



Human Palaeontology and Prehistory

First hominin settlements out of Africa. Tempo and dispersal mode: Review and perspectives



*Les premières occupations d'hominines hors du continent Africain.
Tempo et modalités de dispersion : bilan et perspectives*

Sandrine Prat^{a,b,*}

^a UMR 7194 « Histoire naturelle de l'homme préhistorique », musée de l'Homme, 17, place du Trocadéro, 75116 Paris cedex 16, France

^b UPR 2147 « Dynamique de l'évolution humaine », 44, rue de l'Amiral-Mouchez, 75014 Paris, France

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ABSTRACT

Current discussions generally focus on “when” the first ‘Out of Africa’ hominin settlements occurred. We propose a short review of some of the assumptions underlying the ‘Out of Africa’ dispersal scenarios and their reappraisal in the light of the palaeoanthropological and archaeological records. Globally, these scenarios are still hypotheses; however, some of them can be outlined in more concrete terms, based on the discoveries in the Levant, the Caucasus and Eastern Asia. Dispersals from Africa were multidirectional, with many successive discontinuous occupations and episodes of turning back. Hominins displayed strong adaptive capacities to new environmental conditions, linked to the notion of versatility, which is already present in Early Pleistocene hominins. Factors often proposed to explain the first ‘Out of Africa’ settlements, such as climatic change, new cultural behavior, and increase in body size and brain size do not seem to be relevant according to the fossil and archaeological records.

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R É S U M É

Les discussions relatives aux premières occupations d'hominines en dehors du continent Africain se concentrent généralement sur le « quand ». Nous proposons un aperçu des hypothèses sous-jacentes aux scénarios de cette première dispersion, à la lumière des données paléanthropologiques et archéologiques. Bien que ces scénarios restent hypothétiques, certains d'entre eux peuvent être décrits en termes plus concrets, sur la base des découvertes du Levant, du Caucase et de l'Asie orientale. La dispersion a été multidirectionnelle, avec plusieurs occupations discontinues successives et des épisodes en sens opposé. Les hominines présentent de fortes capacités d'adaptation à de nouvelles conditions environnementales, liées à la notion de versatilité, que possédaient déjà les hominines du Pléistocène inférieur ancien. Les facteurs souvent liés aux premiers peuplements hors

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* UMR 7194 « Histoire naturelle de l'homme préhistorique », musée de l'Homme, 17, place du Trocadéro, 75116 Paris cedex 16, France.

E-mail address: sandrine.prat@mnhn.fr

d'Afrique, tels que les changements climatiques, de comportement technique, une augmentation de la taille corporelle et de la taille cérébrale, ne semblent pas être validés par le registre fossile.

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1. Introduction

In 1871, Charles Darwin proposed in *The Descent of Man* that the cradle of humankind should be sought in Africa. After more than a century of palaeoanthropological research in Eurasia and Africa, this conviction is still relevant and discoveries made since the middle of the 1990s have amply confirmed this hypothesis. The palaeoanthropological remains found in Ethiopia dated to 2.8 Ma (Villmoare et al., 2015) and the 2.3–2.4 Ma discoveries in Ethiopia (Howell et al., 1987; Kimbel et al., 1996), Malawi (Schrenk et al., 1993) and Kenya (Hill et al., 1992; Prat et al., 2005), for example, show that the *Homo* genus is about 2.8 million years old (Ma), although it is not useful to recognize the genus *Homo* before 1.9 Ma. Indeed, the specimens before 2 Ma are scarce and highly fragmentary (two mandibles, one maxilla, one frontal bone and few teeth). Furthermore, morphological comparisons have to be undertaken in more detailed to define the genus *Homo* (e.g., Schwartz and Tattersall, 2015; Wood and Collard, 1999) and to define the number of species within the early *Homo* hypodigm (e.g., Hublin, 2015; Prat, 2004, 2005; Spoor et al., 2015). The evolutionary history of hominins now resembles a bushy tree, where it is difficult to understand the processes of speciation and expansion.

As noted by Lewin and Foley (2004), in order to reconstruct human evolution, we must first ascertain and define its pattern (i.e., who, when and where), and then explain this pattern (i.e., how/why). Most of the discussions have focused on “when” the first dispersal occurred, some on their “frequency”, but very few on the “success” of this dispersal (Dennell, 2003).

The first point (who, when and where) seems to be less and less questioned. As regards the timing of expansion, the long or short chronology question has been widely debated in recent years (Dennell and Roebroeks, 1996, 2005). Until the beginning of the 1990s, the earliest expansion of hominins from Africa to other parts of the world was presumed to have occurred around one million years ago. However, several major discoveries have since contested this point of view (see below and Fig. 1).

