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The Qesem Cave hominin material (part 1): A morphometric analysis of the mandibular premolars and molar

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ABSTRACT

The Mid-Pleistocene Qesem Cave near Tel Aviv in Israel yielded several hominin teeth and abundant faunal and cultural remains. The geological sequences of the cave were dated to 420,000–200,000 years ago. In this contribution, we focus on the three lower postcanine teeth which are among the oldest material from the cave. We used both Geometric Morphometrics and qualitative observations on the outer enamel surface and the internal enamel–dentine junction to investigate shape and size variation in a sample of Early-to Late-Pleistocene fossils (Sangiran, Mauer, Bilzingsleben, Ehringsdorf, Qafzeh, Ohalo), Neanderthals, and geographically diverse recent humans. Our approach based on three dental traits from three tooth types is able to distinguish quite well between dental specimens from anatomically modern humans (AMH) and Neanderthals (NEA). It also confirms an intermediate morphology of Mid-Pleistocene specimens in general, and the close proximity of Ehringsdorf to NEA. While the Qesem premolars display an intermediate shape between NEA and AMH, their size is definitely modern-like. The Qesem molar features a morphology and size closer to NEA. A possible explanation is the evolutionary dissociation of size and shape in premolars, and molars that are morphologically closer to NEA than premolars. It can be noted that a Mid-Pleistocene hominin population was present in Southwestern Asia that shows some Neanderthal affinities, probably more than Mauer and Bilzingsleben, but less than Ehringsdorf. With the current data, however, we cannot confidently assign the Qesem teeth to any existing taxon, nor exclude that it is an autochthonous phenomenon in the Levant.

1. Introduction

The Mid-Pleistocene is undoubtedly one of the most interesting epochs in human evolution, and at the same time one of the most enigmatic. It was characterized by alternating glacial and interglacial stages, accompanied by numerous short but severe climatic oscillations within these stages. While ice shields expanded, vegetation zones shifted southwards, and likely also human occupation in harsh regions disappeared, respectively, were limited to southern refugia (Dennell et al., 2011). In contrast, in warmer periods hominins survived as far north as Suffolk in East Anglia, 52° N (Parfitt et al., 2010). While we have not more than vague ideas how the genus *Homo* evolved in this phase of changing environmental conditions, we know that towards the late Mid-Pleistocene two different human demes appeared in the Old World: Neanderthals (NEA), and anatomically modern humans (AMH).

The hominin fossil record of the Mid-Pleistocene is characterized by a high morphological variability, sometimes referred to as the “muddle in the middle” (Harvati et al., 2010; Buck and Stringer, 2014). Fossil findings from this period are regarded by some as members of *Homo heidelbergensis*, but a clear definition of this taxon is lacking (Stringer, 2012). Specimens from Africa (e.g., Bodo, Kabwe, Elandsfontein, Ndutu), Asia (e.g., Dali, Jinniushan, Yunxian),

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and Europe (e.g., Mauer, Petralona, Arago, Bilzingsleben) show a mosaic of primitive and derived features to a different extent and are lumped into this taxonomical container by some, but not all authors (see Stringer, 2012 and references therein).

Whether Neanderthals developed via a gradual "accretion process" based mainly on genetic drift which requires partial or complete isolation (Hublin, 1998; Harvati et al., 2010), or via a model involving selection and continued genic exchange with other populations (Hawks and Wolpoff, 2001), is unclear. The approximate timeframe when NEA and AMH demes separated can be estimated using morphological or genetic data. Gómez-Robles et al. (2013), for instance, find no suitable candidate for the last common ancestor in the fossil record, but hypothesized that a European clade originated around 1 million years ago. Based on genetic data, the split between the populations leading to modern humans and Neanderthals is placed within the Mid-Pleistocene [370 thousand years ago (ka) (Noonan et al., 2006); 440–270 ka (Green et al., 2010); 480–425 ka (Endicott et al., 2010); 589-553 ka (Prüfer et al., 2014)] but the taxonomy of the last common ancestor to NEA and AMH remains undetermined. The *Homo* remains from Sima de los Huesos (SH; Spain), currently dated to 427 ka (Arnold et al., 2014), show very close morphological relationships with Neanderthals (Martinón-Torres et al., 2012). As Stringer (2012) stated, reclassifying the SH material as an early form of *H. neanderthalensis* would remove most of the data supporting a European chronospecies of *H. heidelbergensis-H.neanderthalensis*.

