

**Structural Organization and Tooth Development in a *Homo aff. erectus* Juvenile Mandible from the Early Pleistocene Site of Garba IV at Melka Kunture, Ethiopian Highlands**

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## ABSTRACT

**Objectives:** The immature partial mandible GAR IVE from the c. 1.7 Ma old Garba IV site at Melka Kunture (Upper Awash Basin, Ethiopia), the earliest human representative from a mountain-like environment, represents one of the oldest early *Homo* specimens bearing a mixed dentition. Following its first description (Condemi, 2004), we extended the analytical and comparative record of this specimen by providing unreported details about its inner morphology, tooth maturational pattern and age at death, crown size and tooth tissue proportions.

**Materials and Methods:** The new body of quantitative structural information and virtual imaging derives from a medical CT record performed in 2013.

**Results:** Compared to the extant human condition and to some fossil representatives of comparable individual age, the GAR IVE mandible reveals absolutely and relatively thick cortical bone. Crown size of the permanent lateral incisor and the canine fit the estimates of *H. erectus s.l.*, while the dm2 and the M1 more closely approach those of *H. habilis-rudolfensis*. Molar crown pulp volumes are lower than reported in other fossil specimens and in extant humans. The mineralization sequence of the permanent tooth elements is represented four times in our reference sample of extant immature individuals (N=795).

**Conclusions:** The tooth developmental pattern displayed by the immature individual from Garba IV falls within the range of variation of extant human populations and is also comparable with that of other very young early fossil hominins. Taken together, the evidence presented here for mandibular morphology and dental development suggest GAR IVE is a robust 2.5-3.5 year old early *Homo* specimen.

Melka Kunture is a complex of archaeological and paleontological sites of the Ethiopian highlands (c. 2000 m asl) extending along the Upper Awash Valley on the western shoulder of the Rift Valley, 50 km south of Addis Ababa (Chavaillon and Piperno, 2004a). Following its first identification in 1963, within the development of a UN water program, preliminary archaeological survey was undertaken one year later by G. Bailloud (Bailloud, 1965). From 1965 to 1998 the activity of the French Archaeological Mission was directed by J. Chavaillon (Chavaillon et al., 1979; Chavaillon and Piperno, 2004b). Since 1999, research in the area has been carried on by the Italian Archaeological Mission at Melka Kunture and Balchit (Chavaillon and Piperno, 2004b; Mussi et al., 2014; <http://www.melkakunture.it/>).

The sites at Melka Kunture (Atebella, Garba, Gombore, Gotu, Karre, Kella, Simbiro, Tcheri-Arussi, Tuka, Weraba, Wofi) are named after the gullies shaped by the nearby seasonal tributaries of the Awash River (Chavaillon and Berthelet, 2004; Gallotti, 2013: fig. 1). Their fluvial-lacustrine and volcanic deposits accumulated and eroded during most of the Pleistocene in a semi-graben depression of c. 3000 km<sup>2</sup> whose southwestern edge is the Melka fault (Taieb, 1967; Kieffer et al., 2002, 2004; Bardin et al., 2004; Chavaillon and Piperno, 2004a; Raynal and Kieffer, 2004; Raynal et al., 2004; Piperno et al., 2009; Morgan et al., 2012; Gallotti et al., 2014; Tamrat et al., 2014).

Relative and absolute chronological assessment of the alluvial and tuffaceous deposits outcropping in the nearly 100 km<sup>2</sup> area of Melka Kunture have been established on the ground of litho- and archaeostratigraphic unit correlations (Taieb, 1967, 1971; Chavaillon and Taieb, 1968; Chavaillon et al., 1979; Kieffer et al., 2004; Raynal et al., 2004) and by K/Ar and <sup>40</sup>Ar/<sup>39</sup>Ar radiometric ages thanks to the presence of volcanic deposits (in Morgan et al., 2012). Supported by an updated magnetostratigraphic record (Tamrat et al., 2014), available evidence shows that the exposed sections cover approximately the entire Calabrian Stage (Early Pleistocene), from the top of the normal polarity Olduvai Subchron to the early Brunhes (Morgan et al., 2012; Tamrat et al., 2014). The archaeological record starts at c. 1.7 Ma with the Oldowan levels of Karre I, Gombore I, Gombore I<sub>γ</sub>, and Garba IVE-G (Piperno et al., 2009; Morgan et al., 2012; Gallotti, 2013; Gallotti and Mussi, 2015), while the first evidence of Acheulean from Garba IVD is referred to c. 1.5 Ma (Gallotti, 2013). The occurrence of the Acheulean then lasts nearly one million years (Chavaillon and Berthelet, 2004; Gallotti et al., 2010, 2014). So far, the early Middle Stone Age is represented at the site of Garba IIIB (Mussi et al., 2014), while Late Stone

Age occurrences lack geochronological resolution because volcanic ashes did not cover the Middle-Late Pleistocene sites (Hivernel-Guerre, 1976; Chavaillon et al., 1979; Chavaillon and Berthelet, 2004; Mussi et al., 2014).

Besides *Homo* (see below), the mammal fossil assemblage from Melka Kunture, particularly rich at Garba and Gombore, includes bovids (notably, Alcelaphini and some Antilopini and Reduncini), hippopotamids, equids, suids, giraffids, and some proboscideans, rhinocerotids, carnivores and non-hominin primates (Oussedik, 1976; Geraads, 1979, 1985; Chavaillon and Berthelet, 2004; Geraads et al., 2004a; Gallotti et al., 2010, 2014; Beaudet et al., 2015). This assemblage associates *Hippopotamus* sp. (cf. *amphibious* and cf. *aethiopicus*) and other artiodactyls indicative of relatively wet grasslands (*Kobus*) along with grazer (e.g., *Connochaetes*, *Damaliscus*) and primate taxa (*Theropithecus*) more commonly found in drier open environments (Geraads et al., 2004a, b; Beaudet et al., 2015). While the latter scenario is also consistent with information from the microfauna (Sabatier, 1980-82; Geraads et al., 2004b; Gallotti et al., 2010) and with some biogeochemical (Bocherens et al., 1996) and palynological data (Bonnefille, 1976) supporting the presence of spread C4 grasslands in the area across most Early to early Middle Pleistocene (in Morgan et al., 2012), paleoecological interpretations at Melka Kunture require caution, as the proportions of mammal taxa, notably the ungulates, reflect strong taphonomic biases (Gallotti et al., 2010: 298). However, a more recent palynologically based paleoenvironmental reconstruction (Mussi et al., 2015) supports a landscape across most of the Pleistocene compatible with the so-called "dry evergreen afro-montane forest and grassland complex" (Friis et al., 2011; Kebede et al., 2013), with no evidence whatsoever of vegetation encountered in the present-day Rift Valley and of any savannah tree species (Mussi et al., 2015).