A preamble to the corpus of data is necessary. Archaeological and palaeoanthropological occurrences are always fragmentary, and therefore only depict a partial picture of hominin settlements (see Figure 2-2, Prat, 2008), and as noted by Dennell (2010) our knowledge of hominin dispersal is plagued by uncertainty and speculation. Fossil discoveries depend on different taphonomic filters and biases (circumstances and environment of death, damage and transport by animal agents, fluvial damage and

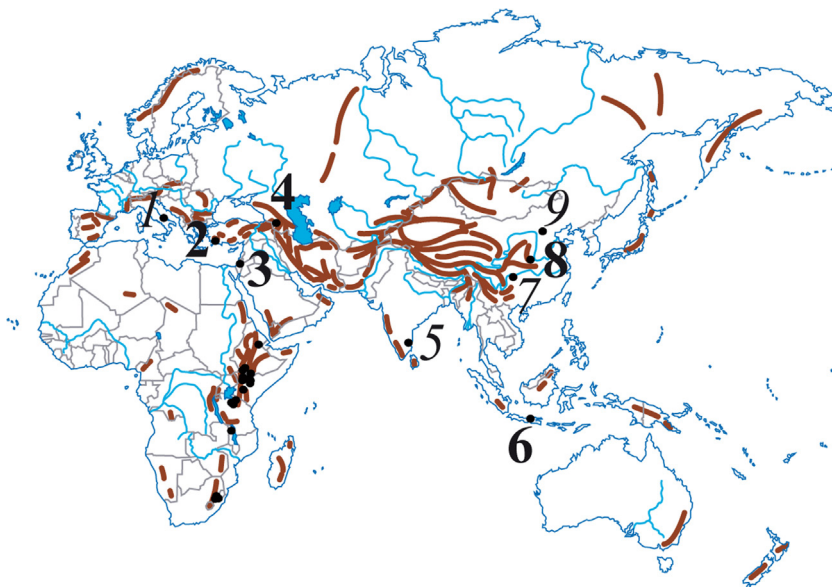


Fig. 1. Location of the sites between 2.8 and 1.5 Ma. Main Eurasian sites with *in situ* material (in bold: hominin remains; in italic, lithic assemblage): [1] Pirro Nord, [2] Kocabaş, [3] ‘Ubeydiya, [4] Dmanisi, [5] Attirampakkam, [6] Bapang (Sangiran), [7] Longuppo, [8] Gongwangling (Lantian), [9] Majuangou. **Fig. 1.** Localisation des sites entre 2,8 et 1,5 Ma. Principaux sites en Eurasie avec du matériel *in situ* (en gras, restes d’hominines ; en italique, assemblage lithique) : [1] Pirro nord, [2] Kocabaş, [3] ‘Ubeydiya, [4] Dmanisi, [5] Attirampakkam, [6] Bapang (Sangiran), [7] Longuppo, [8] Gongwangling (Lantian), [9] Majuangou.

transport, damage during exposure and finally the context of the discovery itself and potential collector bias (White, 1988)). Several datasets provide information relating to hominin settlements: first, the hominin remains, which are often scarce; and second, indirect evidence such as cultural data or intentional cut marks. The link between the culture and tool maker is generally unequivocal if only one hominin species is present, but much less so for time periods during which several hominin species occur.

Sites (Fig. 1) with early *Homo* specimens in Africa between 2.8 and 1.5 Ma are located in Ethiopia, Kenya, Tanzania, Malawi, and the Republic of South Africa, with fewer than 50 specimens (with a majority of dental remains) before 1.8 Ma and more than 200 remains between 1.8 and 1.5 Ma. Concerning the Early Pleistocene sites outside Africa between 1.8 and 1.5 Ma, we report in Fig. 1 the main well-dated sites, with *in situ* material from east to west: [1] Pirro Nord, Italy, 1.3–1.6 Ma, lithic artefacts (Arzarello et al., 2009); [2] Kocabaş, Turkey, 1.2–1.6 Ma, hominin remains (Lebatard et al., 2014; Viallet et al., 2012); [3] 'Ubeydiya, Israel, 1.5 Ma, lithic assemblage and hominin remains (Belmaker et al., 2002); [4] Dmanisi, Georgia, 1.77–1.81 Ma, lithic assemblage and hominin remains (e.g., Ferring et al., 2011; Lordkipanidze et al., 2007); [5] Attirampakkam, India, 1.5 Ma, lithic assemblage (Pappu et al., 2011); [6] Bapang (Sangiran), Indonesia, 1.5 Ma, human remains (Zaim et al., 2011); [7] Longuppo, China, 2.2 Ma, lithic assemblage (Han et al., 2016); [8] Gongwangling (Lantian), China, circa 1.63 Ma (Zhu et al., 2015) or 1.15 Ma (An and Ho, 1989), human remains and [9] Majuangou, China, 1.66 Ma, lithic assemblage (Zhu et al., 2004).

