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MIGRATION OF HOMININS WITH MEGAHERBIVORES INTO EUROPE VIA THE DANUBE-PO GATEWAY IN THE LATE MATUYAMA CLIMATE REVOLUTION

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Abstract. We update critical reviews of sites bearing hominin remains and/or tools from Europe (including the Balkans and Greece) and conclude that the only compelling evidence of hominin presence in these regions was after ~0.9 Ma (million-years-ago), bracketed by the end of the Jaramillo subchron (0.99 Ma) and the Brunhes/Matuyama boundary (0.78 Ma) and straddling the climatic late Early Pleistocene revolution (EPR) at the onset of enhanced glacial/interglacial activity that reverberated worldwide. Europe may have become initially populated during the EPR when, possibly for the first time in the Pleistocene, vast and exploitable ecosystems were generated along the Danube-Po Gateway. These newly formed settings, characterized by lowlands with open grasslands and reduced woody cover during glacial/interglacial transitions, represented the closest analogues to the savanna environment to which several large mammals linked with hominins in a common food web were adapted. It was only after stable and vast grassland-savanna environments opened that large mammals (e.g. megaherbivores) could expand into Europe along the Danube-Po Gateway in conjunction with the attached food web to which hominins belonged.

Introduction

The chronology of early hominin presence in Europe has been considerably improved in the last two decades. Proponents of a 'long' chronology (e.g., Bosinski 1992; Gibert et al. 1998; Toro-Moyano et al. 2013; Garcia et al. 2014) expect the earliest evidence from Europe to date to >1 Ma and correlate with the pre- or syn-Jaramillo portion of the Matuyama reverse geomagnetic polarity chron, and possibly be as old as the earliest dates claimed for Asia: ~1.7 Ma at Dmanisi in Georgia (e.g., Gabunia et al. 2000; Lordkipanidze et al. 2007), ~1.8 Ma in Java (Swisher et al. 1994), or ~1.66 Ma in China (Zhu et al. 2003; 2004). Those advocating a 'short' chronology claim instead that Europe was a peripheral peninsula of the Asian landmass, uninhabited for up to a million years after hominins first appeared in Asia. For example, Roebroeks and van Kolfschoten (1994) proposed that the first solid traces of hominin activities in Europe do not occur until around 0.5 Ma, which would lie well within the Brunhes normal geomagnetic polarity chron (<0.78 Ma). However, after new convincing findings from Spain (e.g., Carbonell et al. 1995), Dennell and Roebroeks (1996) and Roebroeks (2001) concluded that this short chronology applies only to Europe north of the Alps and the Pyrenees (although more recent findings at Happisburgh, England, definitely documented Europe colonization up to the boreal zone since the late Early Pleistocene [Parfitt et al. 2005, 2010]), whereas the Mediterranean region, and especially Spain, saw an earlier occupation starting around the end of the Early Pleistocene (late Matuyama Chron, >0.78 Ma). Dennell (2003) examined the archeological evidence and concluded that even if hominins occupied parts of Europe (as well as northern Africa and southern Asia) shortly after 2 Ma, there is little evidence of colonization and permanent settlement in these regions before the Middle Pleistocene (early Brunhes Chron, <0.78 Ma). Antón and Swisher (2004) reviewed multiple lines of evidence that support a long chronology of hominin presence outside of Africa in

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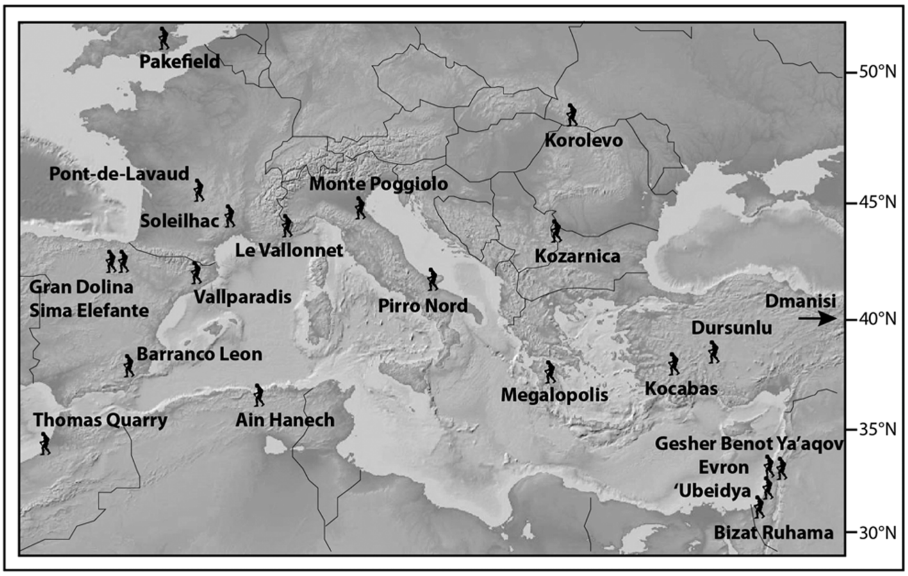

Fig. 1 - Geographic sketch map showing location of hominin sites discussed in the text.

western Asia and Indonesia at as far back as 1.8 Ma and a short (but not so short) chronology of earliest occupation of Europe (e.g., Spain) at ~0.8 Ma.

More recently reported cosmogenic burial dates from Sima del Elefante seem to indicate that hominin occupation in northern Spain was earlier, at around 1.2-1.1 Ma (Carbonell et al. 2008). Moreover, electron spin resonance (ESR) ages on quartz grains, coupled with magnetostratigraphic and biochronologic data, on a human tooth from the Barranco León site would seem to indicate that hominins were present in southern Spain as early as ~1.4 Ma (Toro-Moyano et al. 2013).

From a critique of the Barranco León evidence (Muttoni et al. 2013), we can agree that the precise chronology of earliest hominin presence in Europe remains a complicated and controversial issue especially because the age estimates of several key sites are still very uncertain (e.g., Villa 2001; Roebroeks 2001; Antón and Swisher 2004; Muttoni et al. 2009). In this paper, we expand our previous critical analyses of earliest hominin sites constrained in time by magnetostratigraphy and/or radiometric age data from the circum-Mediterranean region (Muttoni et al. 2010, 2011, 2013), discussing data from key sites bearing hominin remains and/or lithic industries from Europe and including a new critical review of data from the Balkan region, Greece, Turkey, and the Levant. We conclude that the first occurrence of hominins in Europe took place between the Jaramillo subchron and the Brunhes/Matuyama boundary (0.99-0.78 Ma), therefore in between the classic 'long' chronology of earliest peopling of Europe in the pre-Jaramillo Matuyama (>1 Ma; e.g., Garcia et al. 2014), and the classic 'short' chronology of earliest peopling after the Brunhes/Matuyama boundary in the Middle Pleistocene (<0.78 Ma; e.g., Roebroeks and van Kolfschoten 1994). We also improve our previous hypothesis (Muttoni et al. 2010, 2011) on possible paleoclimate causes of hominin migrations during the late Early Pleistocene climate revolution.

