

The origin of Neandertals

J. J. Hublin¹

Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany

Edited by Richard G. Klein, Stanford University, Stanford, CA, and approved August 6, 2009 (received for review April 14, 2009)

Western Eurasia yielded a rich Middle (MP) and Late Pleistocene (LP) fossil record documenting the evolution of the Neandertals that can be analyzed in light of recently acquired paleogenetical data, an abundance of archeological evidence, and a well-known environmental context. Their origin likely relates to an episode of recolonization of Western Eurasia by hominins of African origin carrying the Acheulean technology into Europe around 600 ka. An enhancement of both glacial and interglacial phases may have played a crucial role in this event, as well as in the subsequent evolutionary history of the Western Eurasian populations. In addition to climatic adaptations and an increase in encephalization, genetic drift seems to have played a major role in their evolution. To date, a clear speciation event is not documented, and the most likely scenario for the fixation of Neandertal characteristics seems to be an accretion of features along the second half of the MP. Although a separation time for the African and Eurasian populations is difficult to determine, it certainly predates OIS 11 as phenotypic Neandertal features are documented as far back as and possibly before this time. It is proposed to use the term "*Homo rhodesiensis*" to designate the large-brained hominins ancestral to *H. sapiens* in Africa and at the root of the Neandertals in Europe, and to use the term "*Homo neanderthalensis*" to designate all of the specimens carrying derived metrical or non-metrical features used in the definition of the LP Neandertals.

Acheulean | climate | *Homo heidelbergensis* | *Homo sapiens* | Pleistocene

Continuous research since the middle of the 19th century on the Neandertals has resulted in an unmatched accumulation of data, combining biological and cultural characteristics in their environmental context. This has allowed for the analysis of their morphological variability and geographical distribution with a level of detail unparalleled in other hominins. The close phylogenetic relationship between Neandertals and *Homo sapiens* also makes this group particularly interesting as understanding its status undoubtedly sheds light on the definition of our own species. As a matter of fact, anatomical descriptions of Neandertal remains have most often focused on comparisons with extant or recent humans. Occasionally, this has led to some misleading assessments of the differences between the two groups by confusing genuine derived Neandertal features with primitive retentions lost only recently in *H. sapiens*. Historically, this confusion provided the grounds for the notion of a generalized "Neandertaloid phase," allegedly present throughout the Old World (1), and for debates surrounding the identification of supposed "Neandertal features" in early modern humans. Until the 1970s, Neandertals were considered to date exclusively from the Late Pleistocene (LP) and were assigned to a time period ranging from OIS 5 to OIS 3—between 100 and 40 ka. "Early Neandertals" were also recognized in the early OIS 5 between 130 and 100 ka. For the earlier time periods, the Middle Pleistocene (MP) fossils discovered in Europe were then attributed to diverse groups such as the "ante-Neandertals," the "pre-Neandertals," or the "pre-*sapiens*," each possibly connected to the origins of the modern Europeans to some degree. A better definition of the Neandertals, and the reinterpretation of a range of European MP specimens, resulted in the conclusion that none of these fossils were actually connected to modern humans and that

some of the non-metrical and metrical characteristics used to determine the Neandertal phenotype were already observed in Europe during the MP (2). The discovery of the extensive MP series of Sima de los Huesos (SH) (Atapuerca, Spain) (3) confirmed the long evolutionary history of this Western Eurasian lineage. However, debate continues over its exact date of differentiation as well as over various phylogenetic and taxonomic implications.

Neandertals as a Sister Group

Neandertals lived in Western Eurasia below 55° N. latitude. Significantly, although they were present South of Haifa (Israel), none have been documented in North Africa. In the East, paleogenetic data demonstrate their presence as far as Southern Siberia (4). On its northern edge, this distribution represents what was the limit of the eco-geographical domain of humans in the Late MP and Early LP. This had important implications regarding the biological adaptations, landscape occupation pattern, and demography of the Neandertals. They were large-bodied hominins who required a higher energetic intake than most recent hunter gatherers (5, 6). All of the available isotopic studies suggest that their primary protein source was animal (7), and the archeological record provides us with an image of efficient hunters who focused on medium to large mammals for meat and fat. The range of environments in which they lived covered a variety of climates, most often cool or cold, but occasionally temperate. Although Neandertal body proportions are primarily explained as adaptations to climatic stress caused by cold temperatures (8), they might also be seen as resulting from technical limitations in responding to this stress. In fact, Neandertals seem limited in their ability to live on peri-arctic landscapes. During cold episodes such as OIS 6 and OIS 4, large portions of the European territory were abandoned and later recolonized (9, 10). Different estimates suggest that the Neandertal populations had very low densities and limited resilience (11). Archaeological, paleontological, and paleogenetic evidence also suggest that these changes in geographical distribution primarily resulted from local extinctions rather than from migration and habitat tracking (10).