The discovery of hominin remains in Dmanisi in layers dated to 1.77 Ma (stratum B, Lordkipanidze et al., 2007) and the presence of artefacts found in layers dated to 1.85–1.78 Ma (stratum A, Ferring et al., 2011) provided secure evidence of hominin settlements in Eurasia at least 1.8 million years ago. This confirms the long chronology scenario. Furthermore, these palaeoanthropological remains have largely challenged the hypothesis that the “who” should be a late *Homo erectus*. Indeed, the anatomical features of the hominin from Dmanisi are close to those of early *Homo erectus* specimens (also referred to *Homo ergaster*) (Gabunia et al., 2000a,b). Some of them are closely related to early *Homo* (*Homo habilis*) (Vekua et al., 2002). The Georgian discoveries led to the recognition of a new *Homo* species: *Homo georgicus* (Gabunia et al., 2002). Thus, expansion Out of Africa by hominins should be pushed back more than 2 million years, and even before 2.2 Ma, if we take into account the date of the Longuppo *in situ* lithic assemblage at ~2.2 Ma (layer C III-2, Han et al., 2016), which is 1.5 million years after the oldest archeological record (i.e. 3.3 Ma, Lomekwi 3, Kenya (Harmand et al., 2015)).

The purpose of this article is to propose a review of some of the assumptions underlying the second point (i.e., the pattern, the “reasons”) and to compare them to palaeoanthropological and archaeological records. Indeed, many of these assumptions are still hypotheses and cannot yet be confirmed or invalidated. However, owing to discoveries made over the past 20 years, in the Levant, the Caucasus and Eastern Asia, some of these expansion scenarios can be defined in more concrete terms.

After a discussion concerning the terms migration, dispersal and expansion, several hypotheses related to the first settlements Out of Africa are reviewed and discussed. In this paper, we focus on the exogenous (i.e. climate change) and endogenous (i.e. cultural scenario, body size, brain expansion) hypotheses proposed to explain this dispersal.

2. General considerations: migration, dispersal or expansion?

The hominin occupation of new areas is not comparable to migratory phenomena (i.e., traveling from one place to another at regular times of year, often over long distances) as observed among extant animal populations. We prefer to use the term dispersal, following Croteau's definition (Croteau, 2010): an ecological process that involves the movement of an individual or several individuals from their native population to another place, where they will reproduce and settle. We consider that hominin occupation is an opportunistic event to occupy new available and viable areas, constrained by population growth and nomadic behavior. This occupation is the result of settlement in new areas, which are located close to previous settlement areas and offer suitable conditions for new settlement. The long-distance dispersal involves numerous stochastic movements. These movements occurred with no predetermination, and would have been contingent on food availability and environmental conditions, with no predefined direction (see below and Table 1). The first long-distance hominin dispersal outside Africa should be thus considered as a process resulting from the simple occupation of new adjacent territories. An ecological niche can become saturated for different reasons, leading to strong competition, due for example to an increase in the number of individuals, linked to better reproductive success. A simple scenario can be proposed:

- an increase in the number of individuals in area x;
- competition for resources inside area x;
- occupation of ecological niches (area y) close to area x, if area y is conducive to new settlements;
- increase in the number of individuals in area y, etc.

As noted by Croteau (2010), the dispersal can be active or passive. The former is a density-dependent process and its magnitude is linked to local population size, resource competition and habitat. Highly vagile animals generally have the greatest capacity for long-distance dispersal. Therefore, the extent of dispersal is dependent on the limitations imposed by the habitat and potential geographic barriers. Conversely, passive dispersal involves organisms that cannot move themselves and use dispersal units (i.e. disseminule) to aid in the exploration of new habitats or reproduction. Climate change has a strong impact on dispersal (passive or active) as species that cannot disperse to more favorable conditions may face extinction (Croteau, 2010; Walther et al., 2002). Despite the benefits of dispersal, there is also a price to pay. Indeed, dispersal ability depends on one hand on the degree of specialization within a given ecological niche, and on the other hand on the cost of this dispersal. This is because the mortality risk is

Table 1

Basic model taking into account the distance traveled, model for generation time and territorial exploitation.

Tableau 1

Modèle prenant en compte la distance parcourue, la durée entre générations et l'exploitation du territoire.

Distance: 5000 km	1 km/generation (years)	5 km/generation (years)	10 km/generation (years)
Time generation: 20 years	100,000	20,000	10,000
Time generation: 25 years	125,000	25,000	12,500

high during dispersal, due to increased energy expenditure, unfamiliar habitat and thus potentially reduced reproductive success, and diminished ability to acquire sufficient resources in this new habitat.

Following this definition, Early Pleistocene hominin dispersal is active. The occupation seems essentially sporadic. Indeed, there are few and sometimes no geographical and chronological continuities between the different sites. This discontinuity may partly result from sampling and conservation biases, but may also simply be due to a lack of hominin settlement in this region or time period.

Although the dispersal phenomenon can be perceived as slow on an individual life scale, it is relatively rapid on a geological scale. We propose here a basic model (Table 1), taking into account the distance traveled, and models for generation time and territorial exploitation to discuss the tempo of dispersal.