The human fossil record from Melka Kunture (Coppens, 2004; updating in Mussi et al., 2014) consists so far of the following seven remains: an immature partial mandible (MK 81 GAR IVE 0043) from Garba IV (Condemi, 2004; Zilberman et al., 2004a, b; Zanolli et al., 2014a) and an adult distal humerus (MK 76 GOM IB 7594) from Gombore I (Chavaillon et al., 1977; Senut, 1979; Carretero et al., 2009; Puymeraill et al., 2014; Di Vincenzo et al., 2015), both associated with Oldowan industries; two adult cranial portions (MK 73 GOM II 6169 and MK 76 GOM II 576) from Gombore II (Chavaillon et al., 1974; Chavaillon and Coppens, 1986; Profico et al., 2016), associated with a middle Acheulean industry; and three juvenile to adult cranial fragments from Garba III (MK 78 GAR III A4-W9 n. 1918, MK 78 GAR III B3-A13 n. 1656-1919, and

MK 78 GAR III A4-W9 n. 1917) associated with an early Middle Stone Age industry (Chavaillon et al., 1987; Mussi et al., 2014).

The immature right mandibular portion MK 81 GAR IVE 0043 (hereafter GAR IVE) was discovered in situ in 1981 during excavation of the archaeostratigraphic unit E of Garba IV, a site located on the right bank of the Awash, whose Calabrian deposits belong to the lowest part of the Melka Kunture Formation (Kieffer et al., 2002, 2004; Raynal and Kieffer, 2004; Raynal et al., 2004; Gallotti, 2013; Gallotti and Mussi, 2015). Started in 1972 (Chavaillon and Piperno, 1975), investigations at Garba IV revealed the presence of several archaeological horizons within a stratigraphic sequence of three units almost entirely sandwiched within two tuff layers identified along the Garba gully, tuff A0 and the 'Grazia tuff' (Raynal et al., 2004), which have been recently dated to  $1.429\pm 0.029$  Ma and  $1.719\pm 0.199$  Ma, respectively (Morgan et al., 2012; Tamrat et al., 2014). More specifically, the level E (Piperno and Bulgarelli-Piperno, 1975; Piperno and Bulgarelli, 2004; Piperno et al., 2004a, b, c, d; Gallotti, 2013), whose polarity is normal (Tamrat et al., 2014: fig. 8), lies immediately below the 'Grazia tuff' (Raynal et al., 2004; Morgan et al., 2012: fig. 2a; Gallotti, 2013: fig. 2c; Gallotti and Mussi, 2015: fig. 3). Accordingly, the age of the specimen GAR IVE should be around/slightly older than 1.7 Ma, thus nearly contemporaneous to specimens such as KNM-ER 1805 from the Karari Ridge at Koobi Fora, Kenya (McDougall et al., 2012).

Firstly reported by Condemi (2004; <http://geoserver.itc.nl/melkakunture/biblio/monograph/melka-687.pdf>) and attributed to *H. erectus/ergaster* because of its closer morphological and dimensional similarities to penecontemporaneous *H. aff. erectus* specimens from the Turkana basin (see also Coppens, 2004), notably the subadult mandibles KNM-ER 820 and KNM-WT 15000 and, to some extent, the adult representative ER 992 (rev. and references in Wood and Leakey, 2011), GAR IVE is one of the few dentognathic remains from the Early Pleistocene African human record sampling a child. It is also noteworthy that, together with the c. 1.4 Ma *H. erectus* craniodental remains from the c. 1500 m asl site of Konso, at the southwestern end of the Main Ethiopian Rift (Suwa et al., 2007), this specimen represents the oldest of any human remains from a mountain-like environment.

GAR IVE represents a right mandibular corpus preserved between the central deciduous incisor (di1) broken socket and the first permanent molar (M1) crypt. It bears a heavily worn first

deciduous molar (dm1) and a relatively unworn second deciduous molar (dm2), both in occlusion. Part of the developing crowns of the lateral permanent incisor (I2) and canine (C), as well as the completely formed but still unerupted M1 crown, are also visible. A radiographic analysis performed by Condemi (2004) evidenced the presence of the third and fourth premolars (P3 and P4) still in their crypt. Based on dental development and wear stages, an age at death of 3-4 years has been suggested for this individual (Condemi, 2004). Scanning electron microscopy (SEM) of the outer enamel texture of the dm1, dm2 and M1 suggests the individual may have experienced an inherited pathological condition of enamel formation known as amelogenesis imperfecta (Zilberman et al., 2004a, b). However, while these first studies on GAR IVE presented basic information on this unique fossil, there is still extremely limited data available regarding the structural organization and about skeletal and dental development of early *Homo* immature specimens (e.g., Dean and Smith, 2009; Bermúdez de Castro et al., 2010; Dean, 2016).

By using imaging techniques applied to an X-ray computed tomography record of GAR IVE, the aims of the present study are (i) to integrate details of its outer and inner structural morphology; (ii) to define the developmental stage of each virtually extracted tooth and to estimate the most likely age at death of this child based on modern human standards; (iii) to comparatively assess the size of all, erupted and unerupted, measurable crowns; and (iv) to tentatively quantify crown tooth tissue proportions in the deciduous second and permanent first molars.

## **MATERIALS AND METHODS**

Observations of the external morphology of GAR IVE were carried out in 2012 and 2013 at the Department of Paleoanthropology of the National Museum of Ethiopia, Addis Ababa, where the specimen is permanently stored, by using a Nikon SMZ645 stereomicroscope and a Keyence VHX-600 digital microscope equipped by a 2.11 Mp CCD camera. In November 2013, the specimen was preliminarily detailed by X-ray computed tomography (CT) at the Wudassie Diagnostic Centre of Addis Ababa. The acquisitions were performed with a Philips Brilliance16 equipment according to the following parameters: 140 kV voltage, 100  $\mu$ A current, 1.76 s exposition time per projection. The final volume was reconstructed with a voxel size of

130x130x300  $\mu\text{m}$ . Subsequent 2D-3D elaborations (quantitative virtual imaging and morphometrics) were performed at the ICTP of Trieste.

