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The Status of *Homo heidelbergensis* (Schoetensack 1908)

Chris Stringer

The species *Homo heidelbergensis* is central to many discussions about recent human evolution. For some workers, it was the last common ancestor for the subsequent species *Homo sapiens* and *Homo neanderthalensis*; others regard it as only a European form, giving rise to the Neanderthals. Following the impact of recent genomic studies indicating hybridization between modern humans and both Neanderthals and “Denisovans”, the status of these as separate taxa is now under discussion. Accordingly, clarifying the status of *Homo heidelbergensis* is fundamental to the debate about modern human origins.

THE SPECIES *HOMO HEIDELBERGENSIS*

In 1907, the robustly built mandible that was to become the holotype of *Homo heidelbergensis* was discovered in the Grafenrain sandpit at Mauer, near Heidelberg, Germany, associated with what is now termed a Galerian or Cromerian (early Middle Pleistocene) fauna. The species name was bestowed a year later by Otto Schoetensack,¹ who noted in the Mauer mandible the combination of primitive features (for example, high corpus thickness, very wide ramus, and receding symphysis) and more recent human features, such as small dentition, particularly the canines and anterior teeth. The name

was little used during the earlier part of the twentieth century and, by the 1960s the lumping together of taxa often treated the fossil as a European form of *Homo erectus*.² However, Howell³ took exception to that, arguing that the fossil probably was morphologically distinct enough to represent a separate species.

In 1974, I completed my doctoral thesis, which concentrated on cranial shape comparisons of Neanderthal and modern humans but, along the way, I noted clear phenetic resemblances between the Broken Hill (Zambia) and Petralona (Greece) fossils, and considered both of these to be clearly distinct from Neanderthals.^{4,5} Rather than allocate either of these specimens to *Homo erectus*, I preferred, at that time, to regard them as related primitive forms of *Homo sapiens sensu lato*, eventually assigning them to *Homo sapiens* grade 1 in a gradistic scheme.⁶

Following discussions with Bjorn Kurtén, I became aware of biostratigraphic evidence that elements of the Petralona mammalian faunas were of Cromerian age, potentially comparable to those from Mauer.⁷ Both Kurtén and I considered the possibility that the Petralona cranium could represent a counterpart for the Mauer mandible,^{6,8} even though the

two clearly do not articulate well. In the early 1980s, with a shift to cladistic thinking and influences, I began to gravitate toward the idea that Neanderthals were, after all, a distinct species from *Homo sapiens sensu stricto*, and that this implied the existence of a distinct ancestral species, if *neanderthalensis* and *sapiens* were sister taxa, and *erectus* did not represent the last common ancestor. Through linking Mauer with Petralona and Petralona with Broken Hill, the concept of a Eurafrikan stem species named *Homo heidelbergensis* began to develop.⁹ The following extract and accompanying figure (Fig. 1) summarize the cautious arguments made at that time: “Because at present they cannot be defined satisfactorily by their own distinctive within-group characteristics, it is difficult to justify creating a separate taxon for the Petralona and Broken Hill fossils on the basis of characters they lack, or ones they share with other taxa. Nevertheless, given the need to recognize their similarities to each other, and to other Middle Pleistocene fossils, they could be placed in a separate species, *H. rhodesiensis* or *H. heidelbergensis* (if the Mauer mandible is also included), provided the distinctiveness of the Neanderthals from ‘modern’ *H. sapiens* is also considered worthy of specific recognition (Fig. 1a). Alternatively their possible position as a ‘stem group’ for the Upper Pleistocene hominids could be recognized by the use of a subspecific name for the evolutionary grade they are supposed to represent within *H. sapiens* (Fig. 1b). However, the other possibility that must be considered (Fig. 1c) is that we