Although virtually all of the classic osteometric measurements show some degree of overlap between Neandertals and modern humans, the global assessment of shape by geometric-morphometrics demonstrates a clear separation between the cranio-facial anatomy of the two groups (12). Morphologically, Neandertals postdating OIS 7 display a unique combination of non-metrical features and morphometric architecture that makes them easily distinguishable. Although the estimated time of separation between closely related species of apes, for example, *Pan troglodytes* and *P. paniscus*, is much longer than that of Neandertals and extant *H. sapiens*, the latter species display a greater shape distance. In addition to this large morphological distance, Neandertals seem to display less

Author contributions: J.-J.H. wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. Email: hublin@eva.mpg.de.

morphological variation than extant humans. Gunz et al. (13) have shown that these differences in overall variability are unrelated to the small size of the samples and suggest that modern humans displayed high levels of variability as far back as the Pleistocene. Similarly, Neandertal mitochondrial DNA (mtDNA) variability is lower than that of extant humans and has a magnitude similar to the level observed in a large modern human population (14), both being significantly lower than those of great apes (14, 15). This suggests that different evolutionary processes were at work in Pleistocene humans and in their closest relatives. Drift, with the possible influence of cultural differentiation, might have been prevalent in humans (16, 17), while stabilizing selection would have played a major role in apes. Other differences between Neandertals and modern humans include brain shape (18), developmental patterns (19), obstetric features (20), and possibly life history (21). This has led many scholars to accept the species *H. neanderthalensis* as an operative paleontological species, distinct from *H. sapiens*. However, subspecific divisions have been also proposed (22).

Time of Divergence

Information about the separation of the lineages leading to *H. sapiens* and *H. neanderthalensis* comes from the fields of human paleontology and paleogenetics. However, it is important to stress that the genetic coalescence, population separation, and phenotypic differentiation of the two taxa represent chronologically distinct events. MtDNA from more than 15 Neandertals has been successfully sequenced, sometimes in totality, and provides estimates for the divergence date between *H. sapiens* and *H. neanderthalensis* mtDNA lineages. The most recent estimate is at 660 ka \pm 140 ka, based on a divergence time between 6 and 7 ma for humans and chimpanzees (23). Computations based on the autosomal genome have provided a coalescence time ca. 700 ka and a separation time for the population ca. 370 ka (24).

Crucial to the question of the separation process of the two lineages is the interpretation of the MP European fossil record. Most authors agree that the general cranio-facial architecture of the African and Western Eurasian MP hominins is quite similar, and includes a series of derived conditions relative to *H. erectus sensu lato* (*s.l.*). These features are mostly related to a higher degree of encephalization with various consequences, including a relatively higher cranial vault, a broader frontal and rounder posterior vault, and possibly a more flexed basicranium (25). Authors who emphasize quantitative approaches of the general cranial architecture assign all of the early and middle MP specimens from Africa and Europe to the paleospecies *H. heidelbergensis* (26–28). However, diverse assessments are made of additional endemic features reported in European specimens. It is important to underline that most of these endemic features are non-metrical. They encompass details of the infra-orbital and nasal area on the face (3), aspects of the mandibular morphology (29, 30), the occurrence of a well-defined suprainiac fossa above a bi-laterally protruding occipital torus (9, 31), and the frequent occurrence ($F > 60\%$) of non-metrical dental features such as the mid-trigonid crest on the lower molars, and asymmetrical lower Pm4 with a transverse crest (32, 33) (S. Bailey, personal communication). These features, which characterize later *H. neanderthalensis*, are unknown or very rare in contemporary MP African specimens. Among the metrical Neandertal apomorphies, the sagittally oriented face and the more inferiorly placed juxtamastoid eminence seem to also appear early in the European MP record (34).

Diverse dates have been proposed for population separation, development of phenotypic differences between the two lineages, and finally, species recognition. An early divergence hypothesis is mostly based on the interpretation and dating of the

abundant collection of human remains from SH. This collection represents one of the most convincing pieces of evidence for the recognition of Neandertal apomorphies in the early MP of Europe. High resolution U-Series dates obtained on a speleothem said to postdate the specimens have provided an age of 600 \pm 66 ka (35). If confirmed, this early date raises several issues. It is very close in time to most of the estimated times of coalescence provided by paleogenetics and would predate most of the estimates for the separation time of the populations, including estimates derived from neutrally evolving morphological measurements (36). For supporters of this hypothesis, the SH material and European specimens from as late as 300 ka are assigned to *H. heidelbergensis*, defined as an exclusively Eurasian chronospecies preceding *H. neanderthalensis* and excluding African MP hominins (Fig. 1A). One problem concerns the relationships between the SH material and older European hominins. A series of fragmentary specimens from the layer TD-6 (\approx 800 ka) of the Gran Dolina site at Atapuerca have been assigned to a new species, *H. antecessor* (37). Whether the denomination of this taxon, initially designated as a common ancestor of *H. sapiens* and *H. neanderthalensis*, is valid and to what extent this material represents a group distinct from contemporary African hominins is still debated (38, 39). Martinon-Torres et al. (33) have proposed that *H. antecessor* and the SH material displayed some continuity in their non-metrical dental features. This would push the differentiation of a Western Eurasian clade even further back in time. However, in recent publications, proponents of *H. antecessor* have suggested that it might display more affinities with the Asian *H. erectus* than with the later SH material (40). Another issue is related to the archaeological context. Although Acheulean industries appeared in Africa before 1.6 ma, they occurred for the first time in Europe between 600 and 500 ka. The simultaneity between the emergence of bifaces in Europe and the occurrence of similar forms of hominins on both sides of the Mediterranean can be seen as the likely result of an Out-of-Africa event, the Acheulean being imported into Europe by a new species of large-brained hominins. A date for the SH hominins displaying shared derived features with later Neandertals ca. 600 ka would imply that the phenotypic differentiation of the African and Western Eurasian population would immediately follow this migration.

