The Hominin colonisation of Europe in the Early and Middle Pleistocene: a review

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During the last two decades, the Pleistocene archaeological and palaeontological record from Europe has increased in a significant manner. Several sites, in particular, Atapuerca and Dmanisi, have provided relevant evidence that leads to the refusal of old hypothesis about the first demographic expansions out of Africa and the first colonization of Europe. Other sites, such as Pakefield and Happisburg, in England, have provided interesting data to better understand the dynamics of the evolutionary history of the first European settlers. Despite many unanswered questions and the need for a better chronological frame for several sites, the available data have been already “digested” by the scientific community, who is now ready to accept a different view regarding the first colonization of Europe. In this paper we present a new model to interpret the Pleistocene record that takes into account not only the fossil evidence but also the palaeoclimatic, palaeogeographic and palaeontological data. This model comprises several hypotheses that can be tested as we obtain more information from the Eurasian Pleistocene sites.

Introduction

During the last years, the genus Homo fossil record from Eurasia has increased in a spectacular manner and new dates place the first human occupation of this continent around 1.8 Ma, at least 600,000 years earlier than it was generally accepted ten years ago. New sites, new dates, and new protagonists, like Homo antecessor, Homo georgicus or Homo floresiensis have triggered a hot debate about taxonomic and phylogenetic questions, as well as about the likely evolutionary scenario for these species. This increased body of evidence has significantly improved our understanding of the initial colonisation and settlement of Europe, questioning many notions that were close to become “dogmas” in the field. In its first stages, the debate focused on whether European colonisation was better described by a long or short chronology, i.e. whether Europe was the “empty continent” until 500 ka (Dennell, 1983; Roebroeks & Kolfschoten, 1994). The short chronology was definitely challenged with the discovery of a extraordinary lithic and hominin assemblage from the TD6 level of Trinchera Dolina (TD), Atapuerca, Spain (Bermúdez de Castro et al., 1997, 1999a, b; Carbonell et al., 1995). Thus, a modified version of this theory was proposed (Dennell and Roebroeks, 1996), foreseeing hominins occupying southern Europe in the late Early Pleistocene (ca. 1.0 – 0.8 Ma), whilst excluding them from northern Europe until 500 ka. However, recent archaeological evidence from Happisburgh and Pakefield, England (Parfitt et al., 2005), that is clearly older than 500 ka, forces some further revision of this assessment of the settlement record of northern Europe. Still, the available evidence is sparse before ca. 0.6 Ma, improving its quality and quantity considerably after that date. European hominins before 0.6 Ma are associated to a Mode 1 technology and most hominin groups in Europe used an Acheulean (Mode 2) technology that was not a local development from the previous flake and core transition (see e.g. Carbonell et
al., 1999). Thanks to the extraordinary hominin assemblage recovered during the last twenty years, we have also advanced in identifying the main protagonist of this first settlement, *Homo antecessor* (Bermúdez de Castro et al., 1997). The archaeological and palaeontological findings from the Sierra de Atapuerca sites, in northern central Spain, have been crucial in updating the evidence and the discussion of the first colonization of Europe, documenting a period that was barely known until the discoveries of this region. Despite some initial reluctance to accept an “unexpected guest” in this scenario (e.g. Rightmire, 2001: 82), the last discoveries in the nearby site of Sima del Elefante have definitely ratified *Homo antecessor* as a robust taxon with a chronological span that could stretch back to at least 1.3 million years ago (Carbonell et al., 2008; Stringer, 2009). Still, some questions such as the source population of *H. antecessor* remain unanswered. In accordance with the afrocentric view common in the 90’s, most suggested that it probably derived from an East African population of *H. erectus* s.l. (or *H. ergaster*: e.g. Tattersall 1997; Bermúdez de Castro et al., 1997) that would be in turn the source population of *H. erectus* s.s. in East Asia. As argued below, recent research on the subject envisages an Asian origin for *H. antecessor* (Carbonell et al. 2005; Martinón-Torres et al., 2007).