The distance between Dmanisi in the Caucasus and the Turkana Basin in Kenya is 5000 kilometers, following the Red Sea (south route) and the Levantine corridor. Concerning the generation time (i.e., the mean number of years between successive generations), the estimated generation gap in hunter-gatherer women is 25.6 years (Fenner, 2005); and 18 and 25 years in female gorillas and chimpanzees respectively (Langergraber et al., 2012). According to Hemmer (2007), the estimated age of first breeding is 10 years for *Homo habilis*, 15 years for *Homo ergaster*, 9.9 years for *Gorilla gorilla*, 11.5 years for *Pan troglodytes* and 19.4 ± 1.9 years for hunter-gatherer modern human women (Fenner, 2005). Using the estimated first breeding data as well as the generation gap for *Gorilla*, *Pan* and modern humans, the model *Homo habilis* or *Homo ergaster* lead to an estimated generation time of 20 to 25 years. In order to gauge the distance traveled by each generation, we use three models; one of 1 kilometer per generation; one of 5 kilometers and one of 10 kilometers per generation. These models seem realistic and are probably underestimated if the estimated hominin territorial range is taken into account. Indeed, if we consider that transport distances provide information on hominin ranging behavior, local raw collection has been mainly observed in Early Pleistocene site. Transport distance for Early Pleistocene (Oldowan) lithic assemblages were generally around several kilometers (e.g., in West Turkana (Harmand, 2009), and Dmanisi (Mgeladze et al., 2011)) and less frequently up to 10 km (Plummer, 2004). Furthermore, Lewin and Foley (2004) have suggested that 16 km would be a reasonable average distance traveled per *H. erectus* generation. According to all these models (Table 1), it would have taken between 12,500 and 100,000 years to cover the distance between Turkana Basin and the Caucasus (i.e. 5000 kilometers). Based on the model of 5 kilometers per generation and 25 years for the generation time, this dispersal would

have taken some 25,000 years. These models are strengthened if we assume that dispersal began before or at around 2 Ma, which is at least 200,000 years earlier than the settlement of Dmanisi. According to these models, episodes of turning back could be possible; the dispersal events did not occur on a once-off basis, but as many successive discontinuous occupations, over more or less distant area. This is consistent with Dennell's paper "the hominin record before 1.0 Ma is thus likely to have been one of repeated short-lived and modest dispersal events, rather than continuous residence" (Dennell, 2003: p. 434).

To conclude to these general considerations, rather than "Out of Africa 1", it would be more appropriate to use the term "first settlements Out of Africa" or "first dispersal", since, although some populations expanded Out of Africa, other populations stayed and evolved in Africa. Indeed, East and South Africa have yielded many hominin remains after 1.8 Ma (date of settlement at Dmanisi). Moreover, according to Rightmire et al. (2006), "dating does not presently rule out the possibility that *H. erectus* originated in Eurasia and that some groups then returned to Africa, where they evolved toward *H. erectus ergaster*" (Rightmire et al., 2006: p. 140). As noted previously by Hou and Zhao (2010), it seems necessary to consider Asia in discussions of human origins more seriously but additional research on associated fauna, stone artefacts and hominins are necessary to better understand the important events that took place in Asia. According to dental evidence (Martínón-Torres et al., 2007), Asia has played an important role, with a stronger genetic impact than that of Africa, in the colonization of Europe during the Early and Middle Pleistocene. Furthermore, on a broader scale, initial anthropoid primate expansion occurred from Eurasia to Africa (Chaimanee et al., 2012), and not the opposite, thereby corresponding to "Out of Asia" or "Into Africa".

3. Hypotheses proposed for the first settlements "Out of Africa"

We propose in this section to review the main exogenous and endogenous hypotheses proposed to explain the pattern (the "reasons") often linked with the first Out of Africa settlements.

3.1. Exogenous hypotheses

Dispersal is somewhat limited. Indeed as noted by Croteau (2010), the geographic distributions of species are constrained by a range of environmental variables. Physical barriers to dispersal consist of landscape features that prevent organisms from relocating. Mountains, rivers and lakes are examples of physical barriers that can limit species distribution. But what of the evidence in the fossil

Table 2

List of *in situ* Eurasian sites with associated fauna and secure date, hominin taxonomic allocation or lithic artefacts.

Tableau 2

Liste des sites eurasiatiques *in situ*, présentant de la faune associée et pour lesquels les dates, l'attribution taxinomique des hominines ou de leur culture sont fiables.

	Datation (Ma)	Hominin	Lithic	Stratigraphical context	References
Dmanisi (Georgia)	1.77 1.81	Minimum of 5 individuals	Oldowan	<i>In situ</i>	e.g., Ferring et al., 2011; Gabounia et al., 2002; Gabunia et al., 2000a,b,c; Gabunia and Vekua, 1995; Vekua and Lordkipanidze, 1998; Lordkipanidze et al., 2006, 2007, 2013; de Lumley et al., 2002, 2005, 2006; Rightmire et al., 2006; Vekua et al., 2002 Zhu et al., 2004
Majuangou (China)	1.66 (MJG-III)	No	Oldowan	<i>In situ</i>	
'Ubeidiya (Israel)	1.5	I2 inf (UB 335)	Developed oldowan	<i>In situ</i> (stratum I26a, UB 335)	Belmaker, 2006; Belmaker et al., 2002

record? What geographical or ecological obstacles could have limited the first Out of Africa settlements?