An opposing hypothesis promotes a late divergence of the two lineages (Fig. 1B). In this view, *H. heidelbergensis* is seen as a homogeneous taxon represented in both Europe and Africa (26–28). If Chinese specimens are assigned to it (25), its spread may not be directly related to the diffusion of the Acheulean in Eurasia, as this assemblage did not expand into the Far East. In addition to anatomical evidence, archaeological arguments have been proposed in favor of the late divergence hypothesis. They mostly relate to the supposed synchronous emergence of the Levallois technique in Western Eurasia and Africa, ca. 300–250 ka. Exchanges between the two areas until this date would have allowed cultural diffusion and therefore gene flow. In this view, a European clade distinct from African contemporaries could have developed only later. An extreme version of the late separation hypothesis has been proposed involving the movement out of Africa of a new species of hominin (*H. helmei*) that would have carried the Levallois technology into Europe (41). The late divergence hypothesis is in agreement with the latest range of estimates for coalescence and deduced population separation times. One of its weaknesses is that it hardly deals with the occurrence of Neandertal apomorphies in European hominins predating 300 ka.

An intermediate hypothesis proposes that the population separation time occurred between 500 and 400 ka (Fig. 1C). The existence of endemic phenotypic features in Europe connecting many of the known MP hominins to the later *H. neanderthalensis* would simply result from this geographical and genetic segre-