In this paper we will try to integrate the latest discoveries and theories on the evolutionary scenario of Pleistocene Europe in a wider continental context. Although the debate and the assessments on this subject have been numerous (e.g. Carbonell & Rodriguez, 2006; Carbonell et al., 1999; Peretto, 2006; Roebroeks, 2001, 2006; Roebroeks and Kolfschoten, 1995), the latest evidence from Dmanisi (Georgia), Atapuerca (Burgos, Spain) and Pakefield/Happisburgh (U.K.) obliges to a reconsideration of the issue. With this paper we aim to propose a hypothetical model that explains the evolution of the genus *Homo* in Europe during the Pleistocene. Although the archaeological evidence is important to build this scenario, we will mainly concentrate in palaeontological evidence, which may be integrated with some theoretical issues that are crucial to present a new model for the hominin evolution during the Pleistocene:

1. The evolutionary story of the Eurasian and African populations was relatively independent.
2. During the Early and Middle Pleistocene there was a Central Area of Dispersals in Eurasia (CADE), located in Southwest Asia (not always connected to East Africa), that was continuously inhabited by a “source population”.
3. The “source population” experiments its own evolution in the CADE, changing its genotype by mutation and natural selection, and giving rise to different pulses of populations towards Europe and East Asia.
4. Hominin dispersals follow an expansion/contraction model (with frequent population wipeouts and local extinctions) rather than a lineal and directional emigrational wave.
5. Populations in the central and peripheral areas are connected by narrow corridors where the geographical and climate barriers can favour processes of genetic drift and random allelic variation in the “descendants”.
6. During dispersals, populations experiment genetic processes such as genetic drift, founder effect, local adaptations and eventually, allopatric speciation.
7. Populations with a recent common origin and that occupy the same territory may interbreed.

With these arguments in mind (that will be explored below in more detail) we will propose an evolutionary scenario for the European colonisation and settlement in the Early and Middle Pleistocene.

**Results**

**The first dispersal(s) of hominins into Europe (<1.7 – 0.8 Ma)**

The earliest archaeological evidence for hominin presence in southern Europe prior to 800 ka comes from Sima del Elefante (TE), Atapuerca, with artefacts between 1.0 and 1.3 Ma (Parés et al., 2007). As with all other European localities >0.8 Ma, the lithic assemblages from this site can
be classified as Mode 1. The nearby cave system of Trinchera Dolina (TD) has also yielded artefacts ca. 0.85 Ma old in the TD4 level, 0.8 Ma in TD5 and a larger and better characterized assemblage from TD6, at least 0.78 Ma (Carbonell et al., 1995). Also in Spain, the open-air localities of Barranco Leon 5 and Fuente Nueva 3 have yielded stone tools that are probably ca. 1.1-1.3 Ma (Oms et al., 2000). The earliest evidence from France comes from the site of Pont de Lavaud, which has a very large lithic assemblage dated to ca. 0.905 and 1.187 Ma (Despriée et al., 2003; Falguères et al., 2003; see also Carbonell & Rodríguez, 2006). The recently discovered site of Pirro Nord (Italy) (Azarello et al., 2007) has artefacts probably in the same age range. The earliest lithic assemblages from the cave of Ca’ Belvedere di Monte Poggio in Italy are dated to the Jaramillo Subchron and are thus probably ca. 0.9 Ma (Gagnepain et al., 1992; Peretto, 2006).

Regarding the hominin fossil record, H. antecessor (Bermúdez de Castro et al., 1997; Carbonell et al., 2008) is currently the earliest unequivocal hominin species in Europe and its presence in the Eurasian continent stretches back to at least 1.3 Ma. Recent studies have shed light into the question of the origin of this species, and Southwest Asia, not Africa, appears as the most likely source for the first Europeans. Martínón-Torres et al. (2007) have identified a distinctive “Eurasian dental pattern” in Early and Middle Pleistocene hominins that differed from their African counterparts. Eurasian hominin anterior dentitions were characterized by their “morphological robusticity” with high frequencies of “mass additive traits” such as shovel shape, mesial canine ridge, and strong labial convexity. In the posterior dentition, early Eurasian hominins displayed qualitative traits derived from dental reduction, such as loss of cusps in upper and lower molars, increasing frequencies of groove-patterns different from the Dryopithecine pattern, and simplified occlusal surfaces. The dental evidence is also consistent with the facial and mandibular morphology, where the similarities between the Early Pleistocene humans from Europe and contemporaneous populations in Asia (Carbonell et al., 2005; Bermúdez de Castro et al., 2008) point to the existence of a common ancestor for both human groups.