We propose to review some hypotheses relating to the geographical and/or ecological barriers of this dispersal. In order to infer the first Out of Africa dispersal scenario, we have taken into consideration the published palaeoanthropological, archaeological and palaeoenvironmental data, as well the Palaeobiology Database (www.paleodb.org). We consider in this paper only the well-dated Eurasian sites (Majuangou, 'Ubeidiya, and Dmanisi sites), where the fauna, the hominin or the artefacts are *in situ*, with a reliable association with the stratigraphy (Table 2). Consequently, the other sites illustrated in Fig. 1 (e.g., Kocabaş, Gongwangling (Lantian)...), even if they are important evidence of Eurasian settlements are not included in this table.

3.1.1. Topography and tectonics

The majority of the sites, especially Dmanisi and 'Ubeidiya, are on active tectonic regions, with strong volcanism occurring during site formation (Fig. 1). According to King and Bailey (2006), the choice of these sites could be linked to the varied surrounding topography, which generally provides favorable climatic conditions for settlement. Indeed, these topographic barriers give rise to a mosaic of environments and the long-term persistence of environmental variability.

3.1.2. Environmental and ecological changes

The purpose of this section is to discuss on the one hand, if environmental changes could have impacted the dispersal mode, and on the other hand in which kind of environment the first Out of Africa settlements occurred?

As noted by Mithen and Reed (2002), it is relatively easy to postulate that environmental factors influenced the dispersal mode, but it is, on the other hand, quite difficult to actually assess such propositions. The increasing aridity, accentuated by tectonic processes, is often linked to the first Out of Africa settlements (Martinez-Navarro and Palmqvist, 1995; Turner, 1992). However, as noted by

Antón et al. (2014), new environmental data have challenged the interpretation that the origin and evolution of the *Homo* genus is linked to African aridity and the progressive expansion of open, grassland habitats. Indeed, as noted by van der Made (2011), there is no evidence that the first human dispersal around or shortly before 1.8 Ma coincided with major faunal or environmental changes. The majority of faunal movements happened prior to 3 Ma or between 1.8 Ma and 1.3 Ma, and major climate change occurs in Africa between 1.8 and 1.7 Ma or before 2.5 Ma. There are no major waves of dispersal between Pliocene and Pleistocene African and Eurasian mammals, only few species moved in concert. There is more movement between Europe and Eurasia than between Africa and Eurasia (O'Regan et al., 2011).

Moreover, if we want to consider that environmental change could be a "cause" of dispersal, we need (1) to unearth evidence before 1.8 Ma and even earlier than 2 Ma; and (2) this hypothesis does not take into account the versatility of hominins during this time period. Indeed, early *Homo* specimens as well as *Paranthropus* specimens, contrary to previous belief, occupy a wide range of habitats, and do not display any particular habitat preference (e.g., Wood and Strait, 2004). They are dietary generalist, as shown by isotopic analyses (Cerling et al., 2013) or dental microwear (Ungar et al., 2006, 2008). They were thus able to live in different habitats and environments. This corresponds to the versatility hypothesis advocated by Potts (1998a,b).

In order to discuss the palaeoenvironmental framework of the oldest Out of Africa settlements, we compared the palaeoecological data from the sites presented in Table 2, where hominin occurrences (anthropological and lithic) are unequivocally associated with faunal remains. This consists of inferring past climatic conditions, based on data from the faunal spectrum (Hernandez Fernandez and Peleaez-Campomanes, 2003, 2005).

Palaeoenvironmental reconstructions for the Caucasus site of Dmanisi, which yields a huge amount of information, indicate two phases. During the first hominin occupation

preserved in sector M5 (stratum A), which corresponds to some of the earliest evidence (dated to 1.85–1.78 Ma) of well-known Out of Africa settlements, the climate was humid and hot. The phytolith and pollen assemblages indicate a mixed environment (forest and open ecosystem), adapted to warm and humid conditions (Messenger et al., 2011). After 1.77 Ma, stratum B deposits including all the Dmanisi hominins (Lordkipanidze et al., 2006), the climate was semi-arid Mediterranean to warm with nearby water resources. The landscape was relatively open with sparse forest cover (Gabunia et al., 2000b,c) and palaeoenvironments were dominated by temperate vegetation (Messenger et al., 2010a), with an increase in herbaceous steppe, with abundant grasses and a decrease in forest habitat (Gabunia et al., 2000b,c; Messenger, 2006). According to phytolith data, the occupation of Dmanisi by hominins after 1.77 Ma occurred during a period of increased aridity (Messenger et al., 2010b).

The faunal assemblages (Zhu et al., 2004) from Majuangou (MJG-III or Goudi site (Gao et al., 2005)) in the Nihewan Basin also indicate according to the Indicator Species (IS) an open ecosystem with temperate woodland (*Cervus*) and grassland habitat (*Elephas*, *Equus*, *Pachycrocuta*, *Carnivora*, *Gazella*, *Struthio*, *Coelodonta*) and according to Ecological Diversity Analysis (EDA) woodland, open country and steppe (Belmaker, 2010b). The temperate Nihewan fauna ca. 1.63 Ma briefly overlapped the subtropical taxa in the southern part of the Loess Plateau (Zhu et al., 2015). There was an increasing trend in aridification/cooling of the Nihewan Basin during the Pleistocene (Ao et al., 2010).