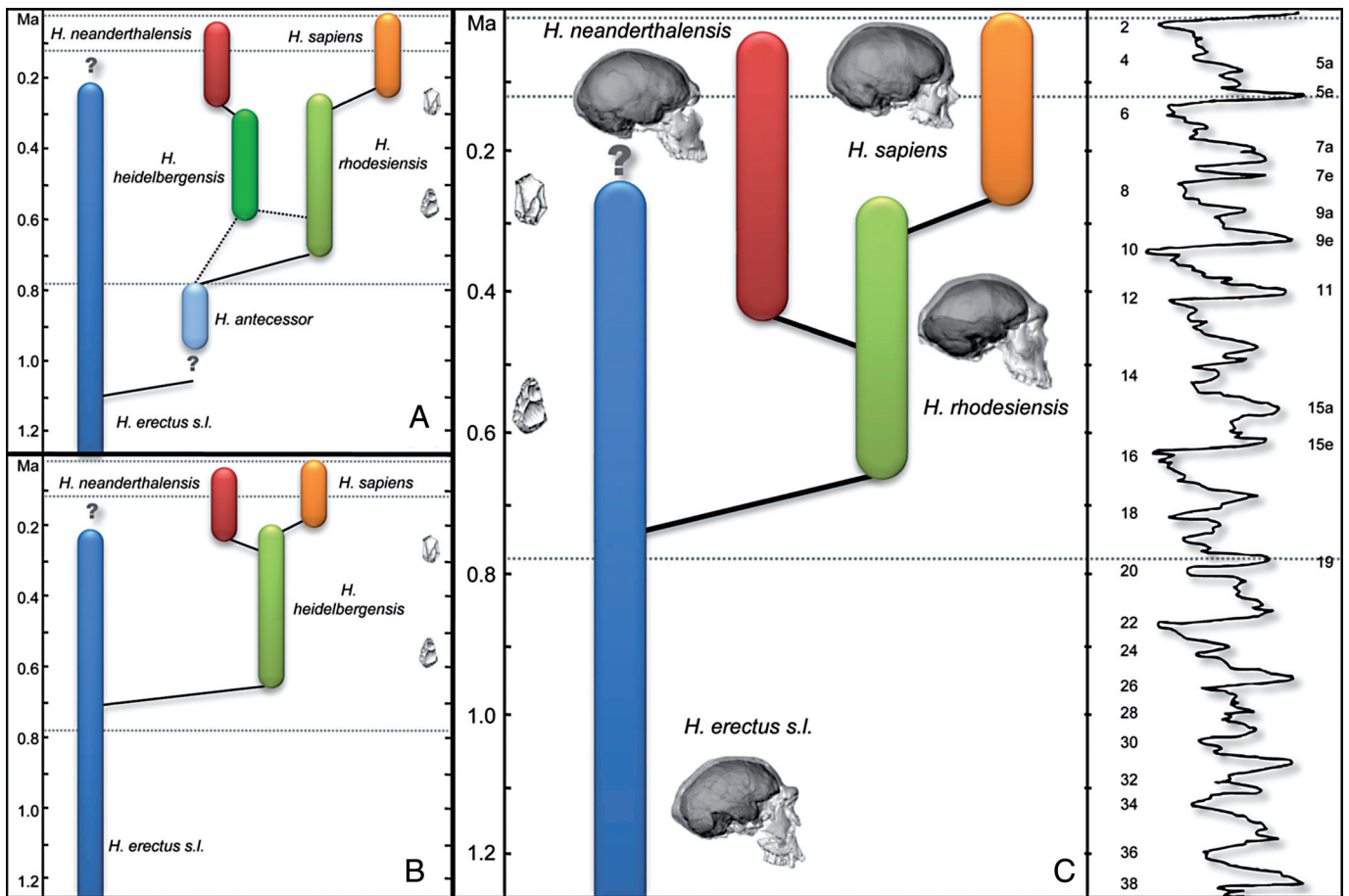


Fig. 1. Three evolutionary scenarios for the origin of the Neandertals: (A) depicts an early, (C) depicts a late, and (B) depicts an intermediate divergence time [modified from Rightmire (25)]. The marine 18O isotope record is indicated on the right of tree C (64). A biface on the chronological scales indicates the time of emergence of the Acheulean in Europe and a flake indicates the occurrence of fully developed *Levallois debitage* in Europe. Horizontal dashes indicate the limits of the Middle and Late Pleistocene.

gation. The age of 400 ka is deduced from the occurrence of clear Neandertal synapomorphies on the Swanscombe (U.K.) skull, which was found in a terrace deposit assigned to OIS 11 (31). The specimen displays a clear suprainiac fossa with a bilateral protrusion of the occipital torus. In posterior view, its braincase shape is intermediate between the pentagonal outline observed in earlier hominins and the circular outline observed in the late Neandertals. This age matches most of the estimates for the coalescence and population separation times, as well as the archaeological evidence, with the exception of the Levallois technique development. However, proto-Levallois productions existed in Europe before OIS 8. The best known and oldest example is represented at Cagny La Garenne (France), in the late OIS 12 (42), and consists of thin flakes extracted from broken handaxes. A later example is provided by the prepared cores from Purfleet (U.K.), dating to OIS stage 9/8 (43). These observations strongly suggest that the Levallois technique is embedded into the development of the Acheulean package. It is significant that the Levallois debitage primarily developed within the geographical domain of the Acheulean. Therefore, the development of Levallois techniques with specific regional features could be seen as independent and parallel processes in a vast geographical area (43). In any case, the existence of proto-Levallois assemblages in Europe is inconsistent with the hypothesis of a late introduction by a hypothetical migrant (41). Such a scheme would inevitably result in the rapid appearance

of this technique, comparable to that of an advanced Acheulean earlier during the MP.

The Evolution of the European Clade

Two models, the “two-phases model” and the “accretion model,” have been proposed to explain the relationships between the European MP forms and the later Neandertals. They have different implications for the taxonomy of the European fossil hominids. However, to some extent, both can accommodate any of the chronological hypotheses discussed above. According to the two-phases model, there is a rapid and marked anatomical change between MP specimens assigned to “*H. heidelbergensis*,” either conceived as a chrono-species of the western Eurasian clade [*H. heidelbergensis sensu stricto* (s.s.)] or as an Afro-European root group (*H. heidelbergensis s.l.*) and later Neandertals. Rosas et al. (44) have proposed that the first phase was characterized by an increase in body size, postcranial robusticity, and mid-facial prognathism. A speciation event occurring in the late MP would result from changes in the dynamics of cranio-facial growth. In particular, they hypothesized a major reorganization of the cranial architecture that would have led to relative increases in the size of the occipital and temporal neural areas. If applicable, this model would allow us to easily identify the MP members of *H. heidelbergensis* and *H. neanderthalensis*.

According to the accretion model (9, 45), changes along the sequence of the Western Eurasian clade mostly resulted from a

shift in the frequency of non-metrical features already occasionally observed in early MP large-brained European hominins.* Eventually, these features were fixed in late *H. neanderthalensis*, primarily through a process of drift and random fixation. In parallel, changes in the cranial architecture occurred in relation to a growing degree of encephalization. This increase in the degree of encephalization, like the reduction of the posterior dentition, likely resulted from selective pressures similar to those at work in the lineage leading to *H. sapiens*. However they followed a different pathway and did not result in a more globular brain overhanging a retracted face but, instead, maintained a more primitive pattern of cranio-facial architecture (49). In this model, there would be no clear divide between *H. heidelbergensis* (however it is defined) and *H. neanderthalensis*.

