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Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins

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ABSTRACT

A better understanding of the evolutionary relationship between modern humans and Neanderthals is essential for improving the resolution of hominin phylogenetic hypotheses. Currently, four distinct chronologies for the timing of population divergence are available, ranging from the late Middle Pleistocene to the late Early Pleistocene, each based on different interpretations of hominin taxonomy. Genetic data can present an independent estimate of the evolutionary timescale involved, making it possible to distinguish between these competing models of hominin evolution. We analysed five dated Neanderthal mitochondrial genomes, together with those of 54 modern humans, and inferred a genetic chronology using multiple age calibrations. Our mean date estimates are consistent with a process of genetic divergence within an ancestral population, commencing approximately 410–440 ka. These results suggest that a reappraisal of key elements in the Pleistocene hominin fossil record may now be required.

Introduction

Background

The resolution of evolutionary relationships amongst Middle Pleistocene hominin populations is an important and long-standing problem in the study of human evolution (Howell, 1994; McBrearty and Brooks, 2000; Harvati et al., in press). Central to this debate is the extent to which it is possible to distinguish between different hominin species and to infer ancestral relationships among them from the limited physical evidence of the Pleistocene fossil record. There remain considerable differences in approaches to hominin classification, with some workers preferring to regard Neanderthals as part of a more broadly defined *Homo sapiens* species (e.g., Bräuer, 2008; Wolpoff, 2009), or simply not to apply taxonomic categories at all (e.g., Trinkaus, 2005). However, most palaeoanthropologists accept the validity of a more restricted diagnosis of *H. sapiens* (sometimes known as "Anatomically Modern Humans") and *Homo neanderthalensis*, to refer to evolutionary, rather than biological, species of hominins (Simpson, 1950).

There is much less consensus, however, regarding the diagnosis and origin of the species ancestral to both modern humans and Neanderthals (see e.g., Stringer, 2002; Tattersall and Schwartz, 2006; Rightmire, 2008; Wood and Lonergran, 2008; Hublin, 2009; Harvati et al., in press). The current palaeoanthropological models for the splitting of modern humans and Neanderthals from an ancestral population can be grouped into four broad chronological categories (Fig. 1). These are the late (~250 ka), middle (~400 ka), and early (~600 ka) periods of the Middle Pleistocene, and the late Early Pleistocene (~800 ka). Whilst these differences might appear to be relatively minor within the broader evolutionary context of *Homo*, they have important taxonomic implications for the genus as a whole, and for the origin of our own species.

Formally evaluating the evidence for each of these four models will help to assess the suitability of the *H. sapiens*–*H. neanderthalensis* species concept overall (Harvati et al., 2004; Trinkaus, 2005; Bräuer, 2008; Wolpoff, 2009). Here, we investigate the potential of genetic data to provide an independent chronology to evaluate the main species diagnoses of *H. sapiens*, *H. neanderthalensis* and the population ancestral to both.

The four models

The late Middle Pleistocene model (Fig. 1a) posits a single ancestral African population of the species, *H. helmei* (~150–300 ka),

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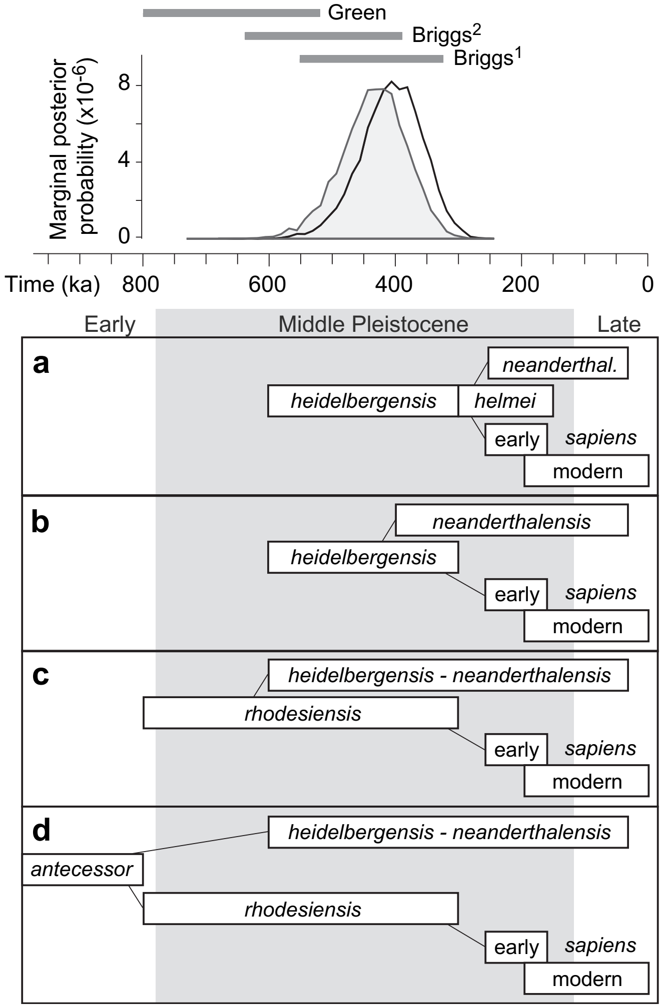