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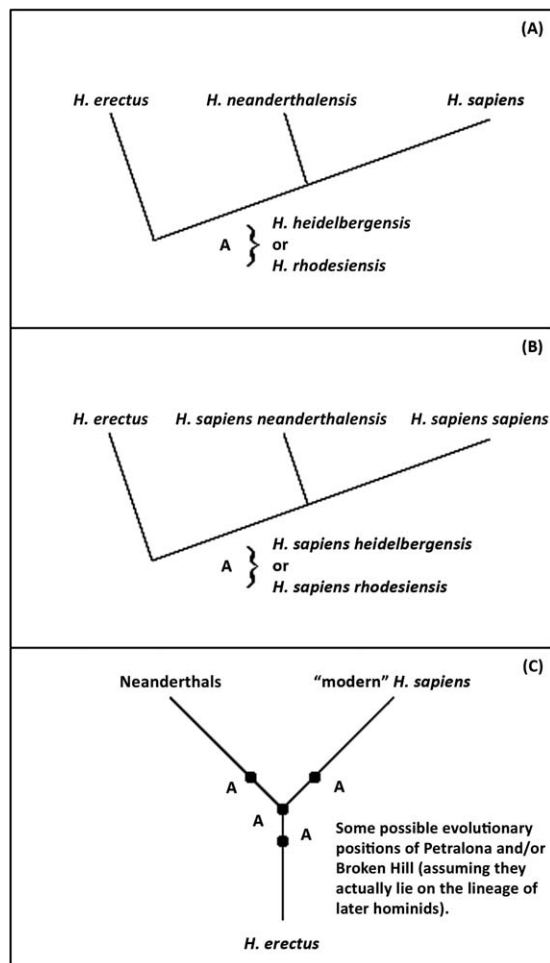


Figure 1. Illustration of the possible phylogenetic relationships of the Petralona and Broken Hill fossils. Redrawn, with permission, from Stringer.⁹

cannot at present resolve the exact phylogenetic position of these hominids because they are close to the point of divergence between Neanderthals and 'modern' *H. sapiens* (assuming that the Neanderthals are not directly ancestral to 'modern' humans). At present I believe this to be quite likely, and that these fossils are close to the morphotype expected in the common ancestor of Neanderthals and 'modern' *H. sapiens*. If this is so, only further careful analysis will allow a decision about the cladistic affinities, and thus the classification, of fossils such as Arago 21, Petralona and Broken Hill."

I began to develop a suite of traits (Table 1; Fig. 2) for grouping Broken Hill and Petralona.¹⁰ European and African fossils such as Bilzingsleben, Vertesszöllös, Bodo 1, and Elandsfontein were added to an enlarged

heidelbergensis hypodigm. A separate study of the first Bilzingsleben cranial finds reinforced their resem-

blance to the Elandsfontein calvaria,¹¹ and the possibility that Middle Pleistocene Chinese and Indian fossils might also belong in this group (Table 2) was raised.^{12,13} Rightmire has adopted a comparable Eurafrikan concept of *heidelbergensis*,^{14,15} while some have preferred to retain a more gradistic concept of *Homo sapiens*, arguing that fossils such as Broken Hill and Bodo are primitive examples of the modern human species.¹⁶ Other workers have used the informal term ante- or preneanderthal for earlier European fossils, including Mauer and Arago, sometimes with a purely chronological meaning, and in other cases implying an evolutionary relationship.¹⁷

This latter option has become increasingly popular with the recognition that the Sima de los Huesos (SH) material displays a mosaic of *heidelbergensis* and *neanderthalensis* features. For such workers, *H. heidelbergensis* could represent an early stage in the accretion model of Neanderthal evolution,^{17,18,35} forming a *heidelbergensis*-*neanderthalensis* continuum. I briefly considered this argument, going so far as to suggest that all *heidelbergensis* material might be lumped into *Homo neanderthalensis*,¹⁹ but I did not persist in that view. However, if the European-only model of *heidelbergensis* is correct, then the non-European components assigned to *heidelbergensis* by workers such as Rightmire and

TABLE 1. Some Traits Observed in *H. heidelbergensis* Fossils

Endocranial volumes overlap those of <i>H. erectus</i> and <i>H. sapiens</i> / <i>H. neanderthalensis</i>
Torus often highly pneumatized laterally, and superiorly into frontal squama
Vault shape parallel-sided in posterior view
Strong and continuous supraorbital torus*
Occipital bone strongly angled*
Strong continuous occipital torus*
Wide interorbital breadth*
Iliac pillar*
Elongated superior pubic ramus*#
Femoral platymeria*#
High arched temporal squama+#
Gracile tympanic+#
Increased midfacial projection expressed through measures of midline nasal prominence+#
In large-faced specimens there may be lack of both canine fossa and infraorbital retraction#
Reduced total facial prognathism+#

*Found in *Homo erectus*; + potential synapomorphies with *H. sapiens*; # potential synapomorphies with *H. neanderthalensis*.