The limited resolution of the CT record available to us currently precludes any investigation of the enamel microstructure. Accordingly, at this stage of the study, which mainly focuses on the previously unreported inner structure of the specimen with the primary aim of refining the overall maturational stage of this juvenile individual, no (re)evaluation was attempted regarding the diagnosis of amelogenesis imperfecta proposed by Zilberman et al. (2004a, b). Nonetheless, we note that, irrespective of the nature of such irregularities at the enamel surface (Hillson, 2005: 168-169) which have been recently observed also in some South African australopith molars (Towle et al., 2016), in terms of morphology and proportions, all tooth crowns lack any evidence of anomalous features at mesostructural scale (Figs. 1, 3, 4). A semi-automatic threshold-based segmentation with manual corrections was carried out following the half-maximum height method (HMH; Spoor et al., 1993) and the region of interest thresholding protocol (ROI-Tb; Fajardo et al., 2002) and by taking repeated measurements on different slices of the virtual stack using Avizo v.6.2. (Visualization Sciences Group Inc.) and ImageJ v.1.48 (Schneider et al., 2012).

Besides detailed analytical and comparative information on the outer aspect of the GAR IVE partial mandible provided by Condemi (2004), here we specifically investigated the buccolingual cross-sectional cortical bone distribution assessed at the dm2 level. For comparative purposes, we used the high resolution microtomographic ( $\mu\text{CT}$ -)based record of three human immature mandibles available in our files representing: the 2.5-3 years old Neanderthal child from Roc de Marsal (OIS 4; Bayle et al., 2009a, 2010; NESPOS Database, 2015); the 3-4 years old late Upper Paleolithic child La Madeleine 4 (OIS 1-2; Bayle et al., 2009b, 2010; NESPOS Database, 2015); and a 3.5-4 years old extant European individual (spec. EH-UdP; Bayle et al., 2010). Given some differences in preservation condition among the specimens and the structural variation of the cortical shell at this level, in all cases we only considered the bony portion immediately below the thinner perialveolar area (see Fig. 2A). Site-specific cortical thickness variation across each section and percent cortical area were assessed using the software package MPSAK v.2.9 (available in Dean and Wood, 2003). For cortical thickness, we automatically performed 3242 linear measurements on GAR IVE (investigated cross-sectional perimeter: 43.3 mm; total area:

215.9 mm<sup>2</sup>), 557 on Roc de Marsal (31.6 mm/132.5 mm<sup>2</sup>), 533 on La Madeleine 4 (31.6 mm/111.6 mm<sup>2</sup>), and 515 measurements on the extant human specimen (26.2 mm/90 mm<sup>2</sup>).

While the resolution of the currently available CT record does not allow for any unambiguous distinction between enamel and dentine, we were able to virtually segment, extract and assess each tooth element. We then combined such information with direct observations performed on the crown morphology visible on the original specimen.

The Bayesian analysis of the dental maturational sequence of GAR IVE is based on a tooth-by-tooth evaluation of the stage of dental mineralization of the teeth according to the scoring system (crown and root calcification stages) established by Demirjian et al. (1973) for the permanent teeth, and by Liversidge and Molleson (2004) for the deciduous teeth, modified and adapted by Bayle et al. (2009a). The estimation relies upon the CT-based examination of the teeth preserved *in situ* within the mandible. The sequence composed by the I2, C, P3, P4 and M1 has been compared to those assessed following the same scoring methods on a radiographic and CT reference sample of 795 living humans (408 females and 387 males) of African, European, and Middle Eastern origins, aged 1-8 years and distributed as follows: 1-2 years (N=14 individuals), 2-3 years (N=21), 3-4 years (N=74), 4-5 years (N=119), 5-6 years (N=153), 6-7 years (N=178), and 7-8 years (N=236) (Braga and Heuzé, 2007; Bayle et al., 2009a, b, 2010; original data). The statistical analysis of each dental mineralization sequence was carried out by applying the method developed by Braga and Heuzé (2007), using Bayes's rule of conditional probability (Vieland, 1998; Aitken and Taroni, 2004), with teeth being considered as statistically dependent units and prior probabilities uniform.

Description of the nonmetric crown outer topography follows Scott and Turner (1997) and is based on the Arizona State University Dental Anthropology System (ASUDAS) scores (Turner et al., 1991). Maximum mesiodistal (MD) and buccolingual (BL) diameters of the two deciduous and the first permanent molars were provided by Condemi (2004: tab. 4) and discussed in a wide comparative context. However, given the position in the alveolar bone of the growing M1, both values were considered underestimated (Condemi, 2004: 694). Accordingly, following the 3D reconstruction and virtual extraction of this crown, we refined such measurements and updated their comparisons. By using the same imaging techniques, we revised the metric record of the dm2 and the M1 and provide here original information on the previously unreported lateral incisor and canine crowns and compare their size with the figures from a number of fossil and



recent human specimens/samples (see Supporting Information). We also digitally measured the crown height of the I2, C, and M1 as the maximum projected distance from the cervix to the highest point on the crown.

Because of the advanced degree of wear affecting the dm1 (stage 6 following Smith, 1984; see below), only the crowns of the dm2 and of the unworn M1 were virtually isolated from their roots for quantifying tissue proportions based on the best-fit plane of the cervical line. The crown pulp volume ( $V_{cp}$ ) and total crown volume ( $V_c$ ) were estimated and the percent of coronal volume that is pulp was then calculated ( $V_{cp}/V_c$ ). Tissue proportions in GAR IVE were then directly compared with the microtomographic-based evidence available to us from: the c. 1 Ma *H. erectus/ergaster* M1/2 specimen MA 93 from the Eritrean Danakil (Zanolli et al., 2014b); the late Early-early Middle Pleistocene *H. erectus* dm2 PCG.2 from the Sangiran Dome, Java (Zanolli et al., 2012); a sample of 6 dm2s and 11 M1s of European Neanderthals from La Chaise-de-Vouthon Abri Suard, Krapina, Combe Grenal, and Roc de Marsal (Macchiarelli et al., 2006, 2013; Olejniczak et al., 2008; Bayle et al., 2009a, 2010; Kupczik and Hublin, 2010; Zanolli et al., 2012, 2014a; NESPOS Database, 2015); 3 dm2s and 1 M1 sample of the two European Upper Paleolithic specimens of Lagar Velho and La Madeleine (Bayle, 2008; Bayle et al., 2009b, 2010; NESPOS Database, 2015); and a nearly unworn sample of 7 dm2s and 11 M1s of recent/extant Europeans (Bayle, 2008; Olejniczak et al., 2008; Bayle et al., 2010; Zanolli et al., 2012, 2014a; and original data).