The main difficulty in comparing and testing these two models relates to the incomplete and discontinuous nature of the fossil record. In the middle of the MP, a group of specimens currently assigned to *H. heidelbergensis* (*s.l.* or *s.s.*) is dominated by the overwhelming series from SH, to which most authors would add the Mauer (Germany) mandible, the Tautavel (France) series, and the Petralona (Greece) skull. The Swanscombe skull, dated around 400 ka, has often been assigned to the same taxon, although it displays rather derived conditions. At the other end of the chronological span of the Eurasian clade, an abundant series of Neandertal remains has been described from OIS 5. Between OIS 10 and 6, fewer specimens have been discovered, sometimes creating the illusion of a morphological gap. The very fragmentary nature of the specimens from Vertésszöllös (Hungary), and Bilzingsleben (Germany), make them difficult to assess. The gracile and distorted skull from Steinheim (Germany), likely from OIS 9, is reminiscent of Swanscombe. The possibly subcontemporary (?) specimen from Reilingen (Germany) displays even clearer Neandertal synapomorphies. The specimens assigned to OIS 7 from Ehringsdorf-Weimar (Germany) and Biache (France) are clearly identifiable as Neandertals.

Different processes of relative or total isolation of the Eurasian and African lineages underlie these two models. Reliable evidence of European hominins predating 1 ma is found in the Mediterranean regions (50, 51). The lithic assemblage of the Cromer Forest Formation at Pakefield (U.K.) is attributed to an interglacial from around 700 ka (52) but there were hardly any continuous populations north of the Alps before the middle of the MP (53). Until then, exchanges between Europe and Africa were very limited, as demonstrated by the absence of the Acheulean in Europe until 600 ka. A second main colonization episode hypothesized around this date coincided with and may be explained by major environmental changes. The “Middle Pleistocene Revolution” is centered around 600 ka and is characterized by an increase in the amplitude and length of alternating warmer and colder climatic stages (Fig. 1) as well as major changes in the sedimentation regime in the North Atlantic (54). OIS 16 represented the first major glaciation in Europe, with an ice sheet extension reaching south of 50° latitude in Eastern Europe (55). It was followed by a long and marked interglacial (OIS 15), during which full-interglacial conditions prevailed longer than during any preceding interglaciation. OIS 15 may have played an important role in the (re-)colonization of the middle latitudes of Europe. Interestingly, the earliest hominin fossil found in Europe north of the Alps (the type specimen of *H. heidelbergensis* itself, i.e., the Mauer mandible), could be

assigned to this stage (G. Wagner, personal communication). Between 470 ka and 360 ka, the succession of OIS 12 and 11 represented one of the largest glacial/interglacial fluctuations in the Pleistocene (55, 56). In particular, as one of the most pronounced and longest interglacials of the MP, OIS 11 provides the best future analogy for the Holocene (57).

During long, severe, and climatically unstable glacial periods, the geography of Europe was markedly modified. In relation to the extension of the icecap and permafrost areas, the continental plates were largely emerged. In Eastern and Central Europe, the climate became a great deal more continental and human population sizes severely decreased (58). In the East, an influx of a large fluvio-glacial system caused the Caspian Sea to double in size and reach up to 50° north, while large glaciers developed on the Caucasus. Population movements between Europe, Central Asia, and the Near East were reduced, and the inhabitable areas in the West were also depleted (9, 10). During the MP, these episodes of periodic isolation and demographic crashes likely resulted in genetic bottlenecks and drift effects explaining the divergence of the Western Eurasian clade, as well as the lower morphological and mtDNA variability observed in late Neandertals (14). In this view, fluctuations of the geographical domains of the Neandertals and specifically, extensions into the Levant or toward Central Asia or Southern Siberia would have been primarily driven by environmental constraints. The lack of deep mtDNA divergence between Central Asian and Western European Neandertals (4) is consistent with a short separation time, and a late colonization or recolonization of the easternmost parts of the Neandertal range.

There is no clear indication that one climatic change alone played a primary role in the emergence of *H. neanderthalensis*, as expected in the “two-phases” model. It has been proposed that OIS 6 could have been catalytic in the evolution of full blown Neandertal features (59). However, this is contradicted by specimens such as Biache 1, which demonstrate that most of the braincase morphology of *H. neanderthalensis* was already established at the end of OIS 7 (60). The fossil record suggests that the cold episode(s) that triggered the process of divergence of the Neandertal clade most likely predates OIS 11.

