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Revising the hypodigm of *Homo heidelbergensis*: A view from the Eastern Mediterranean

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ABSTRACT

The hominin mandible BH-1 from the Middle Pleistocene cave of Mala Balanica suggested the possibility that human populations in this part of the continent were not subject to the process of Neanderthalization observed in the west. We review the paleoanthropological evidence from the Central Balkans in the context of the Eastern Mediterranean geographic entity. The current hominin fossil record of the early Middle Pleistocene in the region suggests that Europe was inhabited by two different populations: a population in the west of the continent with derived Neanderthal morphology; and a more variable population in the east characterized by a combination of plesiomorphous and synapomorphous traits. We suggest that – in order to continue using the nomenclature of *Homo heidelbergensis* – the current hypodigm needs to be revised to include only the specimens from the latter group.

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1. Introduction

The hominin mandible BH-1 from the Middle Pleistocene cave of Mala Balanica (Roksandic et al., 2011; Skinner et al., 2016) suggested the tantalizing possibility that human populations in this part of the continent were not subject to the process of Neanderthalization observed in the west. Neanderthals have been confirmed as descendants of Western European Middle Pleistocene hominins who spread northwards and eastwards in a pulsing fashion dictated by retreating glaciers. The demographic “sinks and sources” model proposed by Dennell et al. (2011) postulated a demographic source population in the central area for the dispersal in Eurasia (CADE) and situated it in South West Asia (SWA). Since there were no significant geographic barriers between SWA and the Balkans during either glacial or interglacial times, they should be examined as a single geographic entity, which we call here the Eastern Mediterranean Area (EMA). We hypothesize that the Pleistocene population within the EMA stayed in more or less

sustained contact – reducing the role of isolation by distance in the evolution of this group; therefore, hominin evolution in the EMA was likely not under the same constraints as in Western Europe. In this paper, we provide an overview of the existing Middle Pleistocene hominin fossil material from the EMA and compare it to the better researched and better understood fossil record of Western Europe. Further detailed cladistic studies on the original material will be necessary to test the proposed hypotheses. Equally important is the need to step up the research effort in the EMA to uncover more (and more complete) hominin material which will help answer some of the questions raised here.

The Middle Pleistocene (MP) fossil record plays a crucial role in understanding later human evolution: this was the period characterized by greater encephalization, accompanied by dental reduction and associated changes in morphology, as well as changes in behavioral repertoire (Ruff et al., 1997; Roebroeks, 2001; Rightmire, 2004, 2013). Since Stringer (1983) re-introduced *Homo heidelbergensis* (Schoetensack, 1908) as a species, the MP human fossil record of Europe has been associated with this nomenclature. The fossil hominin specimens that comprise this hypodigm have been subject to a lot of shifting opinions and debate (for an overview see: Bae, 2010; Stringer, 2012; Rightmire, 2013) variably including European and African, and sometimes, hypothetically,

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even East Asian specimens (Rightmire, 1998; Stringer, 2002). What is currently considered as European *H. heidelbergensis* (*H. heidelbergensis sensu stricto*) is a mixture of specimens clearly ancestral to Neanderthals and those without demonstrable Neanderthal traits (Arsuaga et al., 1997; Rosas and Bermúdez de Castro, 1998; Hublin, 2009). Notably, it includes the Sima de los Huesos material, with a large number of distinctly Neanderthal traits (Arsuaga et al., 2015a). According to Bermúdez de Castro et al. (2011, 2015), even the Early Pleistocene material from Europe (Gran Dolina-TD6) shows derived Neanderthal traits. Along with this direct Neanderthal lineage, represented by the Sima material, Martínón-Torres et al. (2012) suggested that we should recognize an additional lineage in Europe, which is not as closely related to Neanderthals, and Stringer (2012) suggested that the use of *Homo heidelbergensis* could be limited to the latter group. Considering that morphological differences between African and European specimens are not clear cut, *Homo heidelbergensis* could be equated with a purported MP Afro-European population (Rightmire, 1998, 2009; Mounier et al., 2009, 2011; Mounier and Lahr, 2016) which was ancestral to both Neanderthal (European) and modern human (African) lineages. The recognition of continuity between the Sima de los Huesos material and Neanderthals in Europe and the lack of distinct morphology associated with non-European Heidelberg questions the existing definitions of *Homo heidelbergensis (sensu lato)* as a species (Mounier and Caparros, 2015). Stringer (2012) suggested that *Homo heidelbergensis* as a species makes sense only if Sima de los Huesos is removed from the hypodigm which, on the other hand, could potentially include specimens as geographically distant as Mauer in Germany, Bodo in Ethiopia, and Yunxian in China (although the east Asian specimens were tentatively associated with the Denisovans). Thus *H. heidelbergensis* would be distinct enough from smaller-brained Erectines and represent the MRCA of Neanderthals, Denisovans, and modern humans. The occurrence of Neanderthal traits in Heidelberg in Europe would still require an explanation, and would call for limited hybridization events.