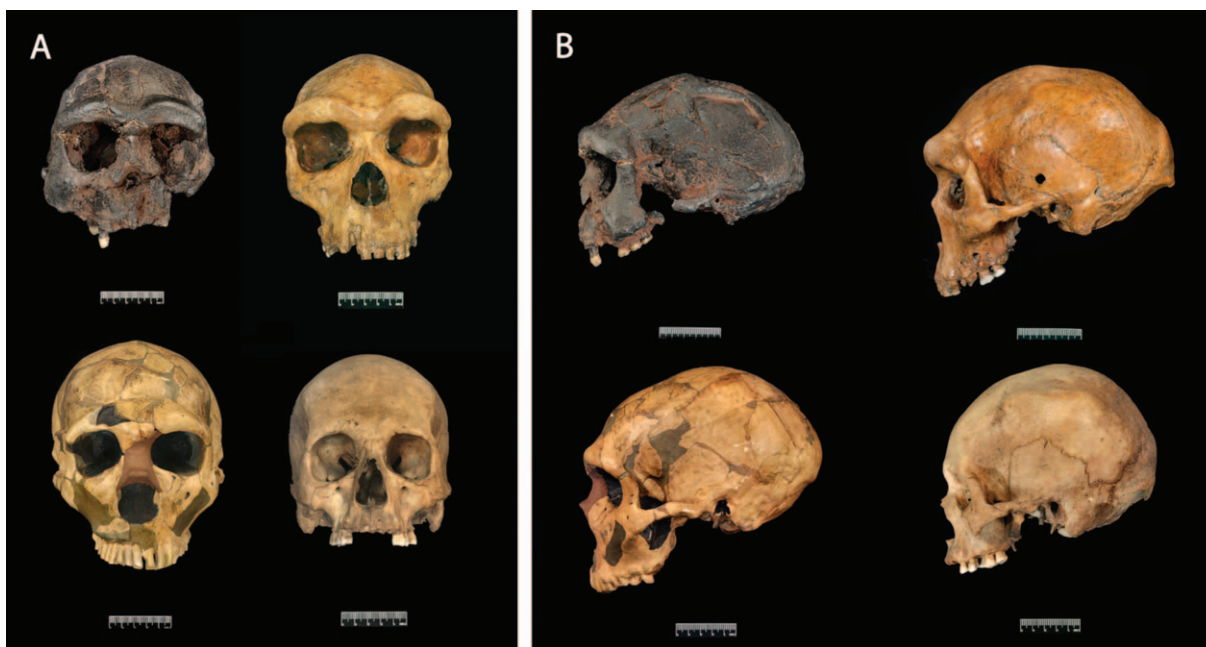


Figure 2. Facial (A) and lateral (B) views of crania. Clockwise from top left: *Homo erectus* (replica, Sangiran, Java), *heidelbergensis* (Broken Hill, Zambia), *sapiens* (recent, Indonesia), and *neanderthalensis* (replica, La Ferrassie, France). All pictures © The Natural History Museum London. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

me, which show few or no Neanderthal apomorphies, would require a separate species names. *Homo rhodesiensis*²⁰ would have priority for that grouping.^{9,21}

RECENT RESEARCH ON THE MAUER MANDIBLE, AND THE SPECIES HYPODIGM

Recently, welcome attention has been given to the Mauer mandible itself, including further dating work.²² Schwartz and Tattersall²³ compared its morphology with that of other Pleistocene hominins, noting its particular resemblance to the Arago 13 mandible. Via the Arago assemblage, they were able to extend their *heidelbergensis* grouping to other European, Chinese, and African fossils, while aligning the SH material with Neanderthals. However, in their view, the derived natures of both the Neanderthal clade and *Homo heidelbergensis* exclude these groups from the ancestry of *Homo sapiens*.

Rak and colleagues⁴¹ noted the idiosyncratic features of the Mauer jaw and argued that “it is not clear whether lumping certain specimens together in this hypodigm is justified

at all. In effect, the morphology of certain specimens does not accord with that of the type specimen. Obviously, the taxonomic identification of skulls lacking a mandible is problematic, but even some mandibles give rise to uncertainty regarding their assignment to the *H. heidelbergensis* hypodigm. In our analysis, the Mauer mandible stands alone in its morphology, which appears to be the outcome of a unique constellation of characters.” This mirrored the view of Hublin,²¹ who argued that the primitive nature of the Mauer mandible and the predominance of cranial material in discussions about Middle Pleistocene hominins rendered it unsuitable as a holotype.