Intra- and inter- tests for accuracy of the estimates were run by two observers. Linear, surface, and volumetric measurements provided for both tests differences of 3.6%, on average, the highest recorded difference reaching 6% for the variable  $V_{cp}$ .

## RESULTS

### External morphology and cross-sectional structure

The specimen GAR IVE represents a 58 mm long incomplete but relatively well preserved and robust right mandibular corpus fragment lacking the ramus and the symphysis (extended description and comparisons in Condemi, 2004). It still preserves the fully erupted dm1 and dm2, as well as five unerupted permanent teeth (I2, C, P3, P4, and M1), three of them (I2, C and M1)

visible at the level of the anterior and posterior breakages of the corpus (Fig. 1). On the lateral aspect, there is an 8.5 mm high and 6.5 mm large hole below the dm1 (Fig. 1A, E), which likely represents a carnivore tooth-mark (Zanolli et al., 2014a). Its inspection by low magnification microscopy shows slightly sunken morphology of its sub-rectangular bony rim, reduction inwards of its diameters, and the presence on the distal aspect of traces of the nerve canal associated to the mental foramen, the latter being no longer preserved (cf. Condemi, 2004). Interestingly, CT-based imaging reveals that, whatever its nature, the impact reached the buccal aspect of the crypt lodging the growing P3 crown, which bears a distinct transverse fracture (Figs. 1A, 1B, 3), but did not reach the inner (lingual) mandibular wall (Fig. 1B). At the dm2 level, height and breadth (width) of this mandibular body correspond to 20.1 mm and 14.5 mm, respectively (Condemi, 2004). Despite damage to the region of the mental foramen, it seems clear GAR IVE, like Ledi-Geraru LD 350, from Ethiopia, and other early *Homo* mandibles (Villmoare et al., 2015), lacks the lateral corpus hollow in which the mental foramen is located, which distinguishes *A. afarensis* mandibles across their size range.

Comparative cortical bone distribution and proportions across the mandibular buccolingual virtual section through the mid dm2 in GAR IVE, in a Neanderthal, a European Upper Paleolithic, and in an extant human representative, all sampling juvenile individuals whose estimated age ranges from c. 2.5 to c. 4 years, are shown in Figure 2. At this cross-sectional level, the Ethiopian specimen exhibits the largest dimensions and absolute greatest robustness of the corpus outline, notably with respect to the condition displayed by the extant child used in this study (Fig. 2A). GAR IVE also shows at all sites absolutely and relatively thicker cortical bone (average:  $2.4 \pm 0.3$  mm) than measured in Roc de Marsal (av.:  $1.8 \pm 0.6$  mm), La Madeleine (av.:  $1.6 \pm 0.5$  mm), and in the extant human mandible (av.:  $0.9 \pm 0.2$  mm) (Fig. 2B). Percent cortical area in GAR IVE (42.3%) also exceeds the estimates obtained for all three comparative specimens (40.5%, 38.4%, and 23.6%, respectively).

### **Dental developmental stages**

At the time of death of the juvenile individual sampled by GAR IVE, the dm1 was in occlusion and heavily worn (stage 6; Smith, 1984), with most of the occlusal enamel removed, more so distally than mesially, but still preserving a thin peripheral enamel ring (c. 0.4 mm thick

lingually and 0.8 mm buccally; *contra* Zilberman et al., 2004b) (Figs. 1, 3, 4). It shows completed mesial and distal roots, with two separated pulp canals in the mesial root but with a reduced pulp cavity distally and an occluded root canal in the distal root (Fig. 3). Both roots show signs of apical resorption in a manner that reflects the P3 crypt outline beneath these roots (Table 1, Fig. 3). However, as 4 mm of each root are exposed above the alveolar crestal bone compared with only 2 mm exposed on the dm2, it seems that the dm1 was slightly extruded from its socket post mortem, as evidenced by the raised contact facet with the dm2 distally.

The dm2 also was already in occlusion at the time of death, but it shows considerably less wear compared to the dm1 (stage 2; Smith, 1984), with small wear facets only appearing on the buccal cusps and on the entoconid (Figs. 1, 3, 4). Its two widely mesiodistally spaced roots, with open apices, are incompletely formed (Table 1, Fig. 3). The pulp chamber displays five well developed horns corresponding to each cusp. There are two separate root canals (buccal and lingual) in the mesial root. Only a single, larger and flat, canal is visible in the distal root (Fig. 3).

The I2 is preserved within the alveolar bone, its incisal edge lying c. 2 mm below the alveolar bone margin (Figs. 1E, 4). Measured from the incisal edge to the farthest point on the base margin, the crown is 9.4 mm high. It is complete down to the cement-enamel junction and beginning of root formation mesially where there is c. 3.8 mm root dentine formed, but only c. 1.8 mm distally (Table 1, Fig. 3). Its pulp cavity is finger-shaped (Fig. 3).

The permanent C germ lies low in the mandibular corpus, with its tip approximately 1.5 mm above the level of the base of the I2 germ, and approximately 2.5 mm below the level of the dm1 root apices (Figs. 1D-F, 4). The germ measures 7.5 mm high from cusp tip to crown base, which may represent 2/3 or less of the final completed crown height (Table 1, Fig. 3). Its pulp cavity only shows a rounded horn (Fig. 3).

The P3 germ, lodged in its crypt under the dm1, measures 7.6 mm from cusp tip to base. It lies higher in the alveolar bone than both the canine germ, mesially, and the P4 germ, distally (Fig. 1D-F). Its base is at the level of the upper margin of the penetrating tooth-mark present on the lateral aspect of the mandibular fragment, and at the level of the distal root apex of the dm2, distally (Fig. 1E). Its cusp tip lies at the level of the mid-crown of the I2. The buccal and lingual cusps of this germ lie directly in the buccolingual plane (Fig. 1F). Crown formation is complete at the occlusal surface and active extension and convergence towards the cervical region is seen (Table 1, Fig. 3). The pulp chamber only shows a pulp horn under the protoconid (Fig. 3).