Magneto-chronology of early hominin presence in Europe

South and Central Europe

For the chronology of key hominin sites in South and Central Europe (either well-dated or less well-dated but highly cited in the mainstream literature) (Fig. 1), we summarize key elements of the critical review of Muttoni et al. (2010, 2011, 2013), including in the selective magnetochronology framework of Fig. 2 only sites with reliable and documented (and accessible) magnetostratigraphy.

Sites in Italy older than the Brunhes/Matuyama boundary are Cà Belvedere in northern Italy and Pirro Nord in southern Italy (Fig. 1). Cà Belvedere was dated to ~0.85 Ma, between the Jaramillo and the Brunhes, based on magnetostratigraphic data buttressed by marine biostratigraphic control from interfingering strata (Muttoni et al. 2011) (Fig. 2). Pirro Nord yielded only reverse magnetic polarity, indicating a pre-Brunhes age (>0.78 Ma) (Pavia et al. 2012); its current age attribution of ~1.7-1.3 Ma is based on mammal biostratigraphy (Pavia et al. 2012). The age of the Pirro faunal unit is strongly dependent on the assumption that it is older than the Colle Curti faunal unit attributed to the Jaramillo (Coltorti et al. 1998). However, the normal polarity interval in the Colle Curti section attributed to the Jaramillo occurs in a clayey interval rich in organic matter and iron sulphides, which are magnetically unstable and frequently of diagenetic origin (e.g., Roberts & Weaver 2005), whereas in the bracketing more sandy layers bearing magnetite, a normal polarity overprint had to be removed before higher unblocking temperature component directions of reverse polarity were revealed (Coltorti et al. 1998). This lithological and mineralogical dependence of magnetic polarity and the likely presence of diagenetic overprinting raise doubts that the purported Jaramillo is real and could instead represent a recent normal polarity overprint. Pending a reanalysis of the section (in progress), we maintain that in the absence of a clear Jaramillo, both the Colle Curti and the Pirro faunal units are, so to speak, 'lost in the Matuyama', without any meaningful numerical age attached other than older than 0.78 Ma.

In Spain, there is compelling magnetostratigraphic evidence of hominin presence before the Brunhes/Matuyama boundary, e.g., at Barranco León (Toro-Moyano et al. 2013), Gran Dolina (Pares and Perez-González 1999; Pares et al. 2013), Sima del Elefante (Carbonell et al. 2008), and Vallparadís (Martinez et al. 2010, 2014) (Fig. 1). At Vallparadís near Barcelona, lithic elements with claimed man-made 'Oldowan-like' features (see Garcia et al. 2013 for a description) have been retrieved from levels constrained to a time interval of reverse polarity comprised between the top of the Jaramillo (0.99 Ma) and the base of the Brunhes (0.78 Ma), and are associated with an average age of 0.83 Ma based on ESR-U/series dating of two equine molars and OSL dating of four quartz grain samples (Martinez et al. 2010, 2014). Martinez et al. (2014) attempted to apply vole clock chronology to assign an age of ~0.98-0.95 Ma to archeological level 10, which would then fall immediately after the Jaramillo. Martin (2014) illustrated that the vole clock method can hardly yield the level of accuracy implied by Martinez et al. (2014) at Vallparadís (and, for similar reasoning, at Fuente Nueva 3 and Barranco Lèon as implied by Lozano-Fernández et al. [2014]). In any case, the Vallparadís site remains at present probably the best magnetostratigraphically constrained site in Spain with the archeological levels falling between the top of the Jaramillo (0.99 Ma) and the base of the Brunhes (0.78 Ma) (Fig. 2). In the framework of a well-established pre-Brunhes and post-Jaramillo chronology of first hominin presence in Spain, there is in our opinion (see also Muttoni et al. 2010) no compelling evidence of hominin presence before (or even during) the Jaramillo, including the human tooth level from Barranco León, whose age attribution to ~1.4 Ma (Toro-Moyano et al. 2013) was recently criticized (Muttoni et al. 2013), and level TE9 from Sima del Elefante at Atapuerca (Carbonell et al. 2008) with cosmogenic burial age estimates that at 2s level (95% confidence) would not preclude that hominin occupation at Sima del Elefante occurred between the Brunhes/Matuyama boundary, which was found a few meters above level TE9, and the Jaramillo, which was not found in the section despite repeated and detailed sampling (Parès et al. 2006; Carbonell et al. 2008).

Hominin sites in France claimed to be older than 1 Ma (Soleilhac, Le Vallonnet, Pont-de-Lavaud, as well as additional sites in the Massif Central and Haute-Loire) typically lack convincing chronology (and sometimes even convincing evidence of human presence) (see critical review and discussion in Muttoni et al. 2010, 2011, 2013). The Le Vallonnet site (Fig. 1) deserves particular mention because it is frequently attributed to the Jaramillo (see for example Toro-Moyano et al. 2013), evidence of which is, however, very elusive. Yokoyama et al. (1988) reported normal polarity directions that they interpreted as pertaining to either the Brunhes or the Jaramillo or the Olduvai, whereas Gagnepain (1996) provided inconclusive paleomagnetic data, which did not allow establishing a clear magnetic polarity for the succession.

In the absence of convincing evidence of Untermassfeld as a Lower Paleolithic site (Baales 2014 vs. Landeck and Garcia 2014), the northernmost tool-bearing site in Europe is Happisburgh (UK; Fig. 1) where sediments are characterized by reverse magnetic polarity attributed, in conjunction with mammal biostratigraphic considerations, to the Matuyama after the Jaramillo and before the Brunhes (both not found), that is to say, to a time interval comprised between 0.99 and 0.78 Ma (Parfitt et al. 2010).

Southeastern Europe (Balkans and Greece)

The Balkan region is a key area for the exchanges between Europe and the Asian and African continents but none of the hereafter discussed sites are thus far provided with reliable and documented (and accessible) magnetostratigraphy that would make them part of the selective magnetochronology framework of Fig. 2.

Korolevo

This site is located in Ukraine along the Tisza River near the border between Hungary and Rumania (Fig. 1). The stratigraphy of the site, discovered in 1974 in a stone quarry, consists of 14 m of loess with seven different paleosols overlying fluvial deposits (Koulakovska et al. 2010). The Brunhes/Matuyama boundary was placed at the base of the loess sequence above the lowermost paleosol (Koulakovska et al. 2010; Stepanchuk et al. 2013), but we could not obtain information on the analytical data used to obtain polarity stratigraphy from the cited references in Russian. The earliest human presence there is testified by the recovery of Mode I (Oldowan) tools coming from two levels in the lower part of the succession, reportedly bearing normal overlying reverse polarity (Stepanchuk et al. 2013; Koulakovska et al. 2010).

