Journal of Human Evolution 93 (2016) 63–81

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

A dental perspective on the taxonomic affinity of the Balanica mandible (BH-1)

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ARTICLE INFO

Article history:
Received 24 January 2014
Accepted 31 January 2016
Available online 3 March 2016

Keywords:
Hominin
Middle Pleistocene
Enamel-dentine junction (EDJ)
Mandible
Molars
MicroCT

ABSTRACT

The Middle Pleistocene represents a period of critical importance in human evolution, marked by encephalisation and dental reduction, and increasing diversification of temporally and spatially distributed hominin lineages in Africa, Asia and Europe. New specimens, especially from areas less well represented in the fossil record, can inform the debate on morphological changes to the skeleton and teeth and the phylogenetic course of human evolution during this period. The mandible from the cave of Mala Balanica, Serbia has recently been re-dated to at least 400 ka, and its well-preserved dentition presents an excellent opportunity to characterize molar crown morphology at this time period, and re-examine claims for a lack of Neandertal affinities in the specimen. In this study we employ microtomography to image the internal structure of the mandibular molars (focusing on the morphology of the enamel-dentine junction, or EDJ) of the BH-1 specimen and a comparative sample ($n = 141$) of *Homo erectus* sensu lato, *Homo neanderthalensis*, Pleistocene *Homo sapiens*, and recent *H. sapiens*. We quantitatively assess EDJ morphology using 3D geometric morphometrics and examine the expression of discrete dental traits at the dentine surface. We also compare third molar enamel thickness in BH-1 to those of *H. neanderthalensis* and both Pleistocene and recent *H. sapiens*, and document previously unreported morphology of the BH-1 premolar and molar roots. Our results highlight the reliability of the EDJ surface for classifying hominin taxa, indicate a primitive dental morphology for BH-1 molars, and confirm a general lack of derived Neandertal features for the Balanica individual. The plesiomorphic character of BH-1 is consistent with several competing models of Middle Pleistocene hominin evolution and provides an important regional and temporal example for reconstructing morphological changes in the mandible and teeth during this time period.

1. Introduction

The hominin fossil record of Middle-Late Pleistocene Europe is typically characterized by the presence of three species: *Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo sapiens*. The definition of *H. heidelbergensis* and its relationship with contemporaneous African forms assigned to *Homo rhodesiensis* are hotly debated (Arsuaga et al., 1997; Hublin, 2009; Stringer, 2012), as are early, intermediate, or late times of divergence between the African lineage leading to *H. sapiens*, and the Eurasian lineage leading to *H. neanderthalensis* (Bischoff et al., 2007; Rightmire, 2008; Hublin, 2009). Furthermore, the evolutionary relationship between material from Sima del Elefante and *Homo antecessor* from Gran Dolina and later *Homo* species requires further investigation (Bermúdez de Castro and Martinón-Torres, 2013; Bermúdez de Castro et al., 2015). For authors defining *H. heidelbergensis* as an Afro-European species, this taxon is considered to be the last common ancestor of Neandertals, Denisovans, and modern humans (Mounier et al., 2009; Stringer, 2012). Other authors define *H. heidelbergensis* as a chronospecies of the Neandertal lineage restricted to western Eurasia

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http://dx.doi.org/10.1016/j.jhevol.2016.01.010
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(Arsuaga et al., 1997; Rosas and Bermúdez de Castro, 1998) and delineate the African Middle Pleistocene specimens as a separate species, *H. rhodesiensis*, which was ancestral to modern humans. Additionally, the timing and process of the emergence of Neandertal morphology in western Eurasia continues to be debated in light of current paleontological and paleogenetic evidence (Hublin, 2009; Green et al., 2010; Martinón-Torres et al., 2012; Meyer et al., 2012, 2014; Bermúdez de Castro and Martinón-Torres, 2013; Arsuaga et al., 2014; Prüfer et al., 2014).

There are a number of models that have been proposed to explain Middle Pleistocene hominin evolution and in particular the eventual appearance of so-called classic Neandertal morphology. The organismic model (Rosas et al., 2006) presents the emergence of Neandertals as rather abrupt with a phenotype that is easy to differentiate from that of its ancestor. This distinct speciation event occurred at around 300–250 ka and coincides with the appearance of the Mousterian industries in Europe (Rosas et al., 2006). An alternative, the accretion model, proposes that western Eurasian populations accumulated Neandertal derived features in a gradual and mosaic manner during the Middle Pleistocene. According to this model, the skull, the occipital, and the facial areas are the first to display Neandertal derived conditions in Europe ca. 400 ka and the mosaic nature of this morphological change makes it hard to delineate early Neandertals from their precursors (Dean et al., 1998; Hublin, 1998, 2009; Stringer and Hublin, 1999; Freidline, 2012; Arsuaga et al., 2014). More recently, the source-sink model (Dennell et al., 2011) and the CADE (central area of dispersals of Eurasia [Bermúdez de Castro and Martinón-Torres, 2013]) models emphasize the likelihood of repeated events of regional extinctions and re-colonisation (Harvati et al., 2003; Hublin and Roebroeks, 2009) leading to complex patterns of morphological change and the eventual appearance of the derived Neandertal morphology. Like the accretion model, this model emphasizes the role of demographic fluctuations and local extinctions. During glacial periods, northern populations would become isolated, resulting in repeated episodes of population fragmentation, isolation, genetic drift and bottlenecks, and, potentially, local extinctions. During interglacial periods, recolonization of the northern areas by southern populations would occur and, in the event of surviving northern populations, result in admixture. The southern populations, located in glacial refugia, would not undergo the same levels of fragmentation, isolation, and extinction as the more northern populations, resulting in different degrees of genetic drift and the fixation of derived morphologies. If the proposed date ca. 430 ka for Sima de los Huesos [Arnold et al., 2014] is accurate, this model can explain why the material from this site shows a stronger derived Neandertal affinity than the more primitive Arago and Ceprano specimens dated to >350 ka (Falguereres et al., 2004) and ca. 350 ka (Nomade et al., 2011), respectively. Critical to evaluating the strength of these various models for explaining Pleistocene hominin evolution are temporally and regionally distinct fossil hypodigms that can elucidate the variation and pattern of craniodental evolution.