In the most extensive comparative analysis to date, Mounier, Marchal, and Condemi²⁴ concluded that the Mauer mandible and *H. heidelbergensis* could be specifically distinguished from *H. erectus*, *H. neanderthalensis*, and *H. sapiens*. They produced a diagnosis for the species hypodigm based on mandibular fossils such as Mauer, Arago, Montmaurin, and SH. Their inclusion of the Tighenif mandibles extended the species to Africa, but unfortunately they did not include other potential African exam-

ples of *heidelbergensis*, such as Thomas Quarry and Kapthurin, in

TABLE 2. Some Fossils That May Represent *Homo heidelbergensis**

<i>Western Eurasia</i>	
Mauer	
Petralona	
Arago	
Vértesszöllös	
?Bilzingsleben	
?Kocabaş	
?Boxgrove	
?Ceprano	
?Zuttiyeh	
<i>Africa</i>	
Broken Hill 1; tibia E.691; pelvis E.719	
Bodo	
Elandsfontein	
Ndutu	
Kapthurin	
?Hoedjies punt	
?Thomas Quarry	
?Salé	
?Tighenif	
?Berg Aukas	
<i>Eastern Eurasia</i>	
?Narmada	
?Dali	
?Jinniushan	
?Yunxian	

*In my view, the inclusion of fossils such as Steinheim and Montmaurin is still doubtful, while Narmada, Dali and Jinniushan may alternatively represent early “Denisovans.”

their analyses. However, it is worth remembering that a fragment of ramus found at Elandsfontein, possibly associated with the “Saldanha” calvaria, was noted as being remarkably similar to that of Mauer in its shape.²⁵

As mentioned, researchers using metric and multivariate techniques have noted metrical and shape similarities between Petralona and Broken Hill.^{5,14,26} This has been confirmed through the use of geometric morphometrics.^{27,28} For example, Friess,²⁸ excluding the Mauer mandible, commented that “the striking affinities between the holotype of *H. rhodesiensis* (Kabwe) and a European fossil (Petralona), as demonstrated previously and confirmed here, are unlikely to disappear, even if more complete specimens were to be included in the analysis. This makes *H. rhodesiensis* an Afro-European species that retains an *erectus*-like plesiomorphic calvarial shape, but no Neanderthal/*H. sapiens* apomorphies, unless one lumps it with SH5 and Steinheim.” In a further study, Mounier, Condemni, and Manzi²⁹ added the Ceprano calvaria to their comparative analyses. They grouped the Ceprano specimen with Eurasian fossils such as Petralona, SH5, Steinheim, Dali, and Jinniushan, as well as with the Broken Hill cranium. They concluded that in spite of its relatively young chronological age (385–430 ka), the Ceprano fossil could represent a morphologically primitive example of the widely dispersed species *heidelbergensis*.

ARE THE SIMA DE LOS HUESOS FOSSILS PART OF HEIDELBERGENSIS?

Although Mounier and coworkers^{24,29} felt able to include the SH material in their *heidelbergensis* hypodigm, I believe that this inclusion has led to the most serious confusion surrounding the status of the species. From the first detailed descriptions of the Sima fossils, their combination of *heidelbergensis*-like and Neanderthal-like features has been recognized.¹⁹ Increasingly old age estimates for the SH assemblage (now >530 ka^{30,31}) have reinforced

the Atapuerca team’s preference for assigning the material to *heidelbergensis*. However, for some time I have preferred to regard the SH material as an archaic form of *neanderthalensis*,¹³ based on the presence of Neanderthal-like features such as an incipient suprainiac fossa and midfacial projection in the crania, dental and mandibular traits, and numerous postcranial characters. More recently, I have also challenged the older age estimates obtained for the SH sample from a dated speleothem.³² That challenge was based on taphonomic issues rather than the age determination itself, but dating work on the speleothem is continuing (J.-L. Arsuaga, personal communication).