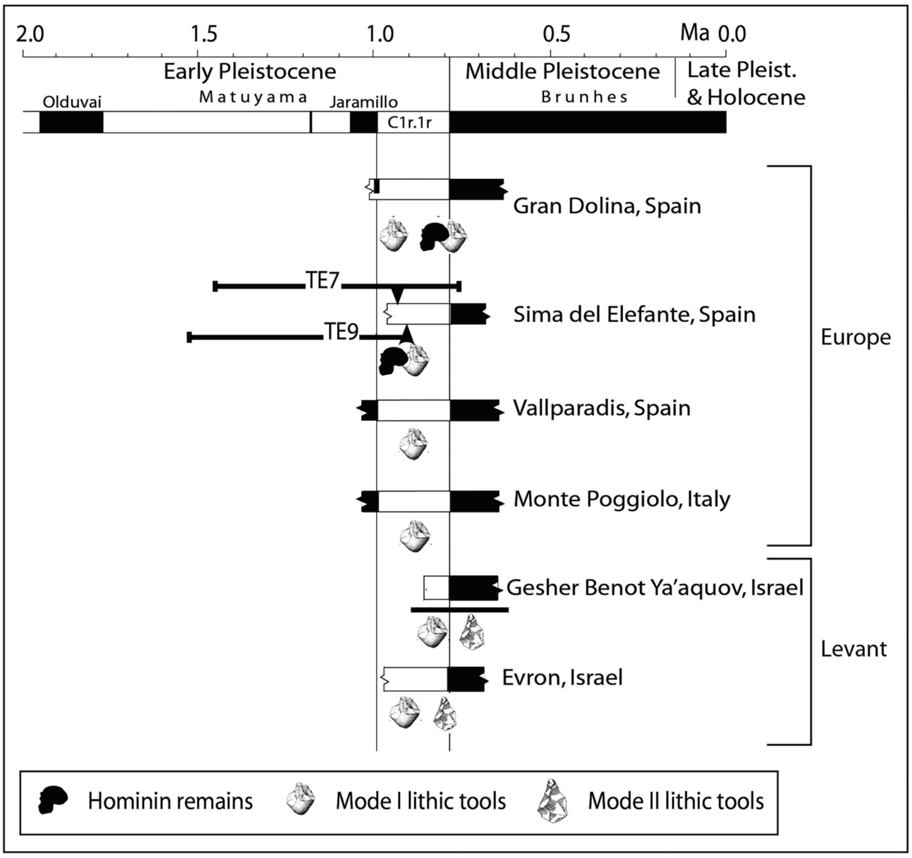

Fig. 2 - Our preferred interpretation of evidence for the earliest human occupation of Europe and at the gates of Europe in the Levant with respect to the astrochronological polarity time scale (APTS) (Lourens et al. 2004). Oldest key hominin sites with reliable magnetostratigraphy tend to occur within the reverse polarity interval between the Jaramillo and the Brunhes (0.99 to 0.78 Ma). Europe: Gran Dolina (Pares and Perez-González 1999; Pares et al. 2013), Sima del Elefante (Carbonell et al. 2008; with cosmogenic burial ages from levels TE7 and TE9 expressed at 2s level; Muttoni et al. 2013), Vallparadís (Martinez et al. 2010), Monte Poggiolo (Muttoni et al. 2011). Gates of Europe: Gesher Benot Ya'aqov (Goren-Inbar et al. 2000), Evron (Ron et al. 2003). Other sites with magnetostratigraphies that are debated or poorly documented or inaccessible that are discussed and referenced in the text (but not shown in the figure) include Soleilhac, Le Vallonnet, Pont-de-Lavaud in France, Kozarnica in Bulgaria, Korolevo in Ukraine, Megalopolis in Greece, Dursunlu in Turkey, and 'Ubeidyia in Israel, whereas Erk-el-Ahmar in Israel and Kocabas in Turkey are excluded because the hominin levels could not be securely traced into the magnetostratigraphic profiles. Other sites with valuable (and well illustrated) but incomplete (single polarity only) magnetostratigraphies are also provisionally excluded from this summary figure: Bizat Ruhama in Israel, Pirro Nord in Italy and Happisburgh in the U.K.; see text for references.

Kozarnica

This site is located in the northwestern part of the Lower Balkans, in the Danube plain of Bulgaria (Fig. 1). Human artifacts from different periods and industries were found inside a 210 m-long cave (Sirakov et al. 2010). The lower levels with lithic tools (from bottom to top, layers 13, 12, 11c and the basal part of 11b) were targeted for magnetostratigraphy. According to preliminary data, for which no analytical information was provided (Sirakov et al. 2010), sediments down to the middle part of layer 11b are characterized by normal polarity magnetization interpreted as a record of the Brunhes Chron; low magnetic inclination values in the lower part of layer 11b have been tentatively interpreted as indicating transition to reverse polarity of the Matuyama Chron but problems of consolidation of blocks from the lower part of the sequence (i.e., from underlying levels 11c-13) did not allow to retrieve a paleomagnetic signal (Sirakov et al. 2010).

Chronologic assessment was also supported by mammal biochronology. Using a statistical (probability) approach, the archeological layers were attributed to Mammal Neogene/Quaternary Zone (MNQ) 17 for layer 13, MNQ 18 for layer 12, and MNQ 19 for layers 11c and 11b (Sirakov et al. 2010). Sirakov et al. (2010) then concluded in favor of an age of 1.6-1.4 Ma for the earliest hominin evidence at Kozarnica. According to ^{40}Ar/^{39}Ar radiometric age assessments on key mammal sites in France, MNQ 17 is dated to well in excess of 2 Ma and MNQ 18 broadly corresponds to the Olduvai chron (1.95-1.78 Ma) (Nomade et al. 2014). Thus the MNQ 17-18 biochronologic attribution is in contrast with the (preliminary and partial) magnetostratigraphy and the 1.6-1.4 Ma age proposed by Sirakov et al. (2010). The Gelasian MNQ 17 age would make Kozarnica an outstanding outlier in hominin chronology with an age of > 2 Ma, i.e. older by as much as 1 Myr than any other dated site in Europe and, more in general, older than virtually all known hominin evidence outside Africa. Additional data are required in order to better assess the chronology of the Kozarnica cave infill and confirm if the lower archeological levels with lithic tools predate the Brunhes/Matuyama boundary.

Megalopolis

The Megalopolis basin is an intermontane depression located in the Peloponnesus, Greece (Fig. 1). A single human tooth was found in the early 1960's

(Harvati et al. 2009) in reworked material attributed to the Marathousa Member of the Choremi Formation, comprised of lacustrine muds intercalated with lignite seams (Okuda et al. 2002; Harvati et al. 2009; Tourloukis and Karkanas 2012 a, b). A magnetostratigraphic study was performed by Van Vught (2000) on outcropping sections of the Marathousa Member. The results showed an upward transition from reverse to normal polarity interpreted as the Brunhes/Matuyama boundary, in agreement with the biostratigraphic data based on micro- and macro-mammals such as *Hippopotamus antiquus*, *Praemegaceros verticornis*, *Pliomys* aff. *episcopalis*, *Mimomys* aff. *savini*, and *Mus spretus* (Tourloukis and Karkanas 2012 a, b). Unfortunately, it has not been possible to relocate the human tooth in the stratigraphic sequence studied by Van Vught (2000) (Tourloukis and Karkanas 2012 a, b); a new magnetostratigraphic investigation of the human tooth-bearing sequence is in order.