Discussion and Conclusions

In assessing the different hypotheses and models discussed above, it is important to provide an evolutionary scenario that is as consistent as possible with the paleontological evidence, the paleogenetic data, and the archaeological record. As already discussed, a hypothesis of very early divergence of the Western Eurasian and African clades could be difficult to accommodate to some genetic data. However, it is important to recall that estimates of genetic coalescence time and deduced population separation times are based on a number of assumptions and are associated with very large confidence intervals. Furthermore, although they have raised new questions and problems (39), recent reinterpretations of *H. antecessor* that posit a phase of population recolonization of Europe between *H. antecessor* and *H. heidelbergensis* (61) have reconciled the paleontological and archaeological evidence. The main problem with Scenarios A and B, presented in Fig. 1, lies in the difficulty of proposing operational diagnoses that would clearly assign all of the European MP specimens (and not only the earliest and latest range of the fossil record) to either *H. heidelbergensis* (*s.l.* or *s.s.*) or *H. neanderthalensis*. To date, the species paradigms proposed with the various definitions of *H. heidelbergensis* are not able to properly deal with the European specimens met between OIS 11 and 6.

The European fossil and climatic records provide more support for the accretion model than for the “two-phases” model. From a cladistic point of view, the accretion model implies that *H. neanderthalensis* should be pushed as far back in time as

*Hawks and Wolpoff (46) have criticized this model on the basis of a statistical test. Among other problems, this test does not address the non-metrical features on which the accretion model was primarily established. It also combines two incompatible mathematical models: one (47) that addresses variance in the phenotypic means of groups connected by gene flow and in a state of equilibrium, and a second (48) that assesses a “scaled” square of generalized genetic distance, based on a model for splitting populations not connected by gene flow and not in equilibrium.

derived features used in the diagnosis of later Neandertals are observed (Fig. 1C). In this scenario, the main difference between Africa and Europe lies in the fact that morphological evolution has been more spectacular in the African clade, with a likely speciation event at the origin of *H. sapiens*. However, similar discussions occurred regarding the taxonomy of the MP African record (62). Although the scenarios previously discussed here relate to different taxonomic choices, it should also be underlined that they are not so distant in terms of evolutionary history. Scenario B emphasizes the symplesiomorphic heritage of the MP hominins from Africa and Western Eurasia and regards the differences observed between the two areas as an effect of geographical (“racial”) variations with little taxonomic value. In this regard, *H. heidelbergensis s.l.* could be seen as a “stem group,” difficult to distinguish from its direct descendents in Europe. Scenarios A and C emphasize the role of these variations in the taxonomic assignment of the available fossil material, but one cannot overlook the similarities between the initial stages of the Western Eurasian clade and its African counterpart (34).

From a nomenclature point of view, a main difficulty results from the very nature of the type specimen of *H. heidelbergensis*. The Mauer mandible is essentially primitive and not directly associated with any cranial material. This situation has allowed for the development of the two current concepts of *H. heidelbergensis* (Fig. 1A and B). However, both are based on anatom-

ical definitions mostly or exclusively derived from cranial but not mandibular features and are therefore hardly applicable to their proposed type specimen, which, from this point of view, might well be an *incertae sedis*. Because of the fragmentary nature of the Mauer specimen and the ambiguity of most mandibular remains (30), on a strict anatomical ground, it is (and may always be) difficult to establish whether this specimen predated or postdated the beginning of the accretion of Neandertal features. An alternative model, which also resolves the nomenclatural issue, recognizes African large-brained hominins preceding the emergence of *H. sapiens* as “*Homo rhodesiensis*.” Such a taxonomy, which has also been proposed by supporters of Scenario A, has the advantage of relying on a very complete type specimen, the Kabwe (Zambia) skull (63), on which most of the definitions of “*H. heidelbergensis*” as a Afro-European taxon are, in fact, based. This terminology also underlines the geographical origin and main distribution of the taxon. However, in this view *H. rhodesiensis* must have occurred at least briefly in Western Eurasia at the root of the oldest forms of *H. neanderthalensis* and in relation to the expansion of the Acheulean domain.

ACKNOWLEDGMENTS. I thank R. G. Klein, who invited me to contribute this article to the Proceedings of the National Academy of Sciences’ special feature; C. Rowney, S. Tüpke, and S. Neubauer who helped me in the preparation of this paper; and E. Delson, S. Bailey, T. Weaver, and an anonymous reviewer provided helpful comments.