Regarding the fossil mandible found at the Sima del Elefante site (ATE9), the morphology of the anterior surface of the symphysis and the position of the anterior marginal tubercle suggest similarities with early Homo specimens, in particular with those from Dmanisi. In contrast, the morphology of the posterior surface of the symphysis and the shape of the alveolar part of the corpus are clearly derived, suggesting a speciation event in this extreme part of Eurasia during the Early Pleistocene (Carbonell et al., 2008). From this evidence we conclude that the earliest Europeans probably were descendants of an “early” expansion of hominins out of Africa rather than a later one at the end of the Early Pleistocene (Aguirre and Carbonell, 2001; Martínón-Torres et al., 2007).

In this context, the Dmanisi specimens would represent a very early dispersal of H. erectus out of East Africa, or they indicate an earlier dispersal of Homo from East Africa in the Late Pliocene that later evolved into H. erectus s.l. and became the source population of H. erectus (or H. ergaster) in East Africa as well as H. erectus s.s. in East Asia (see Rightmire et al. 2006). In both scenarios we posit the existence of a source population of hominins in Southwest Asia that was closer both geographically and morphologically to H. antecessor and later European hominins than to any East African hominin (Carbonell et al., 2005; Martínón-Torres et al., 2007; Bermúdez de Castro et al., in press). Our own assessment of the Dmanisi dental evidence points to a hominin taxon that retains some Australopithecus and H. habilis features in combination with some derived features particularly related with a dentognathic reduction that characterizes H. erectus from the Far East (Martínón-Torres et al., 2008). If these traits reflect phylogeny rather than homoplasy, Dmanisi hominis bear all of the chronological, morphological and geographical conditions to have contributed to the later population of the Eurasian continent (Kaifu et al., 2005; Martínón-Torres et al., 2007). The dental morphology of the African Lower Pleistocene populations is generally more derived than the Dmanisi fossils, although the degree of reduction with regard to Australopithecus
and other early Homo is less pronounced than that seen in contemporaneous Asian populations. We cannot exclude genetic drift as one of the processes that could have accentuated this trend in the Eurasian continent (Suwa et al., 2007), but the Dmanisi dental pattern would point to an early emergence of this hominin lineage, prior to the emergence of the African Lower Pleistocene lineage (Wood, 1991; Suwa et al. 2007). In addition, it is noteworthy that among the human remains found in ‘Ubeidiya (Israel) (Tobias, 1966) dated to 1.4 Ma., there is an upper third molar that shows a remarkable reduction, similar to that found in Dmanisi and Asian H. erectus, and out of the variability range of the contemporaneous African populations (see Suwa et al., 2007). This could point to certain continuity or “residency” of the Dmanisi –or related- populations in the CADE. Postcranial remains would also support this scenario. Despite their primitive traits, which include a low encephalization coefficient, Dmanisi hominins exhibit some derived morphologies in their limb proportions and lower limbs morphology (Lordkipanidze et al., 2008) that point to the Dmanisi hominins as better candidates than H. habilis for the ancestry of the African and Asian Lower Pleistocene populations.

**Hominin dispersals into and within Europe (0.8 – 0.6 Ma)**

For the 0.8-0.6 Ma period, there are two new sets of information that need to be considered: the discovery of artefacts ca. 600-700 ka from eastern England and the ongoing research on the relationship between TD6 and SH, since the TD6 hypodigm has increased substantially since the first discoveries.

**Evidences from Happisburgh and Pakefield**

The discovery at Happisburgh and Pakefield of lithic artefacts ca. 600-700 ka old (Parfitt et al., 2005) obliges to a reconsideration of previous notions about the settlement of Europe. On one hand it demonstrates that hominins first inhabited northern Europe considerably before 500 ka, even if briefly. In addition, before the discoveries at Happisburgh and Pakefield, it appeared that the northern limit of hominins in Eurasia before the late Middle Pleistocene was ca. 40-45º N (e.g. Atapuerca-Dmanisi-Kuldara [Tajikistan]-Nihewan [North China]), perhaps because of the constraints that short winter days would have had on the foraging schedule of a diurnal hominin. However, these British sites are along 53º N of latitude. This implies that previous suggestions (see e.g. Dennell 2003, 2004) were erroneous, and that winter temperatures and/or precipitation (rain, sleet, snow) may have been more significant than winter day-light length. Finally, the climatic context of the artefacts from Pakefield indicates a “warm, seasonally dry Mediterranean climate” that was favourable to frost-sensitive insects and plants that are no longer native to Britain (Parfitt et al. 2005: 1010), and in which mean July temperatures were probably 3°C higher than today (Coope, pers. comm.).