Summary of magneto-chronology of early hominin sites in Europe

Considering all the uncertainties and ongoing controversies (Muttoni et al. 2010, 2011, 2013, this study), we conclude that at present the best available data as summarized in Fig. 2 seem to indicate (or do not contradict) a vision of earliest hominin main presence in Europe between the top of the Jaramillo subchron (0.99 Ma) and the Brunhes/Matuyama boundary (0.78 Ma); that is to say, the European region, including the Balkans and Greece, was hominin-free prior to ~0.9 Ma. Although Turkey and the Levant could have been inhabited earlier (see below), our interpretation on the magnetochronology of earliest occupation of Europe starting at ~0.9 Ma lies in between the classic 'long' chronology of earliest peopling of Europe in the pre-Jaramillo Matuyama (>1 Ma; e.g., Garcia et al. 2014; see also Toro-Moyano et al. 2013 vs. Muttoni et al. 2013), and the classic 'short' chronology of earliest peopling after the Brunhes/Matuyama boundary in the Middle Pleistocene (<0.78 Ma; e.g., Roebroeks and van Kolfschoten 1994). We stress that within the broad magnetochronological framework indicated above, subtle age differences (on the order of ~100 ky) between sites in southern Europe and sites in central Europe could exist, but that these differences are at present difficult to resolve with the applied numerical age methods (e.g., magnetostratigraphic, ESR, cosmogenic isotopes).

We review now how this chronology of earliest hominin presence in Europe can be related to key climatic events that occurred globally in the late Early Pleistocene.

Pleistocene climate variability

Expanding previous considerations (Muttoni et al. 2010), the reasons hominins first migrated to Europe at ~0.9 Ma may be linked with Pleistocene climate variability and associated environmental and ecological changes. High frequency (~40 ky) and low amplitude glacio-eustatic (climatic) oscillations characterized the Early Pleistocene whereas lower frequency (~100 ky) and higher amplitude oscillations have dominated since the Middle Pleistocene (e.g., Berger et al. 1993). The transition to higher amplitude climate variability occurred in the late Early Pleistocene between the Jaramillo subchron (0.99 Ma) and the Brunhes/Matuyama boundary (0.78 Ma) (e.g., Head & Gibbard 2005; Lourens et al. 2004; Lisiecki & Raymo 2005) (Fig. 3A, B), the same magnetochronologic window that we believe includes the best-dated sites with evidence of earliest peopling of Europe (Fig. 2). Within the transition, marine isotope stage (MIS) 22 at ~0.9 Ma represents the first major northern hemisphere continental glaciation of the Pleistocene (Shackleton and Opdyke 1976; Berger et al. 1993; Shackleton 1995; Head and Gibbard 2005) (Fig. 3A, B). This major climatic transition is hereafter referred to as late Early Pleistocene Revolution (EPR) that substitutes for the often-used term Middle (or mid-) Pleistocene revolution (e.g., Berger et al. 1993) in deferrence to modern geologic time-scales in which the base of the Middle Pleistocene is placed at the Brunhes/Matuyama boundary at MIS 19 (Head and Gibbard 2005).

Larrasoaña et al. (2013) established a link between Mediterranean sapropels, traditionally attributed to increased Nile (or similar fluvial system) runoff during summer insolation maxima (Rossignol-Strick 1983), and recurrent humid episodes in North Africa – the so-called green Sahara periods (GSPs) – with savanna expansion throughout most of the desert. The sapropel-based GSP record was shown to be relatively continuous throughout the Pliocene and Pleistocene (Larrasoaña et al. 2013) (Fig. 3C), with only one apparent gap characterized by three oxidized sapropels/possible GSPs broadly occurring during the EPR from ~0.9 Ma to ~0.7 Ma (Larrasoaña, personal communication to GM; Fig. 3C), which temporally coincides with an a step-increase in Sahara dust production as revealed by data from Ocean Drilling Program (ODP) Site 967 (Larrasoaña et al. 2003; Trauth et al. 2009) (Fig. 3D). Our point here is that there seems to have existed as many as 63 GSPs since 2 Ma during which hominins and other mammals could have crossed the Sahara desert barrier and migrated back and forth from/to the Levant (Almogi-Labin 2011) as well as China (Zhu et al. 2004) and southeast Asia (Swisher et al. 1994), but apparently not according to our critical review until much later into Europe.