The P4 germ, measuring 5.4 mm from the cusp tip to the base margin, lies in the mandibular corpus at approximately the same level as the canine germ, but now with its occlusal surface facing buccally (presumably having rotated post mortem). It is positioned at the same level of the tooth-mark puncture, but distal to it (Fig. 1D-F). It still lies low between the apical portions of the dm2 roots. The outline of the occlusal surface is complete, but the lateral enamel extension towards the cervical region had barely begun (Table 1, Fig. 3). The pulp chamber roof only shows a low relief, but with evidence of a forming protoconid pulp horn (Fig. 3).

The M1 is still contained within its bony crypt within the corpus, but is partially visible in lingual view (Figs. 1B-E, 4). The mesial cusps lie 4 mm below the alveolar crestal margin, just distal to the mid-point of the distal root of the dm2, and at the level of the inferior aspect of the bifurcation of the mesial and distal roots of the dm2 (equal also to approximately the level of the middle of the I2 crown, anteriorly). The M1 crown is complete and measures 7.4 mm high from the mesial cusps to the mesiobuccal cervix. The pulp chamber roof displays five well developed horns corresponding to each occlusal cusp (Fig. 3). Approximately 3 mm of root formed below the crown distolingually were preserved (Fig. 4I), but likely slightly less than this buccally beneath the protoconid cervix. The radicular bifurcation had not begun to form at the time of death (Table 1, Fig. 3). The mandibular corpus is incomplete immediately distal to the M1 (Fig. 1B), leaving no trace of any M2 crypt.

### **Maturational pattern**

The maturational pattern of GAR IVE and the associated scores of each tooth element are shown in Table 1, while the results of the Bayesian analysis of the mineralization sequence (D/C/C/B/D) displayed by the preserved permanent teeth (I2/C/P3/P4/M1) are presented in Table 2. Within the comparative sample of 795 extant children aged 1-8 years used in this study (Braga and Heuzé, 2007; Bayle et al., 2009a, b, 2010), the maturational sequence displayed by GAR IVE has been found four times. All the posterior probabilities associated with the observed combinations (N=30) have been efficiently calculated and all are higher than 0.75. Although 0.75 does not represent an absolute cutoff in a continuous probability distribution (ranging from 0 to 1), probabilities higher than this formal threshold indicate very likely events, whereas values

comprised between 0.25 and 0.75 are more likely to be associated with random events, and values lower than 0.25 with unlikely events (Braga and Heuzé, 2007).

In summary, according to the present Bayesian statistical analysis, the occurrence of a mineralization sequence like that found in GAR IVE is relatively common in extant humans of African, European, and Middle Eastern origins. In the comparative record specifically used in this study, the four children sharing their mineralization sequence with the Ethiopian fossil are one boy and three girls aged 2.67, 3.92, 4.54, and 6.42 years, respectively.

### **Occlusal morphology and tooth crown size**

Given the amount of occlusal wear extensively affecting the dm1, a mesial fovea and a transversal ridge are the only features detectable on its crown (Fig. 4); also, its considerably reduced crown dimensions (MD: 8.8 mm; BL: 7.6 mm) cannot be used for any reliable comparison.

The dm2 crown presents five main cusps, including a large hypoconulid (C5; score 5), organized in a + occlusal groove pattern (Fig. 4). It lacks both tuberculum intermedium (C7) and tuberculum sextum (C6). The anterior fovea is sub-triangular and moderately deep (score 4). It is enclosed by a thick uninterrupted mesial marginal ridge with three accessory tubercles (Condemi, 2004) and by a low incised mid-trigonid crest (score 1B). In addition, a short ridge subdivides the mesial fovea. The entoconid, C5 and the low thick distal marginal ridge enclose a groove-shaped distal fovea. The protostylid includes two small pits located at mid-crown height at the mesiobuccal angle of the protoconid, and a V-shaped groove between protoconid and hypoconid. However, in absence of information about the underlying dentine morphology and considering that all these features are at a comparable crown height, we cannot discard the possibility they result from enamel hypoplasia (see Zilberman et al., 2004a, b). Because of the extremely low degree of occlusal wear, measures of its crown size (MD: 12.0 mm; BL: 10.2 mm; crown height: 5.5 mm) are highly reliable. However, the comparative dimensional record available for moderately worn Early-Middle Pleistocene human lower dm2s is rather scanty (Wood, 1991; Condemi, 2004; Moggi-Cecchi et al., 2006, 2010; Zanolli et al., 2012; see Supporting Information, Table S1). Nonetheless, in the comparative record considered in this study, we note

that GAR IVE is intermediate between *H. habilis-rudolfensis*, South African early *Homo* and *H. erectus s.l.* for both MD and BL diameters (Fig. 5).

While the virtually extracted I2 crown exhibits smooth labial and lingual aspects (Fig. 3) and is thus suitable for size assessment (MD: 7.4 mm; BL: 7.1 mm), we measured but did not compare its mesiodistal diameter because of the occlusal wear commonly affecting the lower front teeth in fossil specimens (cf. Wood, 1991). Conversely, among the Early Pleistocene specimens/samples considered in our comparative analysis, its closest fits for the buccolingual diameter are the I2s from Dmanisi, Georgia (Martín-Torres et al., 2008) and the African *H. aff. erectus* assemblage (Wood, 1991), while South African early *Homo* shows smaller dimensions (Moggi-Cecchi et al., 2006) and the values of *H. habilis-rudolfensis*, Indonesian *H. erectus* and *H. antecessor* are systematically higher (Wood, 1991; Grine and Franzen, 1994; Bermúdez de Castro et al., 1999) (Fig. 5; Table S1).

The permanent C crown has high and thick mesial and distal ridges, but no tuberculum dentale (Fig. 3). For its mesiodistal diameter (8.6 mm), it nears the average values of Chinese and African *H. erectus*, South African early *Homo* and *H. habilis-rudolfensis* (Wood, 1991; Moggi-Cecchi et al., 2006), while the canines from Dmanisi commonly display a more mesiodistally expanded crown (Martín-Torres et al., 2008) (Fig. 5; Table S1).

Two well-developed main cusps form the growing P3 crown, and the moderately thick uninterrupted transverse crest linking them circumscribes a small mesial fossa and a larger distal fovea (Fig. 3). As noted above, its buccal aspect is transversally fractured along a plane passing laterally to the metaconid apex (Figs. 1F, 3).

While showing a slightly lower degree of maturation (Table 1), the occlusal morphology of the forming P4 crown is similar to that of the P3 (Fig. 3).