If we assume that the hominins that lived on the “Costa del Cromer” (Roebroeks, 2005) at Happisburgh and Pakefield under a Mediterranean climate were H. antecessor (as these sites predate SH and other examples of H. heidelbergensis), their presence in England at latitude 53º N. can readily be explained as the result of range extension from southern Europe under unusually warm conditions: “The Mediterranean climate reconstruction for […] Pakefield suggests that these pioneers were able to spread northwards in familiar climatic conditions, using existing adaptations” (Parfitt et al. 2005: 1011). On this scenario (and as happened in Britain in every subsequent Middle Pleistocene glacial period [see Stringer 2006], hominins would then have later retreated southwards when the climate became cooler.

An alternative possibility to be explored is that H. antecessor experienced a range shift, rather than range extension ca. 700 ka. ODP 967 from the East Mediterranean shows an exceptional spike of low O18 ca. 650 ka (see Kroon et al., 1997). Further palaeoclimatic data to confirm this hypothesis are needed, but it could be that the Mediterranean zone shifted northwards during this time range. H. antecessor could have moved northwards, and eventually as far north as Pakefield,
but vacated its previous southern range which might be replaced by arid and even desert-like conditions. Climate again would appear as a driving force, but in this case unusually hot parts of interglacials may have been as adverse to hominins at the southern end of their range as severely cold periods were at the northern limits of occupation.

**TD6 and SH populations from Atapuerca**

Initial assessments suggested a phylogenetic relationship between the TD6 *H. antecessor* hominins and the nearby but later SH population of *H. heidelbergensis* (Bermúdez de Castro et al., 1997). Specifically, the convex superior border of the temporal squama, and the anterior position and vertical trajectory of the incisive canal of both species are similar, and are also features shared with *H. sapiens*. These synapomorphies were the basis for proposing *H. antecessor* as the best candidate to represent the last common ancestor of the *H. sapiens* and *H. neanderthalensis* lineages (Bermúdez de Castro et al., 1997). In 2003 we made a comparative study of the TD6 and Sima de los Huesos dental samples. The clear morphological differences found between both populations led us to propose a possible discontinuity between the Early and Middle Pleistocene populations in Europe (Bermúdez de Castro et al., 2003). Within this frame we considered that these differences could be attributed to the influx of a new wave of immigrants of *H. heidelbergensis* that replaced or might have absorbed the indigenous population of *H. antecessor* (Bermúdez de Castro et al. 2003). However, additional studies of the dentition (Martinón-Torres, 2006; Martinón-Torres et al., 2007a, b, Gómez-Robles et al. 2007) compelled us to reconsider this hypothesis. Despite the clear cranio-facial, mandibular and dental differences between both groups, we have identified two synapomorphies exclusively shared by the European Early and Middle Pleistocene populations. These traits correspond to the lower second premolar morphology (Martinón-Torres et al., 2006) and the upper first molar conformation (Gómez-Robles et al., 2007). Other dental traits of *H. antecessor* would fit into the “Eurasian dental pattern” also shared with *H. erectus s.s.*, *H. heidelbergensis* and *H. neanderthalensis* (Martinón-Torres et al., 2007a). This anatomical evidence would point to a phylogenetic relationship between *H. antecessor* and *H. heidelbergensis* but does not directly contradict a scenario of discontinuity between SH and TD6. *H. antecessor* could represent either the true ancestor to the Neanderthal lineage or a dead evolutionary lineage replaced during the Middle Pleistocene by another population (Carbonell et al., 2005) coming from the CADE. In this last scenario, *Homo antecessor* and Neanderthals would have shared a common ancestor, representing two different pulses of hominins into Europe at two different moments in time. As the SH hominin sample is now dated to ca. 0.6 Ma (Bischoff et al. 2007), rather than 0.4-0.5 Ma (Bischoff et al. 2003), this implies that a discontinuity event occurred between 0.6 and 0.8 Ma (0.9 Ma according to Berger et al., 2008).