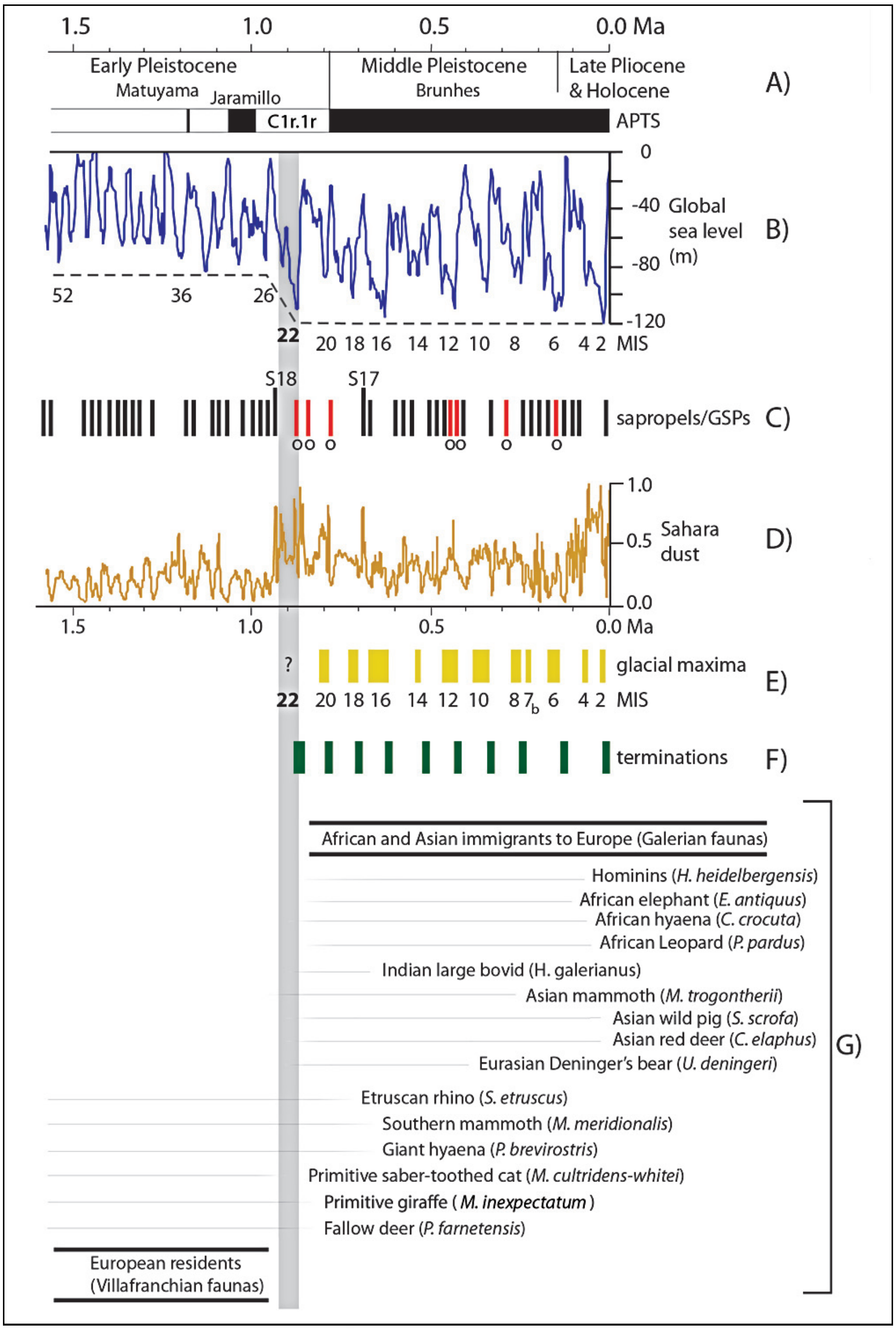

Fig. 3 - A) Astrochronological polarity time scale (APTS) (Lourens et al. 2004) as framework for correlation of B) Pleistocene climate variability as revealed by benthic oxygen isotope data (Shackleton 1995) scaled to the glacio-eustatic drop at the last glacial maximum time (Fairbanks 1989); C) the sapropel-based Green Sahara Period (GSP) record of Larrasoaña et al. (2013; "o" marks represent oxidized sapropels/possible GSPs); D) Sahara dust production as revealed by data from ODP Site 967 (Larrasoaña et al. 2003; Trauth et al. 2009); E) development of loess sequences with steppic vegetation associated with glacial maxima in Europe and the Black Sea area (Cremaschi 1987; Sartori et al. 1999; Dodonov et al. 2006; Fitzimmons et al. 2012; Ujvari et al. 2014; Jipa 2014), and F) main glacial/interglacial transitions characterized by the occurrence of grassland-savanna environments (grasslands or open woodlands; Leroy et al. 2011; de Beaulieu et al. 2013) in the Danube-Po Gateway, which we suggest were exploited for migrations into Europe by hominins and other mammals according to our revised migrate-with-the-herd hypothesis of first colonization of Europe during the Early Pleistocene climate revolution (EPR) centered at ~0.9 Ma (represented by vertical gray band). Panel G is range chart of large mammals in Europe showing the most representative Galerian taxa that entered Europe from Africa or Asia during the EPR at ~0.9 Ma that largely replaced Villafranchian (European resident) taxa (essentially from Van der Made 2011; Masini & Sala 2007).

The Levant and Turkey: a staging area for hominin expansion into Europe at ~0.9 Ma?

The Levant and Turkey represent a natural staging area for the first hominins on the way to Europe at ~0.9 Ma and to Asia perhaps even earlier. In the Levant, the sites of Gesher Benot Ya'aqov and Evron in Israel (Fig. 1) yielded Mode II (Acheulean) lithic tools from levels just below a relatively well documented magnetic polarity transition interpreted as the Brunhes/Matuyama boundary (Goren-Inbar et al. 2000; Ron et al. 2003); these sites are included in our selective chronology of earliest hominin presence at the gates of Europe (Fig. 2). Additional celebrated sites discussed below ('Ubeidiya, Erk-el-Ahmar, and Bizat Ruhama in Israel; Kocabas and Dursunlu in Turkey) are provided with chronologies that would place them in the Early Pleistocene, well before the Brunhes/Matuyama boundary, but lack – in our opinion – sufficient numerical age estimates to place them relative to the Jaramillo or Olduvai subchrons.

The site of 'Ubeidiya in the Jordan Valley (Fig. 1) yielded Mode II (Acheulean) lithic tools from levels of reported reverse polarity attributed (although the magnetics data were not otherwise described) to the Matuyama Chron (Opdyke et al. 1983). Two short normal magnetic polarity intervals were later reported to be found in the Fi member and assigned to the Cobb Mountain and Gilsa subchrons (at 1.18 Ma and 1.57 Ma, respectively; Lourens et al. 2005; Singer 2014) but the results are

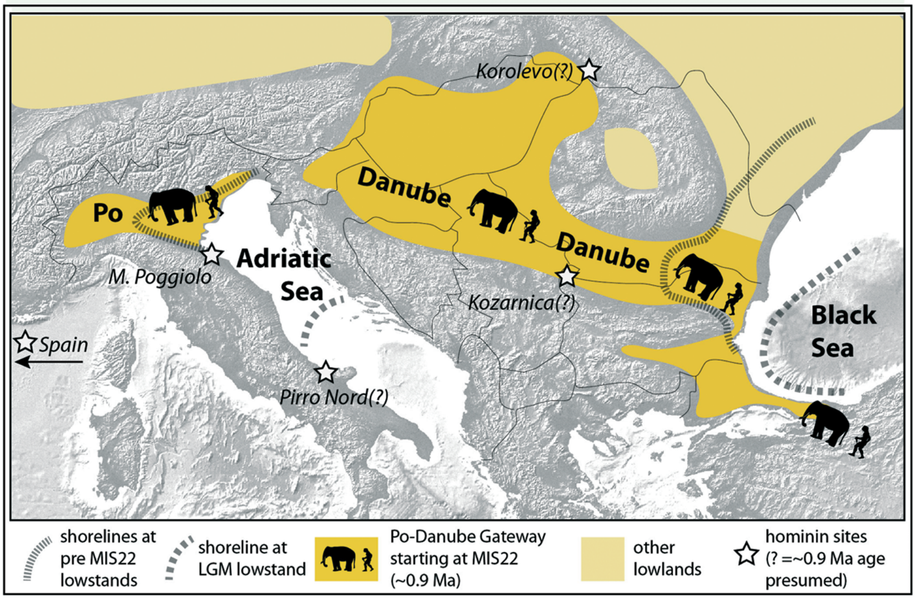

Fig. 4 - Paleogeographic scenario of our revised migrate-with-the-herd hypothesis of earliest expansion of hominins (and large mammals) from the Gates of Europe into Europe across the postulated Danube-Po Gateway during the EPR. Expansion occurred on stable lowlands developed as the Po and Danube deltas prograded over the Adriatic Sea and Black Sea, respectively, since MIS 22 (~0.9 Ma) (Muttoni et al. 2003; Scardia et al. 2006; Winguth et al. 2000). Coastlines at pre-MIS 22 lowstands and at the last glacial maximum (LGM) are tentatively depicted illustrating the advancement of the Po and Danube deltas. Colonization of these lowlands by grassland vegetation with reduced woody cover especially during the onset of glacial/interglacial transitions starting with MIS22/MIS21 provided the closest analogues in the temperate belt of the savanna ecosystems to which migrant mammals (e.g., megaherbivores) were adapted, and into which they expanded only since ~0.9 Ma together with hominins, which depended on them for food provision. Before MIS 22 (~0.9 Ma), these lowlands, reduced in size (see pre-MIS 22 coastlines), were colonized by more permanent closed forests, considered as unadapted to migrant African (or even Asian) large mammals (e.g., megaherbivores) and accompanying hominins.