Figure 1. Summary of genetic date estimates in relation to four candidate chronologies for the evolution of Neanderthals and modern humans. The 95% credibility intervals are given for three published estimates of the *H. neanderthalensis*–*H. sapiens* divergence time, while two estimates from the present study are given as posterior age distributions. Our estimates were obtained using Bayesian phylogenetic analysis of third codon sites from the mitochondrial genomes of 54 modern human, five Neanderthals, one common chimpanzee, and one bonobo. The analyses were calibrated using the radiometric dates of the five Neanderthals, as well as an age calibration for the *Homo*–*Pan* divergence of either 6.0–7.0 Ma (empty curve with black outline) or 6.5–7.5 Ma (filled curve with grey outline). The four candidate chronologies given in the lower panels are: (a) late Middle Pleistocene; (b) mid-Middle Pleistocene; (c) early Middle Pleistocene; and (d) late Early Pleistocene. Details of these four chronologies are given in the text. All species in these panels are recognised here as members of the genus *Homo*.

based on the Florisbad partial cranium. Dated at ~260 ka (Fig. 2), this taxon is presumed to be associated with the beginnings of a novel lithic technology (Foley and Lahr, 1997; Lahr and Foley, 2001). This Mode 3 hypothesis suggests that both modern humans and Neanderthals first appeared in the archaeological context of Levallois prepared cores and that the Florisbad individual is a member of the population ancestral to both species. In this scenario, therefore, population divergence occurred subsequent to the existence of the Florisbad individual and cannot be earlier than ~260 ka.

The mid-Middle Pleistocene model (Fig. 1b) has a single Eurafrican species, ancestral to *H. neanderthalensis* and *H. sapiens*, containing African fossils such as Broken Hill and Bodo, and European specimens such as Arago and Petralona (Fig. 2), with a possible age range of ~300–650 ka. Stringer (2002) and Rightmire (2008) place the Mauer mandible in this assemblage, thus assigning the species name *Homo heidelbergensis*. However, Hublin (2009) has recently argued that this problematic fossil should be excluded from any current species definitions (but see Mounier et al., 2009, for an alternative view), with precedence instead given to the Broken Hill cranium, thus prioritising the name of *Homo rhodesiensis* for this ancestral species.

The early Middle Pleistocene model (Fig. 1c) is based on the alternative suggestion that *H. heidelbergensis* is not known from Africa, but instead is only present in western Eurasia. Under this scenario, there is a European chronospecies of *H. heidelbergensis- H. neanderthalensis*, which is part of a continuum from the early Middle Pleistocene through to the Late Pleistocene. Defined in this way, the lineage leading to the Neanderthals in Europe includes the extensive Atapuerca Sima de los Huesos (SH) sample (Fig. 2), which already displays clear Neanderthal affinities (Arsuaga et al., 1997; Rosas, 2001), particularly in the dentition (Martinón-Torres et al., 2007). According to the latest dates proposed for the SH material, which argue for a minimum age of ~530 ka ($600^{+\infty}_{-66}$ ka) (Bischoff et al., 2007), the population divergence between this European lineage and that leading to *H. sapiens* likely preceded 600 ka. There is currently no strong argument for extending the ancestral population (represented as *H. rhodesiensis* in Fig. 1c) beyond 650 ka, unless the Tighenif fossil material (Klein, 2009) is included in this species diagnosis.

The late Early Pleistocene model (Fig. 1d) has a European hominin (*Homo antecessor*) as the ancestor to a *H. rhodesiensis*–*H. sapiens* lineage in Africa and a *H. heidelbergensis*–*H. neanderthalensis* lineage in Europe, suggesting a population divergence soon after 800 ka (Bermúdez de Castro et al., 1997; Arsuaga et al., 1999). There are variants of this model relating to the various Atapuerca fossil samples; for example, new interpretations of the early Elefante–Gran Dolina material assigned to *H. antecessor* (Fig. 2) favour a hypothetical Asian ancestor derived from *Homo erectus*, which is then either replaced or absorbed by a dispersal of *H. heidelbergensis*, also derived from an Asian (*H. erectus*) ancestor (Martinón-Torres et al., 2007; Bermúdez de Castro et al., 2008; Carbonell et al., 2008). However, this interpretation might push the minimum date for the divergence of the lineages leading to modern humans and Neanderthals back to more than one million years (Carbonell et al., 2008).

An independent chronology

When the Pleistocene fossil record, and different analytical approaches applied to it, permits such disparate interpretations, it is not surprising to find secondary lines of evidence employed to augment the positions of the various models. These have included palaeoenvironmental studies (climate) and archaeology (lithics). However, to avoid a tendency towards circularity, it is preferable to have an independent chronology for the divergence between humans and Neanderthals. This would allow the palaeoanthropological evidence to be assessed without any *a priori* diagnosis of an ancestral species, or the linking of particular taxonomic categories to the production of specific techno-complexes (e.g., Lahr and Foley, 2001; Bermúdez de Castro et al., 2008).

The availability of genomic sequence data from modern humans and Neanderthals provides an opportunity to generate an independent estimate of the evolutionary timescale for the divergence between *H. sapiens* and *H. neanderthalensis*. Molecular phylogenetic analysis can be performed to estimate the age of the most recent common ancestor (MRCA) of the two lineages (e.g., Green et al., 2006; Briggs et al., 2009). This can provide a more concrete *terminus ante quem* (maximum bound) because the reconstructed genealogy provides an uninterrupted line of descent back to a time