While it remains also unclear whether a potential last common ancestor of NEA and AMH might be found in Africa, Europe, or Asia (Rightmire, 2008; Martinon-Torres et al., 2011; Meyer et al., 2012; Stringer, 2012), or if a continuing admixture of several populations from different regions, probably under source-sink dynamics (Eller et al., 2004; Dennell et al., 2011), led to the two demes, the Levant – located at the crossroads between the three continents – is geographically a potential play ground for these developments. Doubts have nevertheless been raised (Martinón-Torres et al., 2011) if a passage from sub-Saharan Africa to the Levant might have been possible in the time frame between 500 and 300 ka due to the large desert areas in north-east Africa. Still, the unique geographical position of the Levant could have allowed admixture of longitudinally migrating population streams between Europe and Asia, and yet also Africa, if a passage was possible. To further complicate the picture, another recently defined hominin group has appeared in Asia, the Denisovans (Reich et al., 2010). They exist rather as a genetic construct than as a morphologically evident taxon, but they seem to be closer related to Neanderthals (and SH; Meyer et al., 2012) than to modern humans. Geneticists calculated a split time between Denisovans and Neanderthals roughly at 380 ka (Prüfer et al., 2014). Their origin is undetermined, but we cannot exclude that Denisovans, or their immediate precursors, inhabited the Levant. Southwestern Asia is also interesting from another, much later, perspective: It is the home of some of the first anatomically modern humans which were found outside Africa [Skhul, Qafzeh, ~120–90 ka (Mercier et al., 1993)], and at the same time it is the home of those Neanderthals [Tabun, 122 ka (Grün and Stringer, 2000, but could be younger); Kebara 60 ka (Schwarcz et al., 1989); Amud 70–50 ka (Valladas et al., 1999)] that were found geographically closest to Africa (which they never reached, according to our fossil record).

Recently, the Mid-Pleistocene Qesem Cave (QC) near Tel Aviv in Israel has yielded several hominin teeth and abundant faunal, as well as cultural remains. The stratigraphic sequence present at the cave was dated between 420 and 200 ka (Gopher et al., 2010; Mercier et al., 2013). The hominins at QC are associated with the Acheulo-Yabrudian Cultural Complex (Barkai et al., 2009; Barkai and Gopher, 2013). A first description of eight teeth has been published by Hershkovitz et al. (2011). Based on qualitative assessments and traditional linear measurements they already pointed out the ambiguous morphological affinities of the Qesem teeth to anatomically modern humans and Neanderthals. Since then, additional five isolated teeth were found in the cave (Hershkovitz et al., 2016). One of them is a right lower second molar which is described and used in this contribution.

We focus on the mandibular third and fourth premolar (P_3 and P_4, respectively) from one individual (Hershkovitz et al., 2011), dated to about 350 ka, and a lower second molar (M_2) from another individual, which at least post-dates 300 ka (Fig. 2). The reason is that these three teeth represent some of the oldest material from the Qesem cave. We use 3D geometric morphometric methods which capture the external and internal geometry of the teeth. This allows analyses of shape and size independent from each other. Our goal is a thorough quantitative description of the 3D geometry of the three QC teeth, and a morphological comparative study with other Pleistocene and Holocene material. Our approach is a phenetic rather than a cladistics one. Given the diffuse picture of Mid-Pleistocene human evolution in general, we do not aim at a definite taxonomic classification at this point.

2. Materials and methods

The sample (Table 1) consists of the three teeth from Qesem Cave P_3-QC9, P_4-QC10, and M_2-QC12, several Neanderthals from Europe and the Levant, Late-Pleistocene (~127–10 ka[1]) anatomically modern humans from the Levant, epipaleolithic Natufians, and a quite diverse sample of recent modern human populations from various geographic regions, among them Khoesan, Papuans, Australian aboriginals, Middle Europeans, Avars (7th–8th century Euro-Asian nomads), and recent Bedouins from Israel. The accessibility of high-resolution 3D data of well-preserved teeth from the Mid-Pleistocene (~781–127ka[1]) is unfortunately very low. Teeth are either missing, or broken, too worn, of a different tooth type, or simply not accessible to us or for scanning in general. Nevertheless, we could consider some Early- (>781 ka[1]) to Mid-Pleistocene lower premolars and molars, including Mauer (the type specimen of *Homo heidelbergensis*), Bilzingsleben E6[2] (*Homo heidelbergensis* or *Homo erectus*; see Vlcek et al., 2002; Stringer, 2012), Ehringsdorf F and G [early Neanderthals according to their old age (Grün et al., 1988; van Asperen, 2012) and their near-Neanderthal or transitional morphology, see e.g. Vlcek (1993) and Smith (1984)], and some Sangiran (S7) Javanese *Homo erectus*.

The QC teeth and most of the comparable material were μCT-scanned at the Core Facility for Micro-Computed Tomography at University of Vienna with a custom built VISCOM X8060 (Germany) μCT scanner with slightly differing scan parameters (adjusted for each specimen): 140–160 kV, 300–400 μA, 1400–2000msec, diamond high performance transmission target, 0.75 mm copper filter, isometric voxel sizes between 9 and 44 μm. X-ray images were taken from 1440 different angles. Using filtered back-projection in VISCOM XVR-CT 1.07 software, these data were reconstructed as 3D volumes with a colour depth of 16,384 grey values. The Ehringsdorf and Bilzingsleben specimens were made available for scanning by the Thüringisches Landesamt für Denkmalpflege und Archäologie Weimar, all the Israeli material by the Tel Aviv University. Other comparable data were obtained from existing collections and data

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[1] http://quaternary.stratigraphy.org/definitions/pleistocenesubdivision/.

[2] The Bilzingsleben E6 specimen is still partly embedded in a stone matrix and not extensively described. It was only classified as "lower P1-2 sin." by Vlcek (2011). Looking at its morphology after virtual removal from the stone matrix, we assess the specimen as a left lower P_4.