in an unpublished Master's thesis (Bar-Yosef & Belmaker 2011 and reference therein). The current age attribution of the site to 1.6-1.2 Ma is based on long distance faunal correlations (Tchernov 1987; Martinez-Navarro et al. 2009; Bar-Yosef & Belmaker 2011). Discarding the site of Erk-el-Ahmar near 'Ubeidiya (Fig. 1), where levels with Mode I (Oldowan) lithic tools could not be correlated to the magnetostratigraphic profiles showing a reverse-normal-reverse polarity sequence (Braun et al. 1991; Ron & Levi 2001), we mention the Israel site of Bizat Ruhama in the northern Negev desert (Fig. 1), where Mode I (Oldowan) lithic tools were found in a reverse polarity interval attributed to the late Matuyama on the basis of integrated paleomagnetic and red thermoluminescence (RTL) data (Laukhin et al. 2001).

In south-central Turkey, the site of Dursunlu (Fig. 1) yielded levels with Mode I (Oldowan) lithic tools correlated to a normal-reverse-normal-reverse (bottom to top) polarity sequence retrieved from a drill core but no information on the procedures adopted to obtain the polarity stratigraphy was provided (Güleç et al. 1999, 2009), and hence this site is discarded from further consideration. The site of Kocabas in southwestern Turkey (Fig. 1) yielded a partial skull of *Homo erectus* s.l. from a travertine-fluvial sedimentary sequence (Lebatard et al. 2014). A well-described composite reverse-normal-reverse magnetic polarity profile was interpreted in conjunction with ^{26}Al/^{10}Be burial ages, as a record of the Matuyama-Cobb Mountain-Matuyama (or, alternatively, of the Matuyama-Jaramillo-Matuyama) polarity sequence comprised between ~1.5 Ma and 1.22 Ma (or ~1.5 Ma and ~1 Ma) (Lebatard et al. 2014). Unfortunately, the stratigraphic position of the skull is uncertain because it was not found directly within the magnetostratigraphic sequence but within a travertine block isolated earlier by quarry workers. The fossil is attributed an age of 1.3 Ma to 1.1 Ma (Lebatard et al. 2014) essentially because this is thought to be the minimum age of travertine deposition in the area.

From the magneto-chronologic framework illustrated above, hominins were clearly present in the Levant and Turkey before the Brunhes/Matuyama boundary (0.78 Ma). Provided the Kocabas hominin fossil has been correctly traced onto the composite magnetostratigraphic profile, and pending additional age constraints from sites in Israel (e.g., 'Ubeidiya, Erk-el-Ahmar), this would indicate hominin presence in Turkey and the Levant before the Jaramillo (i.e., before the EPR). This evidence would fit with the Early Pleistocene dispersal documented by Asian sites in the Caucasus, China and Java, and does not contradict our supposition based on the most reliable data that hominins apparently did not populate Europe until after the Jaramillo at ~0.9 Ma. We surmise that this late entry was due to the opening of a window of opportunity provided by exploitable ecosystems in the Danube-Po area (Balkans and northern Italy) that first started during the EPR.

Opening of the Danube-Po Gateway and first hominin expansion into Europe at ~0.9 Ma

Two main reasons lead us to speculate that hominins and some other mammals could enter the European realm through a postulated Danube-Po Gateway only starting at ~0.9 Ma during the EPR (Fig. 4):

1) Enhanced aridity and glacioeustatic lowstands associated with the EPR starting with MIS 22 (~0.9 Ma) fostered physical erosion in the Alpine-Dinaride mountain belt that promoted large fluxes of detritus that accumulated in peripheral plains. This triggered the formation and development of vast and stable lowlands (on which thick loess/paleosols sequences were deposited) such as the Pannonian Plain in Hungary and Serbia, Dacian Plain in Romania, and Po Plain in northern Italy.

2) Colonization of these lowlands by grassland vegetation with reduced woody cover occurred during onsets of glacial/interglacial transitions. These new environments represent the closest analogues in the temperate belt of the savanna ecosystem to which migrant mammals (and hominins with them) were already adapted.

Regarding the development of stable lowlands, the EPR was a time of profound reorganization of fluvial systems across Europe with the creation of the modern drainage systems of the Danube (Gábris & Nádor 2007) and Po rivers (Muttoni et al. 2003; Scardia et al. 2010), among other fluvial systems (Gibbard & Lewin 2009). The importance of the Po Valley Gateway during late Early Pleistocene mammal migrations was stressed by Muttoni et al. (2010, 2011). The northern Adriatic area was submerged as far west as the modern locality of Milan and as far north and south as the foothills of the Southern Alps and Apennines (Fig. 4) even during lowstands of the Early Pleistocene; it was only since immediately after MIS 22 at ~0.9 Ma that large stretches of the Po Plain started to become more persistently exposed due to enhanced fluvial detritus discharged into the Po Valley during what were becoming much lower glacioeustatic lowstands (Muttoni et al. 2003, 2010, 2011; Scardia et al. 2006, 2010, 2012). The detritus was redistributed as far east as Venice in the Adriatic Sea, promoting the strong progradation of the Po delta (Kent et al. 2002; Muttoni et al. 2010; Scardia et al. 2006, 2012). This may have opened possibly for the first time in the Pleistocene viable new migration routes for large mammals and hominins from the Danube corridor westward across northern Italy to southern France and Spain (Muttoni et al. 2010, 2011) (Fig. 4).

The Danube Gateway seems to have developed similarly and contemporaneously. Winguth et al. (2000) provided a seismo-stratigraphic model in which the Danube reached the Black Sea for the first time at ~0.9 Ma and subsequently built up the Danube fan (Fig. 4). The Dniepr fan started to form at about the same time, around 0.8 Ma (Winguth et al. 2002). These Danube-Po lowlands were covered since the late Early Pleistocene by thick loess sequences associated with enhanced glacial activity as revealed by several magnetostratigraphically dated land sections in Europe and the Black Sea area (e.g., Cremaschi 1987; Sartori et al. 1999; Dodonov et al. 2006; Fitzimmons et al. 2012; Ujvari et al. 2014; Jipa 2014) (Fig. 3E).

