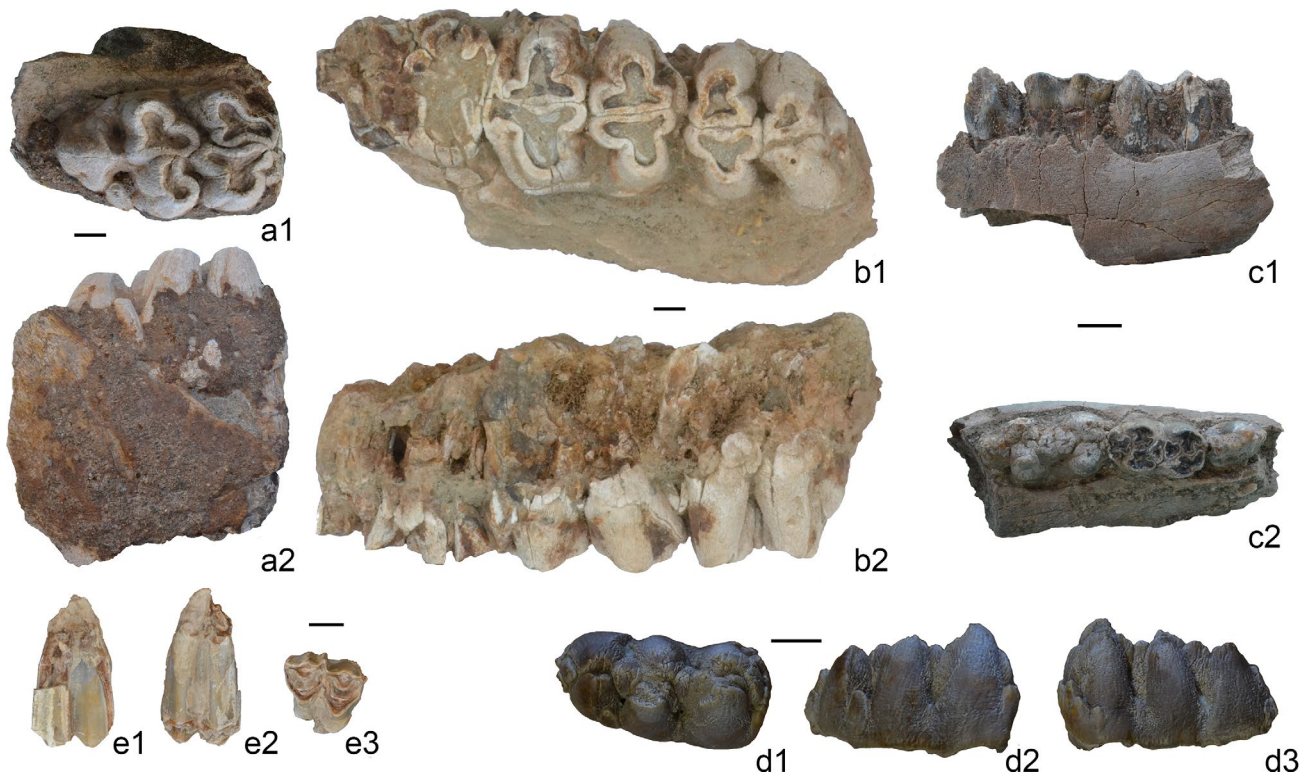


Fig. 9 - (color online) Artiodactyls from Mulhuli-Amo. a) *Hippopotamus gorgops* Dietrich, 1926, MA 138, right mandibular fragment with m3 in occlusal (a1) and labial (a2) views. b) *Hippopotamus gorgops*, MA 973, left upper jaw fragment with M1-M3 in occlusal (b1) and labial (b2) views. c) *Kolpochoerus majus* (Hopwood, 1934), MA 158, left mandibular fragment of a sub-adult individual with p3, dp4, and m1, in lingual (c1) and occlusal (c2) views. d) *Kolpochoerus majus*, MA 943, unerupted left m3 in occlusal (d1), lingual (d2), and labial (d3) views. e) *Kobus cf. K. ellipsiprymnus* (Ogilby, 1833), MA 916, right M2 in labial (e1), lingual (e2), and occlusal (e3) views. Scale bars equal 10 mm.