Concerning 'Ubeidiya, the palaeoecological reconstruction, the layer where the tooth UB 335 (~1.5 Ma) has been found in particular, suggests a huge affinity with the Plio-Pleistocene Mediterranean sites, with open with sparse forest environment (Belmaker, 2006). The southern Levant was a Mediterranean woodland during the Plio-Pleistocene (Belmaker, 2010a).

The palaeoecological data (Belmaker, 2006, 2010a,b; Gabunia et al., 2000b,c; Lordkipanidze et al., 2006; Messenger, 2006; Zhu et al., 2004) from the sites of Dmanisi, Majuangou and 'Ubeidiya show that the first settlements occurred during a relatively humid and warm period (see above, and Messenger et al., 2011). This is consistent with the results of Agustí and collaborators (Agustí et al., 2009), showing that early human occupation in Western Europe took place during mild interglacial conditions in terms of temperature and humidity. These results are also congruous with those of Leroy and collaborators (Leroy et al., 2011), showing that hominin dispersal from East Africa to the southern Caucasus could have occurred during any of the 41 ka climatic cycles during interglacial times between 2.6 and 2 Ma. After 1.78 Ma, hominins encountered a Mediterranean climate, with fauna (e.g., in Dmanisi) made up mainly of Eurasian taxa (Agustí and Lordkipanidze, 2011), with a large proportion of cervid. The data on western Palaeoartic habitat diversity indicate environmental stimuli for the earliest human dispersal in Europe (Kahlke et al., 2011).

Although the climate was rather different in Africa during the same time period (1.77–1.66 Ma) or before, access to dietary resources was not so dissimilar. These

hominins had an adaptive capacity to wide-ranging environments. This is in keeping with the hypothesis of the necessity of pre-adaptation to higher variation in terms of habitat (Belmaker, 2006; Larich and Ciochon, 1996), as suggested by the variability selection hypothesis put forward by Potts (1998a,b). According to the latter author, hominin evolution is not characterized by adaptation to a type of environment (such as the savannah), or to a regular climatic tendency (climate cooling) or the opening of the landscape, but to more or less varied and shifting environments. Dispersal with the crossing of new latitudinal barriers by these hominins was thus possible. Moreover, the publication by Ungar and co-authors of the diet of early *Homo* corroborates this point of view. These species (*Homo habilis*, *H. rudolfensis*, early *Homo erectus*/*H. ergaster*) were adapted to environments with different resources (e.g., Ungar et al., 2006). Furthermore, early *Homo* specimens have been found in varied environments (e.g., DiMaggio et al., 2015; Prat et al., 2005; Tiercelin et al., 2010; Villmoare et al., 2015; Wood and Strait, 2004). They have a high phenotypic plasticity. It seems fundamental to its successful dispersal across diverse habitats: humans have the biology of a "colonizing ape" (Wells and Stock, 2007). It thus seems that one of the most suitable ways of confronting environmental change is versatility, rather than specialization. Furthermore, as noted by some authors (e.g., Bar-Yosef and Belfer-Cohen, 2001, 2013), moving into new territories far from the tropics reduces the danger of exposition to zoonotic diseases and could decrease the mortality and thus increase the number of reproductive individuals.

3.2. Endogenous hypotheses

In order to access to new ecological niches, some endogenous hypotheses implying several theoretical innovations have been put forward in a theoretical view, from both morphological and cultural perspectives. Indeed, many researchers consider that the first hominins outside Africa would have required: a better social organization (e.g., Carbonell et al., 2010; O'Connell et al., 1999; Schröder, 1992; van der Made, 2011); a better control of the environment with access to diversified dietary resources; and the physical and cognitive capacities to access to new ecological niches. For the latter points, the proposed innovations include: better thermoregulation (e.g., Wheeler, 1991); optimization of energetic expenditure (e.g., Aiello and Wells, 2002; Leonard and Robertson, 1997; Steudel-Numbers, 2006); a more diversified diet (e.g., animal protein) (e.g., Aiello and Wheeler, 1995; Antón et al., 2002); and more efficient locomotor capacities (e.g., Bramble and Lieberman, 2004; Pontzer, 2012; Pontzer et al., 2010; Steudel, 1996; Tattersall, 2003).

In this article, we will focus on three other main scenarios, which are also proposed (the cultural, body size and brain expansion scenarios) in order to assess their relevance in the light of the fossil and archaeological records.