Regarding the development of persistent grassland-savanna ecosystems on these loessic lowlands (Fig. 4), the palynological record is relatively clear. Pollen data obtained from magnetostratigraphically calibrated deep cores drilled in the Po Valley and the bordering Southern Alps indicate that during the Early Pleistocene before the EPR (between the Olduvai subchron [1.95-1.78 Ma] and MIS 22 [~0.9 Ma]), climate was generally warm-temperate to cool but not cold, with abundant closed forests characterized by an alternation of deciduous broad-leaved species and conifers (Ravazzi & Rossignol-Strick 1995; Muttoni et al. 2003, 2007; Ravazzi et al. 2005). Even during the coldest spells of this climatic variability, no complete forest withdrawal was observed (Ravazzi et al. 2005).

During the EPR culminating with MIS 22, climate cooled, triggering forest withdrawal (Muttoni et al. 2003, 2007; Scardia et al. 2010). The long pollen record from Tenaghi Philippon in northern Greece (Tzedakis et al. 2006) reveals the vegetational (climate) variability (forest contractions/expansions) since 1.35 Ma across the EPR. This record shows high amplitude and low frequency oscillations with very pronounced expansions of steppe and grasslands during the glacial phases starting with MIS 22 (~0.9 Ma), in agreement with other records from France (e.g., Velay; de Beaulieu et al. 2006, 2013) and Italy (Magri 2010 and references therein).

The occurrence of persistent open vegetation phases only since MIS 22 (Magri 2010) is central to our revised (after Muttoni et al. 2010, 2011) migrate-with-the-herd hypothesis of first colonization of Europe during the EPR, considering that several large mammals on which hominins may have depended on for food provision (e.g., Ben-Dor et al. 2011) were adapted to open environments with limited woody cover (e.g., the African straight-tusked elephant and the Asian steppe mammoth; see Rivals et al. 2012 and discussion below). A recent analysis of faunal and pollen records at several early hominin sites in Europe coupled with climate simulations lead to the conclusion that the environmental context in which the first hominins entered into Europe and dispersed was characterized by the occurrence of open landscapes, essentially grasslands or open woodlands, typical of transitions from glacial to interglacial periods (the full glacials being too cold, and the interglacial to glacial transitions too forested) (Leroy et al. 2011). Well-defined open woodland phases become a persistent component of Pleistocene vegetational variability in southern and southeastern Europe only since ~0.9 Ma during glacial/interglacial transitions (de Beaulieu et al. 2006, 2013). We therefore regard the glacial/interglacial transitions starting from the end of MIS22 (Fig. 3F) as the main time windows of grassland-savanna environments in the Danube-Po Gateway exploited by hominins and other mammals for first migrations into Europe during the EPR starting at around 0.9 Ma (Fig. 4).

The elements outlined above lead us to a reformulation of the migrate-with-the-herd hypothesis of first peopling of Europe at ~0.9 Ma during the EPR.

A revised migrate-with-the-herd hypothesis of first hominin expansion into Europe at ~0.9 Ma

We previously hypothesized (Muttoni et al. 2010, 2011) that hominins seem to have entered Europe together with herds of large African (and Asian) herbivores because they were 'pushed out' of their homelands by enhanced aridity in the Sahara (Larrasoaña et al. 2003) and across Asia during the EPR, finding ultimate refuge in the more temperate Mediterranean realm. In fact, it appears that north subtropical Africa was quite often green (sustainable, traversable) well before and even during the harsh times of the EPR, providing numerous potential windows for mammal migrations in and out of Africa since at least 8 Ma (Larrasoaña et al. 2013).

Instead, we now believe that large mammals, and hominins with them, may have migrated to Europe starting at around 0.9 Ma because the EPR generated for the first time in the Pleistocene vast and exploitable ecosystems for African and Asian mammals especially along the conjunct Danube-Po Gateway (Fig. 4). These new environments were characterized by stable lowlands with open grassland vegetation and reduced woody cover during the onset of glacial/interglacial transitions (starting with MIS 22/MIS 21). The connection between savanna environments and mammal migrations is well established in the literature (e.g., Dennell 2004; but see Bar-Yosef & Belmaker 2011). In our view, the lack of grassland-savanna exploitable ecosystems before the EPR forestalled African and Asian large herbivores from expanding into Europe, should they have reached there. Animal fat from large herbivores (e.g., elephants) was apparently an essential food source for Pleistocene hominins in the Levant (Ben-Dor et al. 2011). It should not come as a surprise, therefore, that *H. erectus* expanded into the newly opened grassland-savanna ecosystems in conjunction with their migrating primary food source (Ben-Dor et al. 2011).

From the staging area in the Levant and Turkey, where hominins survived in diverse Mediterranean environments (Bar-Yosef & Belmaker 2011; Yeshurun et al. 2011), hominis seem to have expanded into Europe as part of a food web in conjunction with African and Asian mammals across the new grassland-savanna ecosystems of the Danube-Po Gateway. Megaherbivores requiring large dietary grass supply such as the African straight-tusked elephant (*Elephas antiquus*), the Asian steppe mammoth (*Mammuthus trogontherii*), the Asian red deer (*Cervus elaphus*), and the Indian large bovid (*Hemibos galerianus)* are among the most representative species of the Galerian mammal assemblage that entered Europe during the EPR at around 0.9 Ma and progressively replaced resident European species of the Villafranchian mammal assemblage, like the Etruscan rhino, the southern mammoth, and the fallow deer (Fig. 3G, essentially from Van der Made 2011, and Masini & Sala 2007; see also Palombo & Ferretti 2005; Palombo & Mussi 2006; Martinez-Navarro 2010; Van der Made 2013).

According to dental microwear analyses on proboscidean teeth (Rivals et al. 2012), the European resident *M. meridionalis* seems to have been more adapted to browsing, whereas immigrants *M. trogontherii* and *E. antiquus* were mixed browsers-grazers, and therefore more adapted to the persistent grassland-savanna ecosystems that developed during the EPR since MIS 22 or the immediately suceeding MIS 22/MIS 21 transition (~0.9 Ma). This dietary flexibility could have given *M. trogontherii* and *E. antiquus* an adaptive advantage relative to more forest-dependent *M. meridionalis*.

In this respect, the fossil record of large grassland-savanna-adapted herbivores may provide valuable clues to the migration routes and timing of hominins with their much more scanty traces. For example, the Serbian site of Kostolac east of Belgrade, located on our postulated Danube-Po Gateway, yielded a specimen of the steppe mammoth *M. trogontherii* from a level overlain by a thick loess-paleosol succession (Lister et al. 2012). *M. trogontherii* is an Asian immigrant that arrived in Europe just before the Brunhes/Matuyama boundary (Lister et al. 2012). We speculate that the level with *M. trogontherii* at Kostolac (for which magnetostratigraphic analyses are in progress by the writers) may represent a regional unconformity marking the EPR in the Danube Valley (similarly to the R surface in the Po Valley dated at ~0.9 Ma; Muttoni et al. 2003; Scardia et al. 2006) along which archeological surveys in search for early hominin sites might fruitfully focus.