	p4		m1		m3		P3		M1		M2		M3	
	L	W	L	WML	L	WML	L	W	L	WML	L	WML	L	WML
MA 138					70.8	39.9								
MA 142							34.9	26.1						
MA 155													62.3	48.2
MA 170									42.7	34.0	50.9	45.7		
MA 937									52.3		60.5	50.4	51.8	47.3
MA 938	24.1		56.0	46.7										
MA 941	30.1	39.2												

Tab. 3 - Measurements (in mm) of Mulhuli-Amo *Hippopotamus gorgops* teeth. L, length; W, width; WML, width of mesial lobe.

Description - The teeth are hypsodont, robust, with thick and corrugated enamel. The canines are labiolingually flattened and extremely elongated, especially the lower ones. The incisors have a cylindrical shape, slightly bending distally. A single unicuspid upper third premolar has been found to date (MA 142). It has a subtriangular occlusal shape and shows well-defined mesial and distal cingula. The tetracuspid upper molars possess strong and large cingula on both the mesial and the distal margins. The upper cheek teeth tend to increase in size from M1 to M3, although the M2 is almost of the same size as the M3. Only one complete p4 (MA 941) has been recovered (being MA 938 fragmentary). It is unicuspid, with a flat occlusal surface, and it possesses a developed distal cingulid. The lower molars share the same overall morphology with the upper ones, but are more compressed labio-lingually and have less-developed cingulids. In addition, the m3 shows a large and robust talonid.

Remarks - The dental material from Mulhuli-Amo can be referred to a large form of *Hippopotamus*. When compared with the material of *Hippopotamus gorgops* from Koobi Fora, West Turkana (Harris, 1991a), and the Dandiero Basin (Martínez-Navarro et al., 2004), as well as with *Hippopotamus behemoth* Faure, 1986 from ‘Ubeidiya (Faure, 1986), and mean values of extant *Hippopotamus amphibius* Linnaeus, 1758 (Fig. 10), the studied sample shows a peculiar distribution, probably due to paucity of the available specimens. In the lower dentition, the Mulhuli-Amo p4 does not group with that of the other species, being wider than long. The m1 of MA 938 falls in the upper part of the distribution of *H. gorgops*, closer to specimens collected from the Dandiero Basin, albeit MA 938 appears to have a more squared occlusal shape. The m3 is slightly larger than that of the analysed specimens of extant *H. amphibius*. Taking into account the upper cheek teeth, even if the number of the studied specimens