1. Hrdlicka A (1927) The Neanderthal Phase of man. *J Royal Anthropol Inst* 57:249–274.
2. Hublin J-J (1988), in *L’Homme de Néandertal N°3*, ed E Trinkaus (ERAUL 30 Liège), pp 81–94.
3. Arsuaga JL, Martínez I, Gracia A, Lorenzo C (1997) The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *J Hum Evol* 33:219–281.
4. Krause J, et al. (2007) Neandertals in central Asia and Siberia. *Nature* 449:902–904.
5. Steegmann AT, Cerny FJ, Holliday TW (2002) Neandertal cold adaptation: Physiological and energetic factors. *Am J Hum Biol* 14:566–583.
6. Churchill SE (2006) in *Neanderthals Revisited: New Approaches and Perspectives*, eds Harvati K, Harrison T (Springer, New York), pp 113–134.
7. Richards MP, Trinkaus E (2009) Isotopic evidence for the diets of European Neandertals and early modern humans. *Proc Natl Acad Sci USA* 106:16034–16039.
8. Holliday TW (1997) Postcranial evidence of cold adaptation in European neandertals. *Am J Phys Anthropol* 104:245–258.
9. Hublin J-J (1998) in *Neandertals and Modern Humans in Western Asia*, eds Akazawa T, Aoki K, Bar-Yosef O (Plenum Press, New York), pp 295–310.
10. Hublin J-J, Roebroeks W (2009) Ebb and flow or regional extinctions? On the character of Neandertal occupation of northern environments. *Pal Evol* 8:503–509.
11. Stiner MC, Kuhn SL (2006) Changes in the “connectedness” and resilience of paleolithic societies in Mediterranean ecosystems. *Hum Ecol* 34:693–712.
12. Harvati K, Frost SR, McNulty KP (2004) Neandertal taxonomy reconsidered: Implications of 3D primate models of intra- and interspecific differences. *Proc Natl Acad Sci USA* 101:1147–1152.
13. Gunz P, Bookstein FL, Mitteroecker P, Stadlmayr A, Seidler H, Weber GW (2009) Early modern human diversity suggests subdivided population structure and a complex out-of-Africa scenario. *Proc Natl Acad Sci USA* 106:6094–6098.
14. Serre D, et al. (2004) No evidence of Neandertal mtDNA contribution to early modern humans. *PLoS Biol* 2:0313–0317.
15. Gagneux P, et al. (1999) Mitochondrial sequences show diverse evolutionary histories of African hominoids. *Proc Natl Acad Sci USA* 96:5077–5082.
16. Weaver TD, Roseman CC, Stringer CB (2007) Were neandertal and modern human cranial differences produced by natural selection or genetic drift? *J Hum Evol* 53:135–145.
17. Premo LS, Hublin J-J (2009) Culture, population structure, and low genetic diversity in Pleistocene hominins. *Proc Natl Acad Sci USA* 106:33–37.
18. Bruner E, Manzi G, Arsuaga JL (2003) Encephalization and allometric trajectories in the genus *Homo*: Evidence from the Neandertal and modern lineages. *Proc Natl Acad Sci USA* 100:15335–15340.
19. Ponce de León MS, Zollikofer CPE (2001) Neandertal cranial ontogeny and its implications for late hominid diversity. *Nature* 412:534–538.
20. Weaver TD, Hublin J-J (2009) Neandertal birth canal shape and the evolution of human childbirth. *Proc Natl Acad Sci USA* 106:8151–8156.
21. Smith TM, Toussaint M, Reid DJ, Olejniczak AJ, Hublin J-J (2007) Rapid dental development in a Middle Paleolithic Belgian Neandertal. *Proc Natl Acad Sci USA* 104:20220–20225.
22. Wolpoff MH (2009) How Neandertals inform human variation. *Am J Phys Anthropol*. 139:91–102.
23. Green RE, et al. (2008) A complete Neandertal mitochondrial genome sequence determined by high-throughput sequencing. *Cell* 134:416–426.
24. Noonan JP, et al. (2006) Sequencing and analysis of Neandertal genomic DNA. *Science* 314:1113–1118.
25. Rightmire GP (2008) *Homo* in the Middle Pleistocene: Hypodigms, variation, and species recognition. *Evol Anthropol* 17:8–21.
26. Stringer CB (1994) in *Origins of Anatomically Modern Humans*, eds Nitecki MH, Nitecki DV (Plenum Press, New York), pp 149–172.
27. Rightmire GP (1998) Human evolution in the Middle Pleistocene: The role of *Homo heidelbergensis*. *Evol Anthropol* 6:218–227.
28. Tattersall I (2000) Paleoanthropology: The last half-century. *Evol Anthropol* 9:2–16.
29. Antonio R, Bermudez de Castro JM (1998) The Mauer mandible and the evolutionary significance of *Homo heidelbergensis*. *Geobios* 31:687–697.
30. Mounier A, Marchal F, Condemi S (2009) Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. *J Hum Evol* 56:219–246.
31. Stringer CB, Hublin J-J (1999) New age estimates for the Swanscombe hominid, and their significance for human evolution. *J Hum Evol* 37:873–877.
32. Bailey SE (2002) Neandertal dental morphology: Implications for modern human origins. PhD dissertation (Arizona State University, Tempe, AZ), p 236.
33. Martinón-Torres M, et al. (2005) in *Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology*, eds Bailey SE, Hublin J-J (Springer, Leipzig), pp 65–79.
34. Harvati K, Hublin JJ, Gunz P (2009) Evolution of Middle-Late Pleistocene human cranio-facial form: A 3-D approach. *J Hum Evol*, in press.
35. Bischoff JL, et al. (2007) High-resolution U-series dates from the Sima de los Huesos hominids yields 600[±]66 kys: Implications for the evolution of the early Neandertal lineage. *J Archaeol Sc* 34:763–770.
36. Weaver TD, Roseman CC, Stringer CB (2008) Close correspondence between quantitative- and molecular-genetic divergence times for Neandertals and modern humans. *Proc Natl Acad Sci USA* 105:4645–4649.
37. Bermudez de Castro JM, Arsuaga JL, Carbonell E, Rosas A, Martínez I, Mosquera M (1997) A hominid from the Lower Pleistocene of Atapuerca, Spain: Possible ancestor to Neandertals and modern humans. *Science* 276:1392–1395.
38. Hublin J-J (2001) in *Human roots: Africa and Asia in the middle pleistocene*, eds Barham L, Robson-Brown K (Western Academic & Specialist Press, Bristol), pp 99–122.
39. Martínón-Torres M, et al. (2007) Dental evidence on the hominid dispersals during the Pleistocene. *Proc Natl Acad Sci USA* 104:13279–13282.
40. Carbonell E, et al. (2005) An early Pleistocene hominid mandible from Atapuerca-TD6, Spain. *Proc Natl Acad Sci USA* 102:5674–5678.
41. Foley R, Lahr MM (1997) Mode 3 technologies and the evolution of modern humans. *Cambridge Archaeol* 7:3–36.
42. Tuffreau A (1995) in *The Definition and Interpretation of Levallois Technology*, eds Dibble HL, Bar-Yosef O (Prehistory Press, Madison, WI), pp 413–427.
43. White M, Ashton N (2003) Lower Palaeolithic core technology and the origins of the Levallois method in northwestern Europe. *Cur Anthropol* 44:598–609.
44. Rosas A, Bastir M, Martínez-Maza C, García-Taberner A, Lalueza-Fox C (2006) in *Neanderthals Revisited: New Approaches and Perspectives*, eds Harvati K, Harrison T (Springer, New York), pp 37–70.
45. Dean D, Hublin JJ, Holloway R, Ziegler R (1998) On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. *J Hum Evol* 34:485–508.
46. Hawks JD, Wolpoff MH (2001) The accretion model of Neandertal evolution. *J Hum Evol* 40:A10–A10.