There are five main cusps forming an X-groove pattern on the M1 crown, including a large hypoconulid (C5; score 5) (Figs. 3, 4). This crown is absolutely and relatively large (MD: 13.7 mm; BL: 12.2 mm). In the comparative context considered in the present study (Fig. 5; Table S1), its best average dimensional fit are South African early *Homo* (Wood, 1991; Moggi-Cecchi et al., 2006, 2010) and the *H. habilis-rudolfensis* assemblage (Wood, 1991; Leakey et al., 2012), but for both diameters it falls near the upper limits of variation displayed by African and Eurasian *H. erectus s.l.* and African *H. heidelbergensis* (Wood, 1991; Widiyanto, 1993; Kaifu et al., 2005; Suwa et al., 2007; Martín-Torres et al., 2008; Lordkipanidze et al., 2013; Zanolli, 2013; Zanolli

et al., 2014b; Maddux et al., 2015), and also exceeds the estimates available for *H. antecessor* (Bermúdez de Castro et al., 1999, 2008).

### **Tooth crown tissue proportions**

For the dm2 and M1 of GAR IVE, crown pulp ( $V_{cp}$ ) and total crown ( $V_c$ ) volumes and their percent ratio are given in Table 3 together with the comparative estimates available from some Pleistocene and recent human specimens/samples. As a whole, while for  $V_{cp}$  and the  $V_{cp}/V_c$  ratio the dm2 from Garba approximates the modern (fossil and recent) human figures and sets GAR IVE systematically apart from the Neanderthal values, for  $V_c$  it perfectly fits the condition displayed by the Early-early Middle Pleistocene Javanese *H. erectus* specimen PCG.2, from the Kabuh Formation outcropping near the Pucung village, in the southern part of the Sangiran Dome (Zanolli et al., 2012). For the M1 of GAR IVE, while it falls within the modern human range for all three variables and is also compatible with the wide range of Neanderthal variation, its crown tissue proportions differ from the condition recently described for the similarly unworn *H. erectus/ergaster* lower M1/M2 crown MA 93 from the 1.0 Ma site of Mulhuli-Amo, Danakil Eritrea (Zanolli et al., 2014b).

## **DISCUSSION**

### *General size and morphology*

For its external morphology and dimensions (Condemi, 2004: tab. 3), the mandibular corpus GAR IVE is similar to other early *Homo* juvenile representatives, such as KNM-ER 820 (Leakey and Wood, 1973) and the more fragmentary specimen KNM-ER 1507 (Leakey and Wood, 1974) from Koobi Fora (Wood and Leakey, 2011), whose age at death has been estimated at 5.3-6.5 and 4-6.1 years, respectively (in Wood, 1991). Even at a much earlier dental age, GAR IVE appears to lack the lateral corpus hollow in which the mental foramen is located in *A. afarensis* mandibles, and is overall more convex here, like dentally older and adult specimens such as KNM-ER 820, KNM-WT 15000, KNM-ER 992. At the dm2 level, the corpus breadth/height index of GAR IVE (72%) is slightly higher than measured across the P4 on the adolescent

skeleton KNM-WT 15000 (left: 66.5; Walker and Leakey, 1993) and intermediate between the values reported at the dm2 position for KNM-ER 820 (average: 67.4%) and the more robust ER 1507 (80%) (Wood, 1991; see tab. 19). Given that both immature specimens from East Turkana are developmentally older than GAR IVE as they share the condition of a fully erupted M1 (even if root development in KNM-ER 1507 is slightly less advanced than in ER 820; Dean, 1987), the mandible from Garba can be considered as absolutely robust. It also has large molar crowns (notably, the dm2 and the M1), whose both mesiodistal and buccolingual diameters are slightly greater than measured on average in *H. erectus s.l.*, rather nearing the estimates available for *H. habilis-rudolfensis* from East Africa. Conversely, because of the still extremely limited amount of information on tooth tissue proportions in fossil *Homo* currently available for direct comparisons, what does seem relevant here is that both GAR IVE's molars display absolutely and relatively low crown pulp volumes. However, at this stage of the research, we cannot confidently interpret the meaning of this structural signature till some supplementary analyses at a higher resolution will be carried out on this specimen and on other penecontemporaneous immature individuals from Eastern and Southern Africa.

Interestingly, evidence for robustness in GAR IVE is compatible with recent suggestions, based on the updated analysis of the markedly robust distal humerus MK 76 GOM IB 7594 from the  $>1.393\pm 0.162$  Ma old site of Gombore I, near Garba (Di Vincenzo et al., 2015), about possible body size adaptations to harsher climatic conditions experienced by early *Homo* on the highlands (at altitudes around 2000 m) compared to those encountered at the time in the lowland regions of East Africa (but, for compelling evidence on penecontemporaneous large body-sized humans in the rift system, see Bennett et al., 2009; Will and Stock, 2015). However, GAR IVE is smaller and less robust compared to mandibular remains from Kenya sampling immature individuals of the sympatric taxon *Paranthropus boisei*, like KNM-ER 1477 and KNM-ER 1820, as well as to South African specimens of *P. robustus* like SK 61, SK 62 and SK 63, from Swartkrans (Wood, 1991; see tabs 3 and 5 in Condemi, 2004). GAR IVE is also less robust compared to the juvenile *P. boisei* mandibular portion KGA10-570 from the 1.4 Ma site of Konso, c. 400 km apart from Melka Kunture on the Ethiopian plateau (Suwa et al., 1997: tab. 1), a specimen representing a left corpus preserving a recently erupted M1 crown and P4 and M2 germs still in their crypts, displaying at M1 position a higher breadth/height index than measured on GAR IVE (Suwa, pers. comm.).



Robusticity in GAR IVE is also revealed by its cross-sectional structure and cortical bone topographic distribution, which closely relate to the functional pattern of masticatory loads (Demes et al., 1984; Daegling, 1989; Daegling and Grine, 1991; Daegling and Hotzman, 2003; Fukase, 2007; Fukase and Suwa, 2008; Gröning et al., 2009). At the best of our knowledge, no directly comparable cortical bone thickness values measured at the same level all along the section have been made available so far for immature human fossil mandibles besides the evidence reported above for Roc de Marsal and La Madeleine. However, it is noteworthy that percent cortical area in the Ethiopian specimen, which largely exceeds the value obtained for a single extant child of comparable age used here for comparative purposes (40.5% vs. 23.6%), fits the proportions (cortical area/total subperiosteal area, i.e., cortical index) measured at the M1 level in extant human adult mandibles and in *P. robustus* (Daegling, 1989: tab. 3; Daegling and Grine, 1991: tab. 4), but exceeds those of *A. africanus* (Daegling and Grine, 1991: tab. 4).