**Middle Pleistocene dispersals of hominins into and within Europe (600 – 300 ka)**

The origin of *Homo heidelbergensis*

As seen above, if we take the morphological differences between TD6 and SH as evidence of discontinuity between the Early and Middle Pleistocene populations in Europe, this would imply that *H. heidelbergensis* lacks a direct European ancestor. However, due to the two dental synapomorphies shared between both lineages (Gómez-Robles et al., 2007; Martinón-Torres et al., 2006, 2007), a phylogenetic link between both populations can be ascertained. Still, the geometry of this relationship is not clear: either TD6 is ancestral to the SH groups or both TD6 and SH share a common ancestor. If we accept the second scenario, and despite the lack of hominin skeletal data from the Early Middle Pleistocene from Southwest Asia, there are two reasons why this region was the most likely area from which *H. heidelbergensis* dispersed into Europe in contrast to the afrocentric view. The finding of a human mandibular fragment in Azykh Cave, Azerbaijan, assigned to *H. heidelbergensis* (Ljubin and Bosinski, 1995) indicates that this taxon was also present in Southwest Asia in the early Middle Pleistocene. Furthermore, the dental evidence suggests that the genetic impact of Asia in the colonization of Europe during the Middle Pleistocene was stronger.
than that of Africa. If the origin of Middle Pleistocene populations of Europe lay in the arrival of African emigrants as it was suggested by several scholars (e.g. Stringer, 1985; Rightmire, 1998; Manzi, 2004), we should expect to find an African influence or discontinuity in the morphological pattern of the European Pleistocene populations. However, the continuity of the “Eurasian dental pattern” from the Early Pleistocene until the appearance of the Upper Pleistocene Neanderthals suggests that the evolutionary courses of the Eurasian and the African continents were relatively independent (Martinón-Torres et al., 2007). In the same line of evidence, the Neanderthal apomorphies that characterize the European Middle Pleistocene specimens are absent in African ones indicating that “the European population constituted the specific lineage of the Neanderthals” (Bermúdez de Castro et al., 2003: 1426). Moreover, with the exception of one specimen of the African hunting dog Nyctereutes at Hayonim, Israel, in the late Middle Pleistocene (Stiner et al., 2001), there is no evidence for a significant faunal exchange between the Levant and sub-African Africa during the Middle Pleistocene. In a more recent assessment, (O’Reagan et al. 2005:235), the only Levantine evidence of a faunal connection with Africa around the Early-Middle Pleistocene boundary is from Evron, Israel (ca. 1 Ma) and Gesher Benot Ya’aqov, Israel (ca. 0.8 Ma). As O’Regan et al. (2006, 241) state, “The idea that the Levant was a route of faunal exchange into and out of East Africa [between 1.0 and 0.5 Ma] is not supported by our results”, and “the modern zoogeographic separation of the Levant and north Africa into the Palaeartic region and sub-Saharan Africa into the African region can be traced back to at least the Early-Middle Pleistocene boundary” (ibid., p. 231). Given these circumstances, we logically hypothesize that the hominin traffic between continents was also severed during that period. “The ‘Levantine Corridor’ was a cul de sac rather than a passageway, as the Saharan belt was too firmly closed to allow free dispersal into sub-Saharan domains” (Tchernov, 1982:118).

Notwithstanding facial similarities between Arago 21 and Petralona, Bodo and Kabwe (Broken Hill) 1, we do not agree with assigning the Middle Pleistocene specimens from Africa to H. **heidelbergensis**, as suggested by Rightmire (2001) and Stringer (2002). The Middle Pleistocene fossils from Africa lack the Neanderthal apomorphies that are present in the European counterparts, and the similarities found between both lineages could be simply sinapomorphies (e.g. Arsuaga et al., 1993, 1997; Martínez and Arsuaga, 1997; Martínez, 1995; Bermúdez de Castro et al., 2004). Instead, we suggest that the African specimens are more appropriately referred to H. **rhodesiensis**, as suggested by Bermúdez de Castro et al. (2003), and McBrearty and Brooks (2000). The calvarium from Daka, ca. 1.0 Ma could represent an ancestral candidate of H. **rhodesiensis** in sub-Saharan Africa, at a time when faunal contacts still existed between Africa and Asia. Thus, Daka and other related specimens still to be found also in Eurasia, could represent the speciation event at around 1 Ma. that according to Rightmire (1996) would preceded the origin of later hominin lineages (Neanderthals and H. sapiens). If we accept that H. **antecessor** is a purely European speciation event (Carbonell et al., 2008), the hypothesis of its relationship with H. **sapiens** lineage (Bermúdez de Castro et al., 1997) should be revisited.