Regarding the dentition, researchers have demonstrated that tooth crown morphology (Benazzi et al., 2011), discrete dental traits (Bailey et al., 2011), and relative enamel thickness (Olejniczak et al., 2008; Smith et al., 2012) can discriminate Neandertals from *H. sapiens*. As briefly mentioned above, the Sima de los Huesos (SH) hominin sample displays a number of features shared with later Neandertals. This is particularly evident in cranial (Arsuaga et al., 2014) and dental (Martinón-Torres et al., 2012) morphology, and the age of the SH sample provides strong support for an early onset of the Neandertal accretion model (Hublin, 2009; Arsuaga et al., 2014). It has also been argued that, dentally, the SH material is so highly derived towards the typical Neandertal condition compared to penecontemporaneous Middle Pleistocene samples (and even to later Neandertals) that a linear version of the accretion model may be untenable (Martinón-Torres et al., 2012). Additionally, characteristics that were previously believed to be indicators of a discrete Neandertal affinity (e.g., the distal displacement of lingual cusps and a large bulging hypocone in the upper first molar morphology [Bailey, 2004]) have been found present in the Early Pleistocene *H. antecessor* specimens from Gran Dolina, whilst lacking in the much younger Arago specimen (Gómez-Robles et al., 2007). It therefore seems that local extinctions may have played a major role in the pruning of varied early Neandertal populations, and in the fixation of the Neandertal phenotype (Hublin and Roebroeks, 2009; Arsuaga et al., 2014). This complex picture of craniodental variation highlights the importance of other Middle Pleistocene hominin material for reconstructing the phylogeny of hominins during this period.

The site of Balanica in Serbia recently yielded a partial mandible (BH-1) that has implications for our understanding of Middle Pleistocene hominin evolution (Roksandic et al., 2011). Based on the observed mandibular and dental morphology of the specimen, Roksandic et al. (2011) concluded that it is plesiomorphic in character and exhibits no Neandertal affinities. The recent re-dating of the Balanica specimen to a minimum age of 397–525 ka (Rink et al., 2013) is in keeping with its primitive morphology. However, given that this specimen overlaps in geological age with the material from SH (which exhibits derived Neandertal features), it is particularly relevant to compare its dental morphology within the context of Neandertal and modern human dental variation. Its location in the Balkans, a glacial refugium at the cross-roads between Europe and Western Asia that did not experience the level of genetic isolation present in the north-western populations, makes this a crucial case study regarding Middle Pleistocene hominin evolution. Based on various animal models of postglacial recolonisation of Europe, Dennell et al. (2011) note that the Balkan region is potentially one of the principal hominin refugia in Europe. The underrepresentation of the Balkan region in the hominin fossil record is therefore a real concern for understanding the timing and nature of Middle Pleistocene hominin evolution.

In this paper we present a detailed description and analysis of the lower molars of the Balanica mandible (Fig. 1) in order to characterize dental morphology in the Balkans at this time and to further clarify its taxonomic affinity. Due to a lack of comparative data for Middle Pleistocene specimens assigned to *H. heidelbergensis* (sensu stricto, s.s., or sensu lato, s.l.), besides the Mauer specimen itself, we focus our analysis on assessing the evidence for Neandertal affinities in the BH-1 dentition. We report on the premolar alveolar morphology, the size and form of the molar roots of BH-1, and examine enamel thickness in the third molar in a 2D mesial plane of section. Finally, we examine the morphology of the enamel-dentine junction (EDJ), which has been shown to carry a strong taxonomic signal (Skinner et al., 2008a, 2009; Crevecoeur et al., 2014) and helps elucidate the expression of discrete dental traits traditionally studied at the enamel surface (Skinner, 2008; Skinner et al., 2008b, 2009; Bailey et al., 2011; Ortiz et al., 2012; Martínez de Pinillos et al., 2014; Martinón-Torres et al., 2014).

2. Materials and methods

2.1. Study sample

The comparative sample for the quantitative analysis of molar roots is from Kupczik and Hublin (2010) and for enamel thickness is from Olejniczak et al. (2008). The study sample for the EDJ and discrete trait analysis is listed in Table 1 and includes specimens of *Homo erectus* s.l., *H. neanderthalensis*, Pleistocene *H. sapiens*, and