47. Rogers AR, Harpending HC (1983) Population structure and quantitative characters. *Genetics* 105:985–1002.
48. Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33:1210–1226.
49. Lieberman D (In Press) *The Evolution of the Human Head* (Harvard Univ Press, Cambridge, MA).
50. Turq A, Martínez-Navarro B, Palmqvist P, Arribas A, Agustí J, Rodríguez Vidal J (1996) Le Plio-Pléistocène de la région d'Orce, Province de Grenade, Espagne: Bilan et perspectives de recherche. *Paleo* 8:161–204.
51. Carbonell E, et al. (2008) The first hominin of Europe. *Nature* 452:465–470.
52. Parfitt SA, et al. (2005) The earliest record of human activity in northern Europe. *Nature* 438:1008–1012.
53. Dennell RW, Roebroeks W (1996) The earliest colonization of Europe: The short chronology revisited. *Antiquity* 70:535–542.
54. Helmke JP, Bauch HA, Mazaud A (2003) Evidence for a mid-Pleistocene shift of ice-drift pattern in the Nordic seas. *J Quatern Sc* 18:183–191.
55. Helmke JP, Bauch HA, Erlenkeuser H (2003) Development of glacial and interglacial conditions in the Nordic seas between 1.5 and 0.35 Ma. *Quatern Sc Rev* 22:1717–1728.
56. Poli MS, Thunell RC, Rio D (2000) Millennial-scale changes in North Atlantic deep water circulation during marine isotope stages 11 and 12: Linkage to Antarctic climate. *Geology* 28:807–810.
57. Loutre MF (2003) Clues from MIS 11 to predict the future climate: A modeling point of view. *Earth Planet Sc Let* 212:213–224.
58. Hoffecker JF (2002) in *Desolate Landscapes: Ice-Age settlement in Eastern Europe* (Rutgers Univ Press, New Brunswick, NJ).
59. Bruner E, Manzi G (2006) in *Neanderthals Revisited: New Approaches and Perspectives*, eds Harvati K, Harrison T (Springer, New York), pp 23–36.
60. Rougier H (2003) in *Etude descriptive et comparative de Biache-Saint-Vaast 1* (Biache-Saint-Vaast, Pas-de-Calais, France) (Universite Bordeaux 1, Bordeaux), p 424.
61. Bermudez de Castro JM, et al. (2008) A new early Pleistocene hominin mandible from Atapuerca-TD6, Spain. *J Hum Evol* 55:729–735.
62. Bräuer G (1989) in *The Human Revolution*, eds Mellars P, Stringer CB (Edinburgh Univ Press), pp 123–154.
63. Woodward AS (1921) A new cave man from Rhodesia, South Africa. *Nature* 108:371–372.
64. Imbrie J, et al. (1984) in *Milankovitch and Climate, Part 1D*, eds Berger AL, Imbrie J, Hays JD, Kukla G, Saltzman B (Riedel, Dordrecht), pp 269–305.