Alternative migration scenarios: the North Africa-Gibraltar Strait connection

An alternative staging area for migration to Europe is represented by northern Africa. At Ain Hanech in northern Algeria (Fig. 1), Parès et al. (2014) obtained a convincing reverse-normal-reverse magnetic polarity sequence from the 29 m-thick type section of the Ain Hanech Formation, revising previous (but not illustrated) results (Sahnouni and de Heinzelin 1998 and references therein). Mode I (Oldowan) lithic tools were found in nearby ~3 m-thick sections at Ain Hanech (not to be confused with the Ain Hanech Formation type section) and El-Kherba (below a calcrete level sealing the Ain Hanech Formation and yielding Acheulean tools) in association with mammal remains, and were correlated by altimetric leveling to within the upper 5 m of the Ain Hanech Formation type section (Parès et al. 2014 and references therein) characterized by reverse magnetic polarity (Parès et al. 2014). After a long debate on the biochronological value of the recovered mammals (Sahnouni et al. 2002; Geraads et al. 2004; Sahnouni et al. 2004), the latest claims for the age of the Ain Hanech and El-Kherba tool-bearing sites are: 1) ~1.7 Ma based on magnetostratigraphy in conjunction with the chronology derived from the morphology of a tooth attributed to the suid *Kolpochoerus heseloni* and the recovery of a tooth fragment attributed to the proboscidean *Anancus* (Parès et al. 2014 and references therein); 2) ~1.5-1.2 Ma based on mammal biostratigraphy alone (Geraads 2010 and references therein), which – we notice – is an age that does not seem to openly violate the recent magnetostratigraphic data of Parès et al. (2014). The ongoing debate seems to still critically depend on the identification and chronological value of a tooth of *Kolpochoerus* and a tooth of *Anancus*, whose occurrences at Ain Hanech are in any case not well documented in the accessible literature.

At the site of Thomas Quarry 1 in the Atlantic Morocco (Fig. 1), Mode II (Acheulean) lithic tools have been found in level L (Raynal et al. 1995; Raynal et al. 2002; Geraads et al. 2004) attributed to the Matuyama Chron based on the presumed presence of reverse magnetic polarity, although no experimental data were illustrated (Raynal et al. 1995; Raynal et al. 1996; Sevket Sen, personal communication to G.M., 2014). Rhodes et al. (1996) reported an OSL-SAR (single aliquot regenerative) age estimate for level L of 0.99 ± 0.2 Ma associated with a 'surprisingly young' OSL-MAAD (multiple aliquot additive dose) age estimate of 0.26 ± 0.06 Ma (both quoted at 1s level). Sahnouni and Van der Made (2009) and Geraads (2010) seem to accept a late Early Pleistocene age for level L based on the available mammal biostratigraphy coupled with the OSL dates.

The relevance of the actual age(s) of the North Africa hominin sites is that they seem to have prompted Parès et al. (2014) to speculate anew about '*the likelihood of North Africa as a plausible routes* [sic] *for hominin expansion into Europe*', which seems to imply the crossing of the Gibraltar Strait into Spain. If so, we would point out (see also Muttoni et al. 2010) that the Gibraltar Strait has experienced Quaternary tectonic uplift as evidenced by a sequence of raised shorelines in Gibraltar as high as 210 m above present sea level (e.g., Rodrìguez-Vidal et al. 2004). This implies that even the lowest Early Pleistocene sea level lowstands (e.g., MIS 22) would have hardly affected the extent of the central channel, now ~5 km wide and ~300 m deep. More importantly, there is a fundamental difference between the Danube-Po Gateway route and a Gibraltar Strait crossing route. In our Danube-Po Gateway hypothesis, the opening of new, stable, and exploitable ecosystems provided a virtual ecological highway for the sustained expansion of mammals and hominins into Europe. On the other hand, a Gibraltar Strait crossing hypothesis inevitably implies a sporadic crossing of a significant barrier, which would be expected to act as a severe filter. In that respect, the Gibraltar Strait seems a much less obvious route, at least for establishing a stable and repeated physical and genetic exchange with Africa for continental-scale peopling of Europe accompanied by a wide variety of megaherbivores.

Summary and Conclusions

- As previously suggested, earliest hominin sites in Europe with reliable age control continue to indicate (or do not contradict) that the earliest peopling of Europe occurred within a narrow time window of the late Early Pleistocene comprised between the top of the Jaramillo subchron (0.99 Ma) and the Brunhes/Matuyama boundary (0.78 Ma). Our preferred late Early Pleistocene chronology (0.99-0.78 Ma) is 'not so short but not too long' as it lies between the classic 'long' chronology that expects the earliest hominin evidence from Europe to date before the Jaramillo (>1Ma) (e.g. Garcia et al. 2014; see also Toro-Moyano et al. 2013 vs. Muttoni et al. 2013), and the classic 'short' chronology claiming instead that Europe was largely uninhabited until after the Brunhes/Matuyama boundary in the Middle Pleistocene (<0.78 Ma) (e.g., Roebroeks & van Kolfschoten 1994). The timing of our preferred late Early Pleistocene (post-Jaramillo) chronology of earliest peopling of Europe may be related to the response of African and southern European climate to the inception of higher amplitude glacial oscillations of the late Early Pleistocene revolution (EPR) centered on MIS 22 (~0.9 Ma).
- We now suggest that hominins entered Europe for the first time during the EPR because it was when vast and exploitable lowlands with open vegetation developed along the conjunct Danube-Po Gateway, thus providing possibly for the first time in the Pleistocene an eco-space for migrations into Europe that grassland-savanna-adapted large mammals, and hominins with

them as part of a common and interlinked food web, could have expanded into (Fig. 4).

- We stress the importance of the opening of land coinduits during migrations of large mammals. A Danube-Po Gateway connecting the Levant and Turkey to Europe would have implied the crossing of only one (limited) waterway – the Bosphorus – which may have been at least intermittently exposed during the Pleistocene (making the Black Sea a freshwater lake; Ryan et al. 2003; but see also Yaltirak et al. 2002). The main point here is that linking the migrations of hominins with large herbivores makes the crossing of extended waterways (e.g. Gibraltar Strait) unlikely, whereas exposed and exploitable plains and lowlands seem more viable routes for the ensemble.

- Finally, the pathways of migration discussed above can be considered valid under the assumption that early Europeans came either accompanying *E. antiquus* from Africa (e.g., Antón 2003) or *M. trogontherii* from Asia (e.g., Dennell 2008), where the records of hominins seem to extend farther back in the Early Pleistocene than in Europe.

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