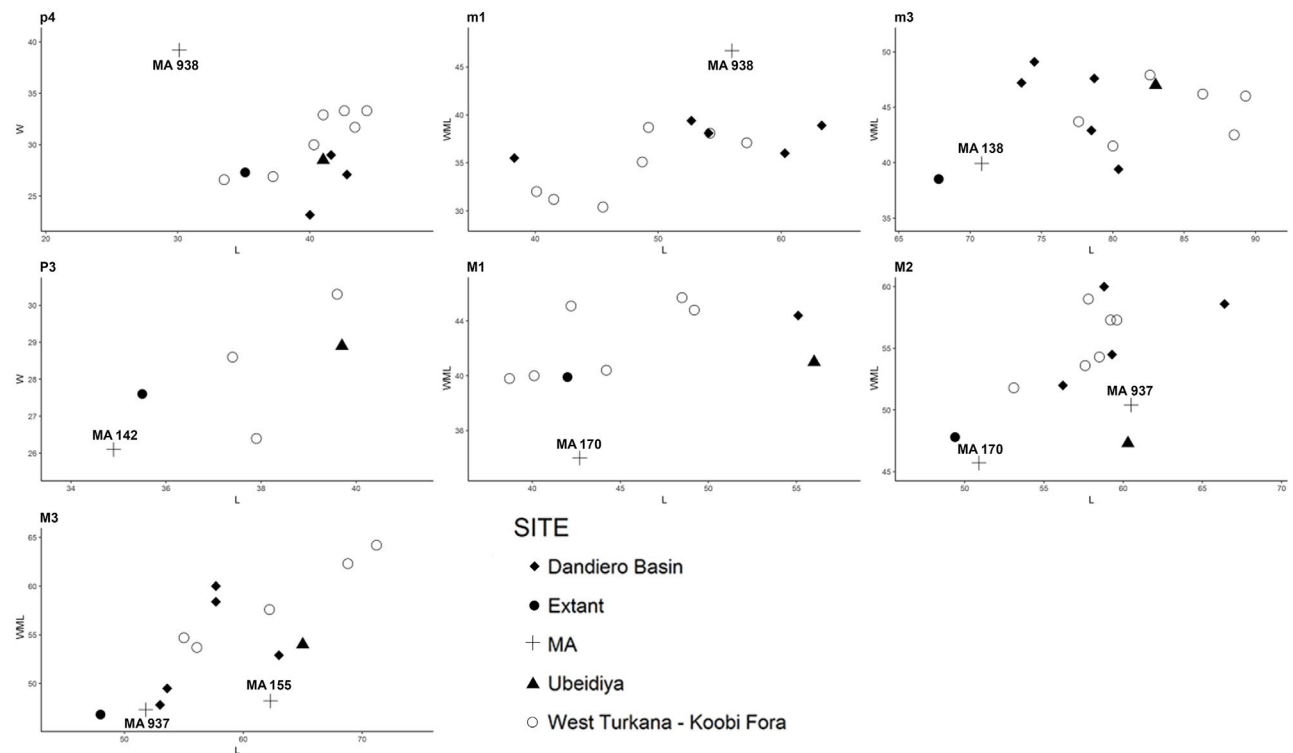


Fig. 10 - Scatter plot of *Hippopotamus* spp. dental remains: *Hippopotamus gorgops* (Mulhuli-Amo, Dandiero; West Turkana - Koobi Fora); *Hippopotamus behemoth* from ‘Ubeidiya; extant *H. amphibius*. L, length; W, width; WML, mesial lobe width.

	p3		dp4		m1		m2		m3	
	L	W	L	W	L	W	L	W	L	W
MA 158	13.1	9.1	22.7	12.3	26.9	15.7				
MA 943									40.5	22.3
MA 958						27.3	30.5	20.1		

Tab. 4 - Measurements (in mm) of Mulhuli-Amo *Kolpochoerus majus* teeth. L, length; W, width.

is reduced, we can identify two different size groups. Three specimens (MA 142, MA 155, and MA 170) belong to clearly smaller individuals than the rest of the sample. In particular, the P3 MA 142 and the M1-M2 MA 170 are particularly labiolingually narrow and even smaller in size than the mean values of *H. amphibius*. The other two individuals, considering both lower (MA 138) and upper (MA 937) dental elements, fall within the range of fossil *Hippopotamus* found in the other localities. The dental morphology and the measurements support attributing the Mulhuli-Amo sample to the species *H. gorgops*.

Family SUIDAE Gray, 1821

Genus *Kolpochoerus* Van Hoepen & Van Hoepen, 1932

Kolpochoerus majus (Hopwood, 1934)
(Fig. 9c-d; Tab. 4)

Material - MA 158: left mandibular fragment with p3, dp4, and m1 (Fig. 9c); MA 958: right mandibular fragment with m1 (broken) and m2; MA 943: unworn left m3 (Fig. 9d).

Description - The p3 is labio-lingually compressed, possesses a strong and sharp median cuspid flanked by two deep lingual grooves. The dp4 is heavily worn, with the cuspids almost completely abraded exposing the dentine. It has a complex conid structure with folded metaconid, protoconid, hypoconid, and entoconid. The m1 exhibits an elaborate occlusal surface. The four principal conids, the two lingual higher than the labial, are distributed on the corners of a generally rectangular shape and show heavily-folded enamel. Two median cuspids emerge within the principal ones, reaching almost half their height. The pentaconid is poorly developed, rugose, aligned with the accessory cuspids. The cingulids are in general scarcely marked. MA 148 and MA 958 share the same lower molar morphology, with the latter being considerably larger.