Regardless of those considerations, morphological and genetic data sug-

Recently, even stronger reasons have emerged to place the SH material within the Neanderthal clade rather than within *heidelbergensis*.

gest that the divergence of the *neanderthalensis* and *sapiens* lineages very likely postdates 530 ka. Therefore, Neanderthal apomorphies would not be expected at such an antiquity. Comparisons using the draft Neanderthal genome produced the following estimate: “Assuming that human-chimpanzee average DNA sequence divergence was 5.6 to 8.3 million years ago, this suggests that Neanderthals and present-day human populations separated between 270,000 and 440,000 years ago.”³³ Using only complete mtDNA sequences, Endicott, Ho, and Stringer³² argued that “our genetic date estimates are inconsistent with the late Early Pleistocene, early Middle Pleistocene, and late Middle Pleistocene models for the divergence between *H. sapiens* and *H. neanderthalensis*.... Rejection of these three models leaves just the mid-Middle Pleistocene model for the time of divergence between mod-

ern humans and Neanderthals.... Here, our 95% credible intervals for the MRCA [most recent common ancestor] (315–538 ka) fall squarely within the proposed dates from palaeoanthropology.... Our estimates are also consistent with dates derived from analysis of neutral morphological characters in both species, 182–592 ka (mean 373 ka).³⁴”

Recently, even stronger reasons have emerged to place the SH material within the Neanderthal clade rather than within *heidelbergensis*. Data from the large SH dental sample have long suggested Neanderthal affinities.³⁵ Most recently, Martín-Torres and colleagues³⁶ concluded: “We find that SH dentitions present all the morphological traits that, either in their degree of expression, frequency, or particular combination, are usually considered as typical of *Homo neanderthalensis*. This study ratifies the deep roots of the Neanderthal lineage in the Middle Pleistocene of Europe. In addition, SH teeth are morphologically ‘more Neanderthal’ than other penecontemporaneous Middle Pleistocene samples such as Mauer or Arago, and even more derived than some classic Neanderthal samples.” Because they adhere to an age of >530 ka for the SH sample, these authors are forced to add, “Thus, our study would not sustain the linearity of the accretion process hypothesized for the origins of the Neanderthals, and we suggest that other evolutionary models and scenarios should be explored for the Middle and Upper Pleistocene of Europe. We propose that more than one hominin lineage may have coexisted during the Middle Pleistocene in Europe.” While I agree with that last statement, it is on completely different grounds. Martín-Torres and coworkers³⁵ argue for this on the basis of an (in my view erroneous) early date for *neanderthalensis* (SH) characteristics. I would instead argue for coexistence on the basis of late *heidelbergensis* age estimates within and outside of Europe.^{29,37–40} In addition, it may well be that significant Neanderthal-like samples such as Krapina, considered to be relatively late in the European sequence, are older than is currently

believed (R. Grün and C. Stringer, unpublished research).

Rak and coworkers⁴¹ have recently added to the data that the SH material is predominantly Neanderthal in its affinities: “The claimed similarities between the characters of the Mauer specimen...and those of Neandertals and the Sima de los Huesos mandibles...cannot be considered homologous, and hence, they are not synapomorphies. Although some of the Mauer characters superficially resemble the ones on the Neandertal and Sima specimens, the Mauer characters stem from a different morphological configuration. On the other hand, the similarities between the Neandertal characters and those of the Sima mandibles are the outcome of identical configurations, making these characters true synapomorphies.” This was reinforced as follows: “The study of mandibles from Sima de los Huesos reveals an identical morphology to that of the corresponding and unique region in the *Homo neanderthalensis* mandible.... This constellation of characters is absent in other early and late hominins, including the type specimen *Homo heidelbergensis* (the Mauer mandible).... We conclude that the mandibles of the Sima sample are virtually identical to the Neandertal mandible. Thus, we regard this morphology as a synapomorphy that the Sima fossils share only with *H. neanderthalensis*. In some other cranial morphologies, the Sima sample does not resemble Neandertals; hence, we place the Sima specimens within the Neandertal clade as a sister group to Neandertals. This conclusion is inevitable regardless of whether one advocates a cladogenetic or anagenetic model.”⁴²