A microtomographic-based virtual cross-section performed just behind the dm2 crypt of the 5.3-6.6 years old ATD6-112A partial mandible of *H. antecessor* (individual H11; Bermúdez de Castro et al., 2010) from the late Calabrian (MIS 21) "Aurora archaeostratigraphic set" at Atapuerca Gran Dolina, Spain (Bermúdez de Castro et al., 2016), has revealed similarly thick, or even slightly thicker, cortical bone compared to the section measured at nearly the same level on GAR IVE (original unpublished record courtesy of Bermúdez de Castro and Martín-Francés Martín de la Fuente). However, while thickest cortex in both specimens is found inferiorly (2.8 mm in GAR IVE and 3.2 mm in H11), H11 is on average thicker lingually (2.7 mm) than buccally (2.3 mm), which is not the case in GAR IVE (2.2 mm vs. 2.4 mm). At any rate, the lack of comparable evidence from Early Pleistocene human specimens inhibits at this stage any functional vs. biological interpretation of these results.

### *Dental developmental pattern*

The Bayesian analysis of the dental developmental pattern in GAR IVE shows that it falls easily within the variation observed in extant African, European, and Middle Eastern human populations. Differences in the sequence, or pattern, of permanent tooth mineralization stages arise between taxa because crowns and roots form over different lengths of time. During the earliest stages, as in GAR IVE before root formation begins, differences in the pattern of dental

development are hard to discern in hominins. For example, figure 3 in Alemseged et al. (2006) shows that the pattern of the developing mandibular dentition of the 3.3 Ma *A. afarensis* infant from Dikika, Ethiopia (Dik-1-1) bears a number of similarities with GAR IVE. However, despite having apparently very similar stages of permanent tooth development to GAR IVE, the permanent canine of Dik-1-1 lies much lower in the corpus, well below the level of all the other developing permanent teeth. The developing I2 in Dik-1-1 also lies well below the level of the alveolar crest in contrast to the I2 of GAR IVE, which is only 2 mm beneath the alveolar crest. Moreover, the M1 in Dik-1-1, despite apparently having less root formed, appears to lie higher in the alveolus with respect to the distal dm2 root than in GAR IVE. It is the disposition of the tooth germs within the mandibles of these specimens that best distinguishes them at this early age, and not so much their pattern of tooth development.

In the future, a comparison of the values collected on GAR IVE with the tooth germ heights assessed in the early *Homo* partial mandibles KNM-ER 820 and KNM-ER 1507 (Wood, 1991; Wood and Leakey, 2011), both more advanced in crown height but not necessarily in proportion of the total crown formed than the Ethiopian specimen (Krovitz et al., 2003), should allow more precise and directly comparable estimates of fractional crown heights.

The pattern of development of the permanent teeth in GAR IVE also closely resembles that in some younger specimens attributed to *Paranthropus*, such as KNM-ER 1477, SK 64, SK 3978, TM 1536, TM 1601 (Skinner and Sperber, 1982; Dean, 1987; Smith et al., 2015). Again, this can in part be attributed to their young age where most tooth crowns are still incomplete. In general, specimens attributed to *Paranthropus* show a greater proportion of incisor crown complete at the time of M1 crown completion than other fossil hominins (Robson and Wood, 2008; Smith et al., 2015) and GAR IVE with its incomplete I2 crown at the time of M1 crown completion and root initiation does not fit the typical pattern seen in *Paranthropus*.

Interestingly, H11 from Atapuerca Gran Dolina is another fossil hominin at a near identical stage of development to GAR IVE, with the dm2 root apex also still open and M1 crown also just complete. But M1 in H11 is slightly delayed with respect to GAR IVE, with only 0.48 to 1.58 mm of root formed (Bermudez de Castro et al. 2010: tab. 1), as opposed to ~3 mm in GAR IVE. In contrast, both permanent incisor germs in H11 are slightly more advanced with respect to GAR IVE and have completed crowns, but with no root formed. This can be interpreted as evidence for a slowing or delay in the time taken to form M1 with respect to many earlier

hominins (Bermudez de Castro et al., 2010). The first evidence for this in the hominin fossil record has been reported in another individual from the Gran Dolina, Atapuerca, ATD6-103 (individual H5; Gómez-Robles et al., 2007, 2011; Bermudez de Castro et al., 2010). The M1s of individual H5 had 8-9 mm of root formed with cuspal wear facets indicating only minimal attrition close to the time of gingival emergence (Bermudez de Castro et al., 2010). This amount of root formed at gingival emergence would have taken more time to form and so provides some evidence (all be it indirect) for a later age of M1 emergence than reported for earlier hominins (Dean, 2016). This would place H5 from Gran Dolina well within the modern human range for age at M1 eruption. However, while the timing of enamel growth and root growth in early *Homo* has been found to be faster on average than in modern humans (Dean et al., 2001, 2010; Dean and Smith, 2009; Dean and Cole, 2013), there is little evidence that there was shift to a more prolonged period of growth and dental development at the time of the transition from australopiths to early *Homo* (Dean 2016). Until such time, as older individuals with later stages of M2 and M3 development can be assigned a secure age at death, it remains difficult to define the origins of prolonged dental development and growth among early hominins (Dean, 2016). In acknowledgement of these limitations, it is still, however, possible to provide a broad estimate of the age at death of this individual (see discussion below). The importance of GAR IVE as a juvenile specimen is, however, not that it currently contributes to the debate about differences in dental and general growth between early *Homo* and australopiths; rather, it provides evidence that the disposition of developing tooth germs within the corpus and evidence that some aspects of external corpus morphology appear already at this young age to differ from those described in *A. afarensis* (Alemseged et al., 2006). This, perhaps for the first, time provides evidence in early *Homo* for what has been clear for some time in infant and juvenile Neanderthals, i.e., that taxonomically diagnostic morphology already exists in very young mandibles (e.g., Ponce de León and Zollikofer, 2001; Bastir et al., 2007).