The unworn lower third molar MA 943 is a stout tooth with developed mesial cingulid. The stylids are low and scarcely marked. A single and simple rounded pillar (the hypopreconulid) marks the trigonid/talonid junction. A pair of strong pillars (hypoconid and entoconid) build-up the talonid, which terminates distally with a couple of smaller pillars (pentaconid and hexaconid), and a small terminal cuspid.

Remarks - The fragmented left mandibular ramus is attributable to the genus *Kolpochoerus*, a medium- to large-sized suid, closely related with the extant forest hog *Hylochoerus* Thomas, 1904 (Pickford & Obada, 2016).

At least five species, *Kolpochoerus limnetes* (Hopwood, 1926), *Kolpochoerus majus*, *Kolpochoerus olduvaiensis* (Leakey, 1942), *Kolpochoerus paiceae* (Broom, 1931), *Kolpochoerus phillipi* Souron et al., 2015, are recorded in the African early Pleistocene (Harris & White, 1979; Alemseged & Geraads, 2000; Suwa et al., 2003; Geraads et al., 2004; Haile-Selassie & Simpson, 2013; Medin et al., 2015; Souron et al., 2015). *Kolpochoerus olduvaiensis* is an advanced form of *K. limnetes*, with increased length of the third lower molars. *Kolpochoerus majus* retains instead a more primitive molar morphology (Haile-Selassie & Simpson, 2013). Both *K. majus* and *K. olduvaiensis* have cheek teeth with thick enamel, heavily folded in the former species, combined with accessory pillars that expand the occlusal surface. The simple morphology of the p3 of MA 158 closely resembles the one found in the *K. majus* material recovered from Konso (Suwa et al., 2014). The m3 MA 943 possesses a relatively low crown height, a generally simple morphology, and very thick enamel. These morphologies overall allow to ground the identification of the Mulhuli-Amo sample to the species *Kolpochoerus majus*.

Family BOVIDAE Gray, 1821 Subfamily BOVINAE Gray, 1821 Tribe BOVINI Gray, 1821

Genus *Bos* Linnaeus, 1758

Bos cf. *B. buiaensis* Martínez-Navarro et al., 2010
(Fig. 11)



Fig. 11 - (color online) Occipital portion of the cranium and horn cores of *Bos* cf. *B. buiaensis* Martínez-Navarro et al., 2010 MA 179A/D on the surface of the Mulhuli-Amo site.

Material - MA 179A/D: fragmentary cranium with horns.

Description - A partial cranium (MA 179A/D) preserving part of the neurocranium, the occipital and frontal regions, and both horn-cores was discovered on the surface of the Mulhuli-Amo palaeoanthropological site. The fossil is heavily weathered and its safe retrieval has not been possible yet. From a preliminary analysis, the cranium presents a very robust structure, with pneumatized frontals that cover part of the parietals and of the nuchal area. The horn-cores, which have an external arch of approximately 1 m each, protrude slightly backwards with tips that bend upwards at almost half of their length. The cross-section is moderately dorsoventrally compressed.

Remarks - MA 179A/D belongs to a large buffalo-like bovine. The lack of dental remains and the poor preservation preclude conclusive and reliable species attribution. However, the anatomy of the protruding parietals, the insertion of the horn-cores on the cranium, and their general morphology and size show strong similarity with the type material of *B. buiaensis* depicted by Martínez-Navarro et al. (2010) and recovered from the Dandiero Basin.

Family BOVIDAE Gray, 1821
Subfamily REDUNCINAE Lydekker & Blaine, 1914
Tribe REDUNCINI Lydekker & Blaine, 1914

Genus *Kobus* Smith, 1840

Kobus cf. *K. ellipsiprymnus* (Ogilby, 1833)
(Fig. 9e; Tab. 5)

Material - MA 916: right M2.

Description - MA 916 is an isolated M2. The tooth is hypsodont with general trapezoid occlusal shape. The cement is abundant in both labial and lingual sides, surrounding the tooth. The labial styles, especially the mesostyle, are strong. The entostyle (Bärmann & Rössner, 2011) is well developed, reaching half the height of the entire crown. The fossae are simple, with no folds. The lower part of the distolabial wall and the roots are missing.