GENOMIC DATA AND THE STATUS OF HEIDELBERGENSIS

As I previously argued,³² reclassifying the SH material as an early form of *H. neanderthalensis* on the basis of its derived Neanderthal features and dating it to no earlier than 400 ka would remove most of the data supporting a European chronospecies of *H. heidelbergensis*-*H. neanderthalensis*. This would open the possibility of a less inclusive diagnosis for the species

that is ancestral to modern humans and Neanderthals, which, in my view, is still most reasonably named *Homo heidelbergensis*. However, new data on the possible eastern representatives of *heidelbergensis* have emerged from the genomic study of fragmentary fossils at the southern Siberian site of Denisova. Initial mitochondrial DNA (mtDNA) study of a large molar suggested an ancient lineage predating the divergence of Neanderthals and modern humans, but genomic reconstruction centered on a phalanx indicated that the “Denisovans” were actually a subgroup of the Neandertal clade.⁴⁷ This finding has fueled speculation that fossils previously considered to be possible Asian representatives of *heidelbergensis*, such as Dali, Jinniushan, and Narmada,¹³ could in fact be Denisovans, but this will remain uncertain until more complete material yields DNA. More ancient Asian specimens such as the Yunxian crania (China) might still represent examples of *heidelbergensis*^{13,43} and potential ancestors of the Denisovans, although biogeographic and archeological arguments can be made against such as assignment.⁴⁴ In addition, the presence of relatives of the Neanderthals in the Far East forcefully reminds us how much our views are biased by the attention paid to the European and African records. We cannot exclude an Asian origin for *heidelbergensis*, given the similar ages (~600 ka) assigned to the earliest (if we exclude Tighenif) potential examples in Germany (Mauer²²), China (Yunxian⁴⁵), and Ethiopia (Bodo⁴⁶).

The new Denisovan genomic data are also consistent with previous evidence of gene flow between *Homo sapiens* dispersing from Africa and native archaic populations (Neanderthals).³³ Limited but viable hybridization events led to an input of “archaic” genes into all non-African people in the case of Neandertal DNA, and Australasian populations in the case of the Denisovans.⁴⁷ Such gene flow is bound to raise serious issues about the validity of specific distinctions between *heidelbergensis* and its daughter species, particularly as such hybridization events may even have occurred in Africa.^{48,58} Nevertheless, on morphological

grounds, I believe that a pragmatic case can still be made for such species distinctions, especially bearing in mind the extensive evidence for interspecific hybridization even in living primates.⁴⁹

Genetic data can provide new perspectives on the evolutionary history of *heidelbergensis* and its daughter species, as can be illustrated by comparing Figure 1c and Figure 3, based on the mtDNA divergence data discussed earlier. Gene trees are not species trees, of course, but Figure 3 may nonetheless serve as a useful heuristic device. First, it is evident that both the modern human (A) and late Neandertal lineages (B) may have suffered bottlenecks, perhaps during the harsh conditions of Marine Isotope Stage (MIS) 6; the slender evidence of Denisovan mtDNA already suggests greater diversity in that lineage.⁵⁰ Genetic diversity that would have been represented within early or archaic members of the *sapiens* (C) and *neanderthalensis* groups (D) has consequently been lost. The hypothetical mtDNA last common ancestor for A+C and B+D is estimated at 338-538 ka (mean 407 ka), while population divergence is placed at 315-506 ka (mean 345 ka). The predivergence segment labeled F would have existed during the time span of *Homo heidelbergensis*. I argue that if we had fossils of the relevant ancestors, we would recognize them as members of that species. While fossils such as Swanscombe and SH might correspond with segments D or E, in my view we have yet to identify specimens showing convincing apomorphies of *Homo sapiens* that could represent the earliest stages of segment C, although fossils such as those from Florisbad and Guomde are possible candidates.

As for what initiated the divergence of these lineages, one possibility is to return to an idea suggested more than 50 years ago by Howell,^{51,52} though framed by him in the context of the last glaciations. There is evidence now that glaciation in the Balkans was much more severe during the Middle Pleistocene than at the Last Glacial Maximum.⁵³ Also, pollen data from Tenaghi Philippon indicate that MIS 12 (~450 ka) was particularly severe.⁵⁴ If, at that time, cold, arid conditions