3.2.1. Cultural expansion scenario

Previous postulates suggested that technological innovations could explain an Out of Africa dispersal. In other terms, humans with a more advanced culture would be

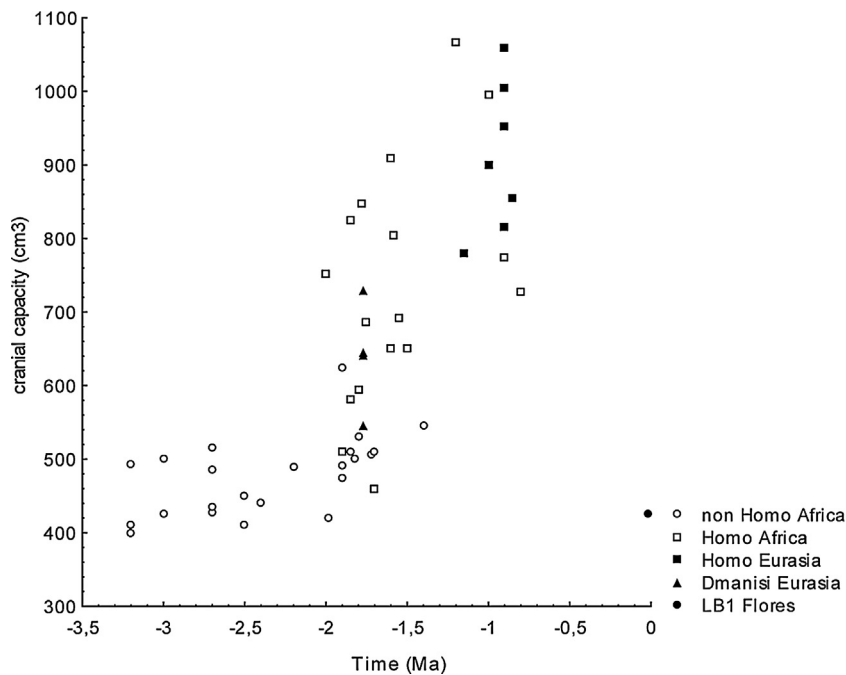


Fig. 2. Cranial capacity versus time.

Fig. 2. Capacité crânienne en fonction de la chronologie.

expected to be more efficient “colonizers”. At the end of the twentieth century, some authors advocated that the technological shift to the Acheulean (Mode 2) in Africa could have pushed some Oldowan (Mode 1) populations to move into Eurasia (Carbonell et al., 1999). However, this was before the discovery of Dmanisi, Majuangou and the new date for Longgupo. The archaeological record for Dmanisi (1.81–1.85 Ma) shows that the Oldowan assemblages are comparable to those from Early Pleistocene Oldowan sites in Africa. They are different from Developed Oldowan, and Acheulean technologies (de Lumley et al., 2005; Mgeladze et al., 2011), which emerged in Africa at the same period as the Dmanisi settlement (e.g., Acheulean technology in West Turkana at 1.76 Ma (Lepre et al., 2011)). In Majuangou (Zhu et al., 2004) and Longgupo (Huang et al., 1995), the lithic artefacts are similar to those from Oldowan assemblages, with some differences in terms of technological development stages (Boëda and Hou, 2011). The new dating framework for Longgupo site shows that the sedimentary layer bearing the artifacts, which is correlated to C-III-2, is dated to ~2.2 Ma (Han et al., 2016), which considerably pushes back dispersal into Asia (more than 2.2 Ma). The three cutmarks found on the surface of 2.6 Ma outcrops in Masol area (India) under light also an old dispersal event (Coppens, 2016; Dambricourt-Malassé et al., 2016).

3.2.2. Body size scenario

Body size (as reflected in body mass and stature) is often considered a contributory factor to the earliest hominin dispersal into Eurasia (e.g., Aiello and Key, 2002; Antón et al., 2002; Holliday, 2012; Pontzer, 2012; Wells and Stock, 2007). However, the body size database for early *Homo* and other Early Pleistocene hominins (e.g., Lordkipanidze et al.,

2007, 2013; Ruff and Burgess, 2015; Will and Stock, 2015), shows that the Dmanisi hominins are within the range of variation estimated for early *Homo* and at the lower end of variation of African *Homo erectus* in terms of body size. The marked increase in body mass and stature took place after 1.7 Ma in Africa (Figures 6 and 8 from Will and Stock, 2015). This implies that the first dispersal Out of Africa could have occurred without significant change in body size (Will and Stock, 2015).

3.2.3. Brain size scenario

Until the beginning of the 2000s, it was common to link brain size and the first Out of Africa dispersal, assuming that the increase of brain size (i.e. cranial capacity and encephalization quotient) could have been quite reasonably the cause of the first spread. However, the data in Fig. 2, which represents cranial capacity throughout time, show that: (1) the variability increases after 1.8 Ma, regardless of the species and the location (Africa or Asia); (2) the increase occurred after the first ‘Out of Africa’ settlement, and (3) there is no distinction between the African and Eurasian Early Pleistocene hominins (including Dmanisi hominin), but an overlap between them. Unfortunately, we cannot plot the specimens allocated to *Homo naledi* (Berger et al., 2015) in Fig. 2, because the date is still unknown. Moreover, as illustrated by the high variability observed in the Dmanisi palaeodeme, this feature (cranial capacity) seems to be a variable trait and thus debatable in terms of taxonomy.

