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The late Early Pleistocene human dental remains from Uadi Aalad and Mulhuli-Amo (Buia), Eritrean Danakil: Macromorphology and microstructure

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ABSTRACT

Fieldwork performed during the last 15 years in various Early Pleistocene East African sites has significantly enlarged the fossil record of *Homo erectus* sensu lato (s.l.). Additional evidence comes from the Danakil Depression of Eritrea, where over 200 late Early to early Middle Pleistocene sites have been identified within a ~1000 m-thick sedimentary succession outcropping in the Dandiero Rift Basin, near Buia. Along with an adult cranium (UA 31), which displays a blend of *H. erectus*-like and derived morpho-architectural features and three pelvic remains, two isolated permanent incisors (UA 222 and UA 369) have also been recovered from the 1 Ma (millions of years ago) *Homo*-bearing outcrop of Uadi Aalad. Since 2010, our surveys have expanded to the nearby (4.7 km) site of Mulhuli-Amo (MA). This is a fossiliferous area that has been preliminarily surveyed because of its exceptional concentration of Acheulean stone tools. So far, the site has yielded 10 human remains, including the unworn crown of a lower permanent molar (MA 93). Using diverse analytical tools (including high resolution μCT and μMRI), we analysed the external and internal macromorphology and microstructure of the three specimens, and whenever possible compared the results with similar evidence from early *Homo*, *H. erectus* s.l., *H. antecessor*, *H. heidelbergensis* (from North Africa), Neanderthals and modern humans. We also assessed the UA 369 lower incisor from Uadi Aalad for root completion timing and showed that it compares well with data for root apex closure in modern human populations.

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Introduction

Geological, paleontological and paleoanthropological field research has been carried out in the Dandiero Rift Basin, northern Danakil Depression of Eritrea since 1994. This research has led to

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the discovery of over 200 late Early to early Middle Pleistocene sites with widespread evidence of vertebrate faunal remains and lithic artefacts within the nearly 1000 m-thick fluvio-deltaic-lacustrine sedimentary succession outcropping 100 km south of Massawa (Abbate et al., 1998, 2004; Ghinassi et al., 2009; review in; Rook et al., 2012). Thus far, in an area covering about 40 km^2, cranial, dental and postcranial human remains have been discovered in two localities near the Buia village: Uadi (Wadi) Aalad and Mulhuli-Amo (Coppa et al., 2012).

The continental basin fill (the so-called Maebele Synthem) consists, from bottom to top, of six lithostratigraphic units: fluvial Bukra sand and gravel, fluvio-deltaic Alat Formation, fluvial Wara sand and gravel, lacustrine Goreya Formation; fluvio-deltaic Aro sand; and alluvial fan Addai fanglomerate (Abbate et al., 2004; Papini et al., 2014). The *Homo*-bearing deposits belong to the upper part of the 70–100 m-thick fluvio-deltaic Alat Formation (Ghinassi et al., 2009).

The upper part of the Alat Formation hosts the top of the Jaramillo subchron (0.99 Ma), which occurs about 10 m below the transition to the overlying Wara sand and gravel. The Matuyama-Brunhes boundary (0.78 Ma) is located about 5 m above the base of the Aro sand unit (Albianelli and Napoleone, 2004). Confirmation of the magnetostratigraphically-based chronological setting comes from fission track dating (Bigazzi et al., 2004) and mammal biochronology (Ferretti et al., 2003; Martínez-Navarro et al., 2004, 2010; Rook et al., 2010, 2012).

All human remains discovered so far occur in the upper part of the Alat Formation, where the transition from a deltaic to alluvial setting is characterized by high frequency, potentially millennial-scale, lake-level oscillations (units DL5, FL2a and FL2b in Ghinassi et al., 2009). Specifically, the concentration of fossil bones at the base of the FL2b was associated with an increase in fluvial discharge that caused winnowing of the immediately underlying fossil-bearing fluvio-deltaic deposits. As a whole, both the sedimentary record documenting the evolution of fluvio-deltaic and lacustrine systems (Ghinassi et al., 2009; Rook et al., 2012), and the vertebrate faunal assemblages predominated by taxa known for their water dependence (Delfino et al., 2004; Martínez-Navarro et al., 2004), clearly indicate a relatively open paleoenvironmental scenario characterized by the presence of moist grassed habitats adjacent to persistent water (Rook et al., 2012).