Reviewing the changes in positions of different researchers becomes increasingly difficult and illustrates that the reintroduction of *Homo heidelbergensis* did not result in a greater understanding of the relationship between MP African hominins at the origin of our lineage and the MP European fossils at the origin of the Neanderthal lineage. Important questions remain open: 1) what was the relationship of European *H. heidelbergensis* to the earlier European specimens from Gran Dolina and Sima del Elefante in Spain (Bermúdez de Castro and Martínón-Torres, 2013; Bermúdez de Castro et al., 2015); 2) what was their relationship to the contemporaneous African specimens assigned to *H. heidelbergensis sensu lato*, or to *H. rhodesiensis* (Arsuaga et al., 1997; Hublin, 2009; Stringer, 2012); 3) when did the split between the African and Eurasian lineages occur (Bischoff et al., 2007; Hublin, 2009; Rightmire, 2009); and 4) what was the relationship of African and European MP hominins with contemporaneous Asian specimens (Bae, 2010)?

On the basis of genetic data, the split between the ancestors of Neanderthals and those of modern humans was postulated to have happened around 300–400 ka (Noonan et al., 2006; Endicott et al., 2010). The oldest hominin aDNA retrieved from Sima de los Huesos shows a mitochondrial genome more closely related to “Denisovans” (Meyer et al., 2014): the latter are a group of hominins only known from their DNA and a small number of teeth (Krause et al., 2010; Meyer et al., 2012) to which any number of currently known morphologies could theoretically be assigned. However, nuclear DNA of an additional two individuals from the same site shows a closer relatedness to Neanderthals (Meyer et al., 2016). Together

with aDNA results and the presence of Neanderthal autapomorphies in Sima de los Huesos, the re-dating of the material to 430 ka (Arsuaga et al., 2014) supports the estimate by Langergraber et al. (2012) of 420–770 ka for the initial separation of Neanderthal, Denisovans and contemporary African populations. Furthermore, interbreeding between Neanderthals and modern humans, long held to be improbable based on the mtDNA evidence (Serre et al., 2004) was confirmed by the examination of whole genome sequences of several Neanderthals (Green et al., 2010), while the putative date for introgression was pushed back to 270 ka (Posth et al., 2017). A recent review by Pääbo (2015: 313) states that the genomes of Neanderthals and Denisovans suggest that “our ancestors were part of a web of now-extinct populations linked by limited, but intermittent or sometimes perhaps even persistent, gene flow” complicating the famous “muddle in the middle” (Isaac, 1975). Hawks’ (2013) assertion that all three groups were part of the biological species of *Homo sapiens* – which could have been far more variable in the Middle Pleistocene than it is today – seems more plausible than ever.

There is no denying that Neanderthals are a morphologically distinct population. With their recognizable derived morphology, long persistence of the population in Europe and remarkable fossil record, Neanderthals dominate both popular imagination and scientific research, and our quest for understanding these remarkable fossil humans and contrasting them to our own condition has produced innumerable treatises, not all of which are to the credit of the science we practice. Their sheer number compared to the less well-known Middle Pleistocene record of Asia and Africa, and a practically nonexistent fossil record from wide stretches of Eurasia – among which the Balkans figure as a gaping hole – ensures that the difference between “us” and “them” is either negated or essentialized by those who either support inclusion or exclusion of this group into our common ancestry. Paleoanthropology seems to go through a pendulum motion of assigning and removing a species status to Neanderthals, prompting many to prefer the usage of colloquial names such as Heidelberg and Neanderthals rather than a taxonomic nomenclature (Cartmill and Smith, 2009). However, morphological and genetic differences exist, and in order to acknowledge the extent of variation in the Middle Pleistocene and compare evolutionary trajectories across the Old World, Howell (1996, 1999) introduced the concept of “paleo-deme” or “p-deme” which allows us to distinguish between local populations and discuss their possible phyletic relationships without implying (or rejecting) speciation events. Based on the current fossil record, Neanderthals are a distinctly western European-derived population whose morphology is likely linked to isolation induced by glacial cycles (Hublin, 2009). This isolation should not be construed as absolute and/or resulting from insurmountable geographic barriers, but rather as a product of the peripheral position of the westernmost peninsula and its geographic distance from other contemporaneous hominin populations. With Sima de los Huesos at the far west of the continent presenting undeniable evidence of derived Neanderthal morphology from at least 430 ka (Gómez-Olivencia et al., 2007; Martínón-Torres et al., 2012; Arsuaga et al., 2014, 2015b), the lack (or attenuation) of Neanderthal traits in contemporaneous specimens from other parts of Europe needs new explanations.

Given the truncated record of MP fossil hominins, the continuous, overlapping, and mosaic nature of morphological variation in ancient populations, and the increasing recognition of some level of admixture across hominin groups (Smith et al., 2016), the fossil records from less well known areas of Eurasia become crucial for understanding the timing and mechanism of the split between the Neanderthal and modern human ancestral lineages. Recognizing

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