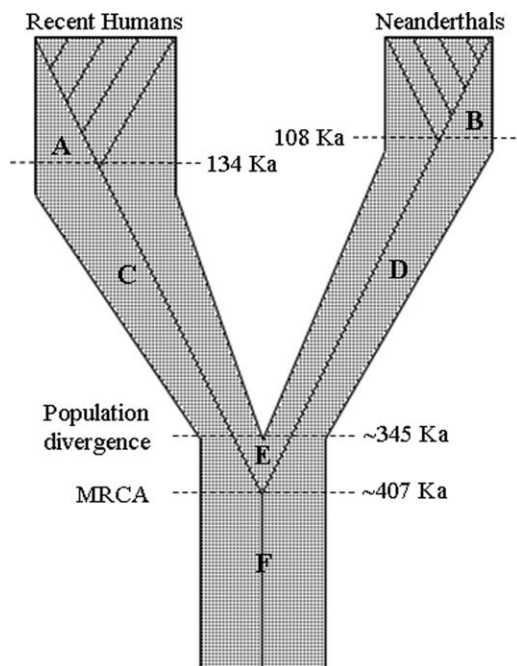


Figure 3. Reconstruction of mtDNA evolution in the *sapiens* and *neanderthalensis* lineages, based on complete genomes from 5 Neanderthals and 54 modern humans. Based on data in Endicott, Ho, and Stringer.³²

extended eastward across the high relief of the Taurus-Zagros mountain systems, coupled with enlarged Caspian and Black Seas, European populations could have been effectively isolated from their African and Asian counterparts. Moreover, increased aridity in North Africa and the Levant could have added to this paleogeographic separation. Whether increased selection or drift then operated to differentiate these separated populations progressively is still uncertain,⁵⁵ but Neanderthal-derived features are evident in Europe from MIS 11 onward.^{13,52,56}

A comparable speciation scenario, using the mechanisms of refugia, has recently been proposed by Stewart and Stringer⁵⁷: “When a lineage adopts a new (or changes its) refugial area, and it survives for a number of Milankovitch cycles, expanding from and contracting into that new refugium instead of its original refugium, it is destined to evolve into a distinct population. Given enough time in isolation, it will become a new species.... A new refugium is unlikely to have the same flora, fauna, and ecology compared to the lineage’s original refugium, which

contributes selective pressure to adapt and diverge.”

CONCLUDING REMARKS

Clearly, many problems in Middle Pleistocene human evolution remain unresolved. Some of these center on chronological issues, others on the lack of data for some important fossils, such as those from China. The relationship of *Homo antecessor*, still definitely identified only from Atapuerca, to succeeding samples is also unclear, although it remains possible that this derivative of *Homo erectus* went extinct during the early Middle Pleistocene.⁵⁹ *Homo antecessor* also seems an unlikely ancestor for *Homo heidelbergensis*, which means that the origin of *Homo heidelbergensis* is obscure. However, in my view, the main uncertainty about *Homo heidelbergensis* is much more fundamental, concerned with its very nature. The idiosyncratic morphology of the type specimen is certainly problematic, but for me an even more vexing issue is whether the species existed only in western Eurasia and gave rise solely to the Neanderthals. The main support for such a view has come from the derived Nean-

derthal features claimed for the species, simultaneously differentiating it from contemporaneous African fossils and linking it to the succeeding Neanderthals.

In this review, I have discussed the growing and, in my view, convincing evidence that the Sima de los Huesos material belongs to the Neanderthal clade, and perhaps represents a primitive form of *Homo neanderthalensis*. Removing the extensive SH assemblage from *H. heidelbergensis* greatly clarifies the situation in also removing most of the unique links to the Neanderthals. This allows a reformulated *heidelbergensis* to approximate more closely the plesiomorphous morphotype expected for the last common ancestor of *Homo neanderthalensis* and *Homo sapiens*. However, if genetic and morphological estimates for *neanderthalensis-sapiens* divergence at <530 ka are accurate, the SH material must be younger, and perhaps considerably younger, than this date.

The addition of “Denisovans” to the hominin lexicon provides a further dimension to these discussions. The relationship of non-*erectus* Asian Middle Pleistocene fossils to those further west has long been problematic, but now we have the potential to properly integrate the hominin records from western and eastern Eurasia for the first time, and to see East Asian fossils like Dali and Jinniushan as counterparts of the evolving Neanderthals further west. Indeed, it may be just as logical to regard the Neanderthals as a western subset of the Denisovan group as to consider, as is usually done, the inverse relationship. The concept of *Homo heidelbergensis* remains at the center of such discussions, as this species represents the probable ultimate ancestor of these three daughter taxa: *sapiens*, *neanderthalensis*, and Denisovans.

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