First identified in the Uadi Aalad (UA) site, the 5–6 m-thick *Homo*-bearing layer produced a virtually complete adult cranium preserving the face (UA 31), two permanent incisors (UA 222 and UA 369), and three pelvic portions (UA 173, UA 405, UA 466) (Abbate et al., 1998; Macchiarelli et al., 2004a; Bondioli et al., 2006). Compared with the Indonesian and Chinese *Homo erectus* sensu stricto (s.s.) sample (review in Antón, 2003), as well as with African specimens such as OH 9 and, to a lesser extent, KNM-ER 3733 (Baab, 2008; Rightmire, 2013) and to the chronogeographically close calvaria from Daka, Middle Awash (Gilbert and Asfaw, 2008), UA 31 displays a blend of *H. erectus/ergaster*-like and derived morpho-architectural features more commonly found in Middle Pleistocene specimens. These features include a high positioning of the maximum parietal breadth, weak parietal keeling along the midline, slight parasagittal flattening, and from sub-vertical to slightly downwards converging parietal walls, documenting extensive variation in late Early Pleistocene East African *Homo* (Macchiarelli et al., 2004a).

Since 2010, the systematic survey of a fossiliferous area near to the exceptionally preserved A006 site (the so-called 'handaxes esplanade') previously reported for its extensive concentration of Oldowan and Acheulean lithic tools (Martini et al., 2004), has led to the discovery of new fossil human remains at the Mulhuli-Amo (MA) locality, 4.7 km south of the UA *Homo* site (Coppa et al., 2012, 2014).

The nearly 15 m-thick sedimentary succession of Mulhuli-Amo consists of deltaic and fluvial sediments. The lower interval (ca. 5 m) consists of a sandy Gilbert-type delta deposit. The middle interval (5 m) is made of pedogenized muddy deposits with isolated sandy fluvial channels responsible for the transport and accumulation of bone remains and stone tools in their basal parts. Finally, the 5 m-thick upper interval of the succession consists of fluvial channelized gravelly sand capped with pedogenized mud. Even if most fossil remains from this site are spread on the eroded surface, most of the bones and Acheulean artefacts occur in situ at the base of the third interval.

The human fossil-bearing levels of Uadi Aalad and Mulhuli-Amo are remarkably similar in sedimentary facies and depositional history (cf. Ghinassi et al., 2009; Rook et al., 2012), and are considered to sample the same stratigraphic horizon belonging to the Alat. Besides the presence of reptile remains including crocodiles (*Crocodylus niloticus*), turtles (*Pelusios sinuatus*), and monitor lizards (*Varanus niloticus*), the vertebrate assemblage at Mulhuli-Amo consists of the same mammal taxa represented at Uadi Aalad (i.e., *Elephas*, *Hippopotamus*, *Kolpochoerus*, *Kobus*, *Pelorovis*).

A total of 10 cranial and dental human remains, likely from two adults and one immature individual, have been collected so far at Mulhuli-Amo. They consist of an isolated frontal fragment bearing a thick right torus (MA 14) and eight parietal fragments (MA 64 and MA 88a–f) associated with a temporal bone fragment (MA 89), all from a single adult cranium showing structural (thickness distribution) and architectural features (proportions, curvature) closely fitting the morphology represented by UA 31. Finally, the assemblage includes an isolated permanent lower molar crown (MA 93) (Coppa et al., 2014).

Compared with the Southeast Asian and Indonesian hypodigm (Indriati, 2004; Kaifu et al., 2005), the human dental assemblage from chronologically well-constrained Early Pleistocene African sites (e.g., McDougall et al., 2012) is qualitatively and quantitatively relatively rich until about 1.4 Ma (millions of years ago) (cf. Wood, 1991), while evidence from the later Early Pleistocene is scanty (Schwartz and Tattersall, 2003; Suwa et al., 2007; Brink et al., 2012). The material we examine here thus enlarges this sample and contributes to partially fill the gap still existing between the dental records available so far for African *H. erectus* sensu lato (s.l.) on one hand, and *Homo heidelbergensis* on the other hand.

Building on the announcement (Abbate et al., 1998) and preliminary general description of the two incisors from Uadi Aalad, collected in 1995 and 1997, respectively (Macchiarelli et al., 2004a), and the molar crown from Mulhuli Amo, collected in 2011, here we provide details of their external and internal morphology. More specifically, we compare the structure of the three Eritrean specimens sampling *H. erectus/ergaster* with some earlier and later human taxa, particularly with the evidence from the early Middle Pleistocene North African sample of Tighenif, using a variety of investigative approaches and analytical tools granting high resolution access to their microstructure (Zanolli and Mazurier, 2013). In doing so, we reveal for the first time the primitive versus derived nature of some tooth structural features in African *H. erectus* s.l. near the end of the Early Pleistocene and investigate their evolutionary polarity at a macroregional scale.

Materials and methods

The three fossil teeth from the Buia area represent an upper left lateral permanent incisor (UA 222) and a lower left central permanent incisor (UA 369) from the *Homo* site of Uadi Aalad (Abbate et al., 1998; Macchiarelli et al., 2004a), and a lower left M1/M2 crown (MA 93) from Mulhuli-Amo (Coppa et al., 2012, 2014; Zanolli et al., 2013). The incisors preserve the crown and root, while the

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