Furthermore, if we take into account the encephalization quotient (EQ) using the data (cranial capacity and body mass) from the same individual and McHenry’s (1992) formula (i.e. $EQ = \text{observed endocranial volume} / 0.0589 (\text{body weight in grams})^{0.76}$) which is a more accurate

Table 3
Quotient of encephalization.
Tableau 3
Quotient d'encéphalisation.

	Endocranial capacity (adult estimation)	Body mass estimation (kg)	Quotient of encephalisation (equation from McHenry, 1992)
AL 288-1	387	27	2.81
Sts5/Sts 14	485	30	3.25
MH1	420	32	2.68
KNM-ER 1470	752	46–51	3.65–3.37
KNM-ER 1813	510	35–31	3.04–3.34
OH 24	594	30–36	3.99–3.47
KNM-ER 3883	804	57–58	3.31–3.27
KNM-ER 3733	848	59–65	3.4–3.16
KNM-WT 15000	909	80	2.89
D2700	645	49.4	2.96
D4500	546	48.8	2.53
DH 1 (male)	560	39.7–55.8	2.34–3.04
DH 2 (female)	465	39.7–55.8	1.94–2.52
Zhoukoutian XI	1015	45.75	4.94
Zhoukoutian XII	1030	51.93	4.56
LB 1	426	16–36	4.61–2.49

Equation from McHenry (1992).

McHenry's formula $EQ = \text{observed endocranial volume} / 0.0589 (\text{body weight in grams})^{0.76}$. Data cranial capacity: KNM-ER 1470, 1813, 3733, 3883 (Holloway, 1983); OH 24 (Tobias, 1991); MH1 (Berger et al., 2010); D2700 (Vekua et al., 2002); D4500 (Lordkipanidze et al., 2013); KNM-WT 15000 (Begun and Walker, 1993); AL 288-1, Sts5/Sts14 (Holloway et al., 2004); Zhoukoutian XI, XII (Weidenreich, 1943); LB1 (Kubo et al., 2013); DH1 (Berger et al., 2015). Body mass: KNM-ER 1470, 1813, 3883, 3733, OH 24: (Kappelman, 1996) and Aiello and Wood (1994), respectively; MH1 (Berger et al., 2010); D2700, D4500 (Lordkipanidze et al., 2007); KNM-WT 15000 (Ruff and Burgess, 2015); AL 288-1 and Sts5/Sts14 (McHenry, 1992); Zhoukoutian XI, and XII (Rightmire, 2004); LB1 (Brown et al., 2004); DH1 (Berger et al., 2015).

indicator, the EQ of the Eurasian hominins from Dmanisi (e.g., D 2700 and D4500), is less than African specimens allocated to *Homo ergaster* (KNM-ER 3733, 3883) or to early *Homo* (KNM-ER 1470, 1813, OH 24) (Table 3). Therefore, the first Out of Africa settlement is not linked to an increase in the encephalization quotient. Moreover, the discovery of LB1, with a small cranial capacity, allocated to *Homo floresiensis* (Brown et al., 2004) dated to 60 000–100 000 years and the data from *Homo naledi* (DH1 and DH2; Berger et al., 2015) yielded that the cranial capacity and/or the EQ is not a relevant indicator in term of hominin expansion as well as species or genus differentiation criteria; thus, hominin brain size evolution is a very challenging question.

4. Conclusions

This review, completed by new models and data, allows some general conclusions. The archaeological and palaeanthropological datasets show an early hominin dispersal before 1.8 Ma. This probably occurred before 2 Ma and even before 2.2 Ma and 2.6 Ma taking into account, on one hand, the date of the lithic assemblage of Longuppo at ~2.2 Ma (Han et al., 2016) and cutmarks from Masol (Coppens, 2016; Dambri-court-Malassé et al., 2016); and on the other hand, the humid period corridor which occurred between 2.6 and 2 Ma.

This paper shows that the expression; “first Out of Africa settlement” should be preferred to terms such as “migration” or “Out of Africa 1” in order to distinguish this expansion to migration as traveling from one place to another at regular times of year and to under light that although some populations expanded Out of Africa, other populations stayed and evolved in Africa. Dispersals were,

sporadic and multidirectional, with no predetermination, and dependent on food availability and environmental conditions. Our basic model shows that these dispersals did not occur on a once-off basis, but as many successive discontinuous occupations, over more or less distant areas and at times with episodes of turning back.

Hominins in Eurasia encountered different environments, with more temperate climates, but dietary resources, such as herbivores, were not markedly different to those in Africa during the same period. Hominins had an excellent ability to adapt to novel habitats and environmental conditions. This is linked to the notion of versatility, which is already present in Early Pleistocene hominins, represented by the early *Homo* specimens found in different habitats.

The “reasons” or “factors” often linked to the first Out of Africa settlement, highlighted in this paper, such as climatic changes, technological innovation (different from Oldowan), increase of body size and brain size (cranial capacity and encephalization quotient), do not seem to fit the hominin and archaeological datasets. As noted by Palombo (2013), we are still far from an exhaustive scenario depicting the relationships among human dispersal, body size and brain expansion, cultural innovation and ecosystem dynamics.

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