As previously suggested, we believe that main influences on developments in Europe in the Early and Middle Pleistocene derived from its immediate neighbour of Southwest Asia rather than Africa. The Near East, together with the Mediterranean coast of Israel and the Lebanon, Georgia and nearby countries at the south, like northern Syria, could be the establishment area for our “source population’. This CADE represents a true crossroad between Africa, Asia and Europe, where theoretically we can expect a more generalized morphology. Populations in the central and peripheral areas are connected by narrow corridors where the geographical and climate barriers can favour processes of genetic drift and random allelic variation in their “descendants”. The genetic variability of the populations that travelled far in Asia and Europe from Africa is lower due to the founder effect and genetic drift (Lohmueller et al., 2008). Inversely, this implies that the core or “source” populations have more variability, the “mixtures” are more likely and the cross-lines to define and separate species, less clear. Groups in the periphery are probably more likely to
suffer isolation and genetic drift processes and, eventually, an allopatric speciation. Still, genetic and consequent morphological changes are not exclusive to the “descent” populations but can also occur in the “source population”, being thus reflected in the morphological variability –not necessarily to a “species level”– of the migrational pulses that enter the continent. In fact, trying to classify the hominid populations into a “species” scheme too rigidly, and the understanding of dispersal events as directional and lineal migrations instead of expansion/contraction hominid pulses, undoubtedly interfere in the understanding of the evolutionary scenario of the genus Homo during the Pleistocene. The pattern of interglacial/interstadial expansion and glacial/stadial contraction in hominin (and other mammals’ ranges) is also a pattern of expansion and local extinctions (Dennell et al., 2010). We should not forget that range contraction of a species is not the same as range contraction of all its groups.

The taxonomic distinctiveness of H. heidelbergensis

Within Europe, the taxon H. heidelbergensis applies to all hominin specimens of the Middle Pleistocene that post-date H. antecessor and predate Neanderthals and H. sapiens. There is a general agreement that the Upper Pleistocene Neanderthals have deep roots in the European Middle Pleistocene (Rightmire, 1997; Arsuaga et al., 1993, 1997, Bermúdez de Castro, 1986, 1987, 1993; Bermúdez de Castro et al., 2009). Most European fossil remains from this period (e.g. Steinheim, Petralona, Arago, Swanscombe and SH) and region exhibit one or more derived cranial traits, exclusively shared with Neanderthals. According to Arsuaga et al. (1997), H. heidelbergensis would be defined by a number of primitive features lost in Upper Pleistocene Neanderthals, other traits that are transitional to the Neanderthal morphology (named “mesomorphies” by Arsuaga et al., 1998), and other traits that are typical of classic Neanderthals. This evidence has led to the consideration of the European Middle Pleistocene populations as direct ancestors of the Neanderthal lineage, even as the same evolutionary species without disruption of their reproductive continuity (Arsuaga et al., 1993, 1997). In this context, it has been proposed a model of local evolution in Europe with increasing frequencies of Neanderthal traits due to isolation for glacial conditions, for the origins of H. neanderthalensis (Arsuaga et al., 1993; Hublin, 1996). The gradual accumulation of Neanderthal distinction was coined as the “accretion hypothesis” (see Hublin, 1988; Condemi, 1987; Rightmire, 1997, 1998). However, the European sample of H. heidelbergensis may be more variable than often assumed. Apart from the lack of a reliable chronological framework to place each preneandertal specimen with reasonable precision, the combination of primitive and derived traits appears to be random and cannot be ordered in a chronological sequence (Bermúdez de Castro et al., in press). Thus, while SH populations exhibit a fully Neanderthal pattern in both dental morphology and proportions (Martinón-Torres, 2006), chronologically younger specimens like Mauer (the holotype of H. heidelbergensis) lacks some of the distinctive morphological traits of the European Middle Pleistocene populations (Rosas, 1991; Rosas and Bermúdez de Castro, 1998). Similarly, the Arago hominins are somewhat anomalous compared with SH and later Neanderthals, and Arago 13 “shows a combination of the ‘Gran Dolina and Sima de los Huesos’ dental traits” (Bermúdez de Castro et al. 2003: 1423). Thus, some later pre-neandertals appear to be “less Neanderthal” than chronologically older specimens.