Remarks - The general morphology of the tooth is very similar to those of the extant waterbuck *K. ellipsiprymnus*, a large-sized hypsodont antelope that lives in grasslands close to fresh water. The species is commonly found in the Pleistocene fossil record of East Africa (Gentry & Gentry, 1978; Harris, 1991b) and in the Dandiero Basin

	m2		
	L	WML	WDL
MA 916	24.7	20.9	18.8

Tab. 5 - Measurements (in mm) of Mulhuli-Amo *Kobus* cf. *K. ellipsiprymnus* specimen. L, length; WML, width of mesial lobe; WDL, width of distal lobe.

(Martínez-Navarro et al., 2004). MA 916 dimensionally and morphologically is overall well comparable with *K. ellipsiprymnus* described by Harris (1991b).

DISCUSSION AND CONCLUSIONS

The vertebrate assemblage of Mulhuli-Amo includes 14 taxa, two fishes (*Clarias* [*Clarias*] sp., ?Cichlidae indet.), four reptiles (*Crocodylus* sp., *Pelusios sinuatus*, *Varanus niloticus*, *Python* gr. *P. sebae*), one bird (*Ardeotis kori*), and seven mammals (*Palaeoloxodon* cf. *P. recki*, *Ceratotherium simum*, *Equus* cf. *E. quagga*, *Hippopotamus gorgops*, *Kolpochoerus majus*, *Bos* cf. *B. buiaensis*, *Kobus* cf. *K. ellipsiprymnus*). The reported occurrence of *Pelorovis* preliminary listed by Zanolli et al. (2014) is here corrected referring the material to *Bos* cf. *B. buiaensis* (following Martínez-Navarro et al., 2010).

With the exception of few taxa (fish, turtle, and bird in particular) most of the vertebrates are of relatively large size. Fish remains are relatively uncommon in the deposits of the Mulhuli-Amo section and certainly represent a small portion of the original fauna that inhabited this part of the Dandiero fluvial system during the early Pleistocene. The evident dominance of the thick and resistant *Clarias* bones appears to be related to a sedimentary selection that occurred during the deposition of the fossiliferous sediments. Both the recognised fish taxa are consistent with riverine palaeobiotopes revealed by the sedimentological analysis. Catfishes of the family Clariidae inhabit a variety of freshwater environments in tropical Africa (Teugels & Adriaens, 2003), where they can easily tolerate poorly oxygenated waters. In general, these fishes primarily occupy the well-oxygenated shallow waters of rivers and lakes where they feed on a number of prey items. Cichlids usually prefer to live inshore in the shallow waters of rivers and lakes.

The absence of amphibians, as for Uadi Aalad, is likely due to taphonomic reasons, but is nevertheless not surprising due to the fact that they have been rarely reported and fully studied for other Plio-Pleistocene palaeoanthropological sites of East Africa (Isaac, 1978; Brugal & Denys, 1989; Woldegabriel et al., 2009; Delfino, 2017).

The mammals from Mulhuli-Amo form a typical late early Pleistocene East African assemblage, characterised by *Palaeoloxodon* cf. *P. recki*, *Equus* cf. *E. quagga*, *Hippopotamus gorgops*, *Kolpochoerus majus*, and *Bos* cf. *B. buiaensis*, associated to forms that persist until present like *Ceratotherium simum* and *Kobus ellipsiprymnus*.

As already concluded for Uadi Aalad on the basis of sedimentology and palaeontology (Ghinassi et al., 2009; Rook et al., 2013; Medin et al., 2015), both lines of evidence agree in suggesting that the palaeoenvironment of Mulhuli-Amo was characterised by moist grassed habitats adjacent to persistent water. The bird *Ardeotis kori*, represented by a single remain, could also indicate the local or distant presence of well-developed savannah with stable grass and scattered trees (Hoyo et al., 1996).

Because of the congruence of all the palaeoenvironmental proxies of both Uadi Aalad and Mulhuli-Amo, it is possible to propose that a large portion of the Buia area was characterized by the same environment when it was inhabited by hominins during the early Pleistocene, about 1 Ma ago.

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