### *Individual age at death*

An age at death of 3-4 years originally suggested for GAR IVE (Condemi, 2004) may well encompass the true age at death of this specimen, but at least one younger individual (2.67 years old) in our extant reference sample shows the same developmental pattern. Perhaps, the best

indication of the age at death of GAR IVE comes from the histological estimates of M1 crown formation times assessed in other fossil hominins. Smith et al. (2015) reported the enamel formation time in another likely early *Homo* M1 specimen from Sterkfontein, South Africa (StW 151; Moggi Cecchi et al. 1998). In this specimen, synchrotron imaging of enamel microstructure shows M1 took between 2.4 years (lower ml cusp) to 2.8 years (upper ml cusp) to complete. Another M1 attributed to *H. erectus* from Sangiran, Java (S7-37; Dean et al. 2001) took 2.47 years to complete the crown. In this specimen, 2.6 mm of root had formed beneath the protocone by 3.56 years of age at an average rate of 6.6  $\mu\text{m}/\text{day}$ . These M1 crown formation times seem to encompass much of the range reported for M1s in several other early hominins such as Sts 2, KNM-KP 31712 and DNH 84 (Smith et al. 2015; tabs 2, 3), but root formation rates are known to vary enormously (Dean, 2012; Dean and Cole, 2013) and remain unknown in GAR IVE.

To summarize, based on what we now know of the microstructure of other early fossil hominin M1s (in Smith et al., 2015) and in the absence of any direct histological evidence for the true crown and root formation times in GAR IVE, the age at death of this juvenile individual from Garba might well have been anything between 2.5 and 3.5 years.

## CONCLUDING REMARKS

Even if they document the earliest phases in Africa of a long-term techno-cultural (Chavaillon and Piperno 2004a, 2004b) and biological adaptation to mountain ecological conditions (Mussi et al., 2015), until recently information on the Early Pleistocene human remains from the sites of Garba and Gombore, at Melka Kunture, on the Ethiopian highlands, has been poorly reported, thus legitimizing the remark that "(t)here is surprisingly limited literature on the Melka Kontouré hominids... Clearly, reappraisal of this heterogeneous assemblage is in order" (Schwartz and Tattersall, 2003: 172-173; among other titles, see also the lack of paleoanthropological information on Melka Kunture in Begun, 2013; Henke and Tattersall, 2015).

Revisited in context within the framework of an ongoing analytical revision of the whole human fossil assemblage from this important Early to Middle Pleistocene site complex (Mussi et al., 2014; Puymerail et al., 2014; Zanolli et al., 2014a; Di Vincenzo et al., 2015; Profico et al., 2016), the present study used a new X-ray computed tomography record to refine and successfully expand the original description of the c. 1.7 Ma old early *Homo* mandibular portion

GAR IVE from Garba IV (Condemi, 2004; Zilberman et al., 2004a, b), notably the radiographic-based assessment of its inner structure and tooth developmental pattern (Condemi, 2004). Nonetheless, given the only modest resolution of our 2D-3D virtual reconstructions, we admit there is still much information to retrieve from this unique specimen, likely representing a 2.5 to 3.5 years old *H. erectus/ergaster* (Condemi, 2004; Coppens, 2004). Specifically, future research relying upon a high resolution microtomographic record should more precisely image details of the enamel-dentine junction of the deciduous second and permanent first molar crowns for comparative geometric morphometric analyses and allow the subtle quantification of tooth tissue proportions, notably in terms of enamel thickness topographic repartition (cf. Zanolli et al., 2014b).

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## CAPTIONS FOR FIGURES

**Fig. 1.** The right mandibular specimen GAR IVE. The original specimen in lateral (**A**), internal (**B**), and superior (**C**) views; a CT-based virtual section passing approximately across its mid portion (**D**); the 3D rendering of the bone (in semi-transparency) and the in situ tooth elements (**E**), where the dotted polygon at the base of the P3 highlights the outer outline of the hole opening into the P3 crypt which erased the foramen mentale (see Condemi, 2004); the virtually extracted tooth elements (**F**), where the arrow indicates a mesiodistal fracture running along the P3. In all images but **B**, posterior is to the left. Scale bar, 5 mm.

**Fig. 2.** (**A**) Inner structural organization of four mandibular bodies of immature individuals virtually sectioned buccolingually across the dm2. From left to right: GAR IVE, the Neanderthal from Roc de Marsal (RdM; Bayle et al., 2009a), the Upper Paleolithic human from La Madeleine (LM4; Bayle et al., 2009b), and an extant human child (EH, spec. EH-UdP; Bayle et al., 2010). The lateral (buccal) aspect of the corpus is systematically to the left. The dotted lines indicate the upper limit of the section considered for quantitative assessment. All images, but GAR IVE (CT-based), obtained from a  $\mu$ CT record (NESPOS Database, 2015). (**B**) Cortical bone thickness distribution (in mm) comparatively assessed across the bony sections shown above (portion below the dotted line). b, buccal; i, inferior; l, lingual. Scale bar, 5 mm.

**Fig. 3.** The virtually extracted and 3D rendered deciduous and permanent tooth elements of the mandibular specimen GAR IVE. Enamel and dentine appear in orange, the pulp cavity in cyan. b, buccal; d, distal; l, lingual; m, mesial; o, occlusal. Scale bar, 5 mm.

**Fig. 4.** The two deciduous (dm1 and dm2) and three permanent (I2, C and M1) tooth elements of the mandibular specimen GAR IVE visible from the outside shown in different perspectives. b, buccal; d, distal; i, inferior; l, lingual; m, mesial; o, occlusal; ol, occlusolingual. Scale bar, 5 mm.

**Fig. 5.** Crown dimensions (MD and BL diameters, in mm) of the deciduous second molar (dm2, **A**), the permanent lateral incisor (I2, **B**; BL only), the permanent canine (C, **C**; MD only) and the first permanent molar (M1, **D**) of the mandibular specimen GAR IVE (black star) compared with the average values of some Pleistocene and recent human specimens/samples. EUPH: European Upper Paleolithic humans; HA: *H. antecessor*; HEA: *H. erectus/ergaster* from East Africa; HEC: *H. erectus* from China; HEG: *H. erectus* from Georgia; HEJ: *H. erectus* from Java; HHA: African *H. heidelbergensis*; HHE: European *H. heidelbergensis*; HHR: *H. habilis-rudolfensis* from East Africa; NEA: Neanderthals; NEEHS: Near Eastern early *H. sapiens*; RH: recent humans. The related data (sources, N, means, range, s.d.) are provided in the Supporting Information (Table S1).