As discussed with more detailed elsewhere (Dennell et al., 2010) a possible explanation for the Middle Pleistocene Europe demographic dynamics could be based on “sources” (a small number of “core” populations in glacial refugia in southern Europe from which hominins expanded northwards in interstadial and interglacial periods) and “sinks” (populations that depend on recruitment from source populations further south to remain occupied). Occupation outside glacial refugia would have been restricted to warm or temperate periods, In extreme situations, Europe may have been a population “sink” (i.e. unpopulated) that was replenished from source populations in Southwest Asia. We suggest that this pattern of repeated colonisation and extinction may help explain the morphological variability of European Middle Pleistocene hominins, particularly
Homo heidelbergensis and its apparent non-lineal evolution towards Homo neanderthalensis (Dennell et al., 2010).

In the game of chance of Middle Pleistocene Europe, some populations would undoubtedly have foundered. Those that survived may have been more resilient, or simply more fortunate. The Iberian Peninsula may have been one of the principal refuges in Western Europe to work as a “source” area during glacial periods, becoming a genetic reserve for subsequent demographic expansions when the climate ameliorated. According to Hewitt (2000), the Iberian and Balkan Peninsulas were also origin of certain number of European animal and land species, and the Alps could have been an important barrier for species dispersals even during interglacials.

Discussion and conclusions

Crucially, the initial colonisation of Europe by hominins such as *H. antecessor*, its subsequent occupation by *H. heidelbergensis*, and the appearance of Acheulean (Mode 2) assemblages in Europe as well as South Asia all probably derived from Southwest Asia rather than sub-Saharan Africa. The source population of both *H. antecessor* and *H. heidelbergensis* was probably Southwest Asia (with the Dmansı hominins currently providing the best example of an ancestral population). We also argue strongly on both morphological and geographical grounds that *H. heidelbergensis* was restricted to Europe and Southwest Asia, and could not have entered (or come from) sub-Saharan Africa because of the desert barriers that persisted throughout the Middle Pleistocene. Overall, Africa is not particularly relevant for the evolutionary history of Eurasia from 800 ka until the appearance of modern humans in the Levant ca. 120-130 ka.

At this point, we can consider the likely processes that resulted in the archaeological and fossil hominin evidence from Europe before and after 600 ka.

1) pattern and process of hominin dispersals into Europe before 600 ka

At a regional level, the evidence now available from the Atapuerca region is providing the first European sequence of hominin populations from ca. 1.4 to \(\leq 0.6\) Ma. This indicates an initial set of dispersals that probably began after 1.75 Ma and involved descendants of the *H. erectus/georgicus* population in Southwest Asia. The discovery of hominin remains and artefacts from Sima Elefante that are ca. 1.3 Ma old (Carbonell et al., 2008) significantly reduces the time that hominins had to wait “at the Gates of Europe”. Indeed, the Sima del Elefante hominins are unlikely to have been the first hominins that dispersed as far and west as Spain, and still less likely to have been the first that entered Southeast Europe. The absence of Early Pleistocene faunal and archaeological evidence from western Turkey, Greece, and the rest of Southeast Europe means that we may well yet be surprised by discoveries in these regions. Indeed, one should expect discoveries of hominins in these areas that are older than those from the West Mediterranean. It is also unlikely that there was only one dispersal event of hominins into Europe in the Early Pleistocene. The process of dispersals would probably have been driven primarily by climatic factors. More specifically, hominins would probably have dispersed westwards from Southwest Asia along the Mediterranean as part of their range extension during interglacials when rainfall and biological productivity were higher. Some dispersals would probably have failed (i.e. have not persisted beyond a glacial-interglacial cycle) but others would have proved more resilient. Evidence from Happisburgh and Pakefield indicate that their latitudinal ranges may occasionally have extended as far as 53° N. when conditions were warm enough to allow it. We might thus expect a pattern in the Early Pleistocene of many “visitors” in warmer and moister periods, but few longer-term “residents”, along the lines previously suggested for Eurasia (Dennell, 2003). The Sima del Elefante hominins might represent one of these resident populations, especially if we accept the morphological similarities with the younger TD6 *H. antecessor* groups. At least one dispersal event in the Early Pleistocene thus appears to have resulted in a speciation event at the western end of the Mediterranean in the later Early Pleistocene. The fact that all Early Pleistocene European hominin groups used simple (Mode
1) flake and core assemblages of stone tools may imply that hominins were already resident in Europe before Mode 2 assemblages were used after 1.4 Ma in East Africa and Southwest Asia.

2) pattern and process of hominin dispersals into Europe after 600 ka

The hypothesis of population discontinuity between H. antecessor (TD6) and H. heidelbergensis (SH) suggests an immigration event by hominins that replaced or absorbed the indigenous H. antecessor population. This dispersal may have originated in Southwest Asia, not Africa as it has been classically proposed. This event occurred between ca. 780 and 600 ka during the Middle Pleistocene transition that ended with the establishment of a 100-ka cycle of glaciations and interglacials at ca. 640 ka. Since its appearance in Europe at least 1.3 Ma ago, H. antecessor survived numerous climatic shifts, and the most likely cause of the population replacement between 780-600 ka could be an exceptionally cold period. This may have been during Marine Isotope Stage (MIS) 16 (ca. 650-620 ka), as this was the earliest European glaciation; or during one or more short periods of extreme cold of the kind shown in marine cores after 500 ka.

The immigrant population of H. heidelbergensis became the resident one in Europe and developed into H. neanderthalensis by the later Middle Pleistocene. The process giving rise to H. neanderthalensis may have not been as linear as previously thought with the accretion model, and the climate probably played a major role in the expansion and the contraction of the occupation range of these hominin populations (Dennell et al., 2010).

As a working hypothesis, we therefore suggest that both H. heidelbergensis and the use of Acheulean bifacial assemblages in Europe originated in Southwest Asia rather than Africa, and that their appearance at approximately the same time (so far as can be judged from the admittedly poor dating evidence) in both western Europe and India indicates a dispersal event, or a series of dispersal events from Southwest Asia, most probably during one or more interglacial periods, by small populations of hominins. Some, but not all, would have used an Acheulean bifacial technology; however, not all “Acheulean” groups would necessarily have used and discarded bifaces on a habitual basis. Regarding Europe, it is likely that the immigrant populations were early ones of H. heidelbergensis that may have absorbed remaining descendents of H. antecessor. This possibility, as well as the likelihood of genetic drift among small and often isolated populations, may help explain some of the variability seen in European specimens of H. heidelbergensis.

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MARTÍNEZ I (1995) La base del cráneo y el hueso temporal en la evolución de los homínidos con especial refe-

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Durante los dos últimas décadas el registro arqueológico y paleontológico del Pleistoceno de Europa ha experimentado un incremento muy importante. Varios yacimientos y en particular los de Atapuerca y Dmanisi, han aportado datos muy relevantes, que han permitido refutar viejas hipótesis acerca de la primera expansión demográfica de los homínidos fuera de África y de la primera colonización del continente europeo. Otros yacimientos, como los de Pakefield y Happisburg, en el Reino Unido, han proporcionado datos de gran interés para comprender mejor dinámica de la historia evolutiva de los homínidos en Europa durante el Pleistoceno. A pesar de que existen todavía muchos interrogantes y faltan datos sobre la cronología de buena parte de los yacimientos, los datos disponibles han sido ya “digeridos” y la comunidad científica está preparada para aceptar una visión diferente acerca del primer poblamiento de Europa. En este trabajo presentamos un nuevo modelo para interpretar el registro, que tiene en cuenta no sólo las evidencias que ofrecen los restos fósiles de homínidos, sino los datos paleoclimáticos, paleogeográficos y paleontológicos. Este modelo comprende varias hipótesis de trabajo, que se irán contrastando a medida que se obtenga nueva información en los yacimientos del Pleistoceno de Eurasia.

Palabras clave: Europa, Pleistoceno, evolución humana

La colonización de los homínidos en Europa durante el Pleistoceno