



## Early Human Evolution in the Western Palaeartic: Ecological Scenarios

José S. Carrión<sup>a,\*</sup>, James Rose<sup>b</sup>, Chris Stringer<sup>c</sup>

<sup>a</sup> Department of Plant Biology, University of Murcia, 30100 Murcia, Spain

<sup>b</sup> Department of Geography, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK

<sup>c</sup> Palaeontology Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK

### ARTICLE INFO

#### Article history:

Available online 6 May 2011

#### Keywords:

Human evolution  
Palaeoecology  
Palaeoclimatology  
Quaternary  
Pleistocene  
Biodiversity  
Biodiversity hotspots

### ABSTRACT

This review presents the themes of a special issue dealing with environmental scenarios of human evolution during the Early Pleistocene (2.6–0.78 Ma; MIS 103–MIS 19) and early Middle Pleistocene (0.78–0.47 Ma; MIS 19–base of MIS 12) within the western Palaeartic. This period is one of dramatic changes in the climates and the distribution of Palaeartic biota. These changes have played their role in generating adaptive and phyletic patterns within the human ancestry, involving several species such as *Homo habilis*, “*Homo georgicus*”, *Homo erectus*, *Homo antecessor* and *Homo heidelbergensis*. In the archaeological record, these species include the Oldowan (Mode 1) and Acheulian (Mode 2) lithic technologies. Taphonomic considerations of palaeoecological research in hominin-bearing sites are provided and evaluated. Syntheses are provided for north Africa, western Asia, the Mediterranean Basin, Britain, and continental Europe. Palaeoenvironmental reconstructions based on multidisciplinary data are given for Ain Boucherit, Ain Hanech and El-Kherba in Algeria, Dmanisi in Georgia, Atapuerca, Cueva Negra, and the Orce Basin in Spain, Monte Poggiolo and Pirro Nord in Italy, Pont-de-Lavaud in France, and Mauer in Germany. The state of the art with the Out of Africa 1 dispersal model is reviewed. A source-sink dynamics model for Palaeolithic Europe is described to explain the morphological disparity of *H. heidelbergensis* (we will sometimes use the informal name “Heidelbergs”) and early Neanderthals. Other aspects debated here are the selective value of habitat mosaics including reconstructions based on mammal and avian databases, and the role of geological instability combined with topographic complexity. This review is completed by addressing the question of whether the appearance of evolutionary trends within hominins is concentrated in regions of highest worldwide biological diversity (biodiversity hotspots). It is concluded that the keys for the activation of evolutionary change in hominins may have been geological instabilities, and a shifting physiographical heterogeneity combined with high biodiversity and ecological interaction.

© 2011 Elsevier Ltd. All rights reserved.

### 1. Introduction

This special issue deals with environmental scenarios of human evolution, an enormously important subject to which Quaternary scientists have not given appropriate attention (Stringer, 2006). Our goal is to shed light on the interplay of environment and evolution during the Early Pleistocene (2.6–0.78 Ma; MIS 103–MIS 19) and early Middle Pleistocene (0.78–0.47 Ma; MIS 19–base of MIS 12) (Rose, 2009) within the western Palaeartic (Middle East, North Africa and Europe).

This volume focuses on the evidence from western Europe and northern Africa, which may be surprising in view of the fact that

early evidence for human evolution is much more abundant in eastern and southern Africa, and the Far East. Conventional wisdom and most evidence indicates that our species, and probably many of its immediate predecessors, arose in eastern Africa, but it is nonetheless ironic how recent data have resulted in a re-examination of the geographical origins of Hominidae. In establishing the sister-group relationships between kenyanthropines and hominids, Moyà-Solà et al. (2009) observed the presence of both groups in Eurasia during the Middle Miocene, and argued in favour of a Eurasian origin of the Hominidae. Begun (2007) suggested that the hominid clade may have been settled in Africa from a European ancestor ape which would have expanded its range between 11 and 9 Ma. Indeed the warming trend experienced in Europe during the Middle Miocene may have built a hospitable scenario for hominoid habitation (Folinsbee and Brooks, 2007), with the cooling episode of the late Miocene having provoked regional extinction, with

\* Corresponding author.

E-mail addresses: [carrión@um.es](mailto:carrión@um.es) (J.S. Carrión), [j.rose@rhul.ac.uk](mailto:j.rose@rhul.ac.uk) (J. Rose), [c.stringer@nhm.ac.uk](mailto:c.stringer@nhm.ac.uk) (C. Stringer).

a refuge in Africa. So, even before the Pleistocene, Eurasia can be identified as a crucial region for the human evolution experiment.

The period under consideration is one of dramatic changes in climates and the distribution of African and Palaeartic biota. From Early to Middle Pleistocene, a general trend towards increased severity of cold episodes is observed (Bradley, 1999; Candy et al., 2010) and it is possible, as we shall see later, that these changes played their role in generating adaptive and phyletic patterns within human ancestry. In addition, it must be emphasized that during the first four million years or so of human evolution, brain size increased very slowly (Stringer and Andrews, 2005) and encephalization is only particularly pronounced over the past 800,000 years, coinciding with the period of strongest climate fluctuation worldwide.

Although multidisciplinary approaches in human palaeoecology have improved their taxonomic and temporal resolution over the last decade (Aguirre, 2008), the topic of this special issue is of immense complexity. While the title may be considered pretentious, we use it as an objective, and we are aware of the pitfalls of this kind of research. Like any other investigation we need critical evidence, and in this case we have to concede that we are constrained by a depressingly fragmentary fossil record and a much-disputed taxonomy. The critical evidence upon which we must depend – species, demes, populations – is, regrettably, diffuse and unstable. Indeed, with each new fossil discovered, or with each new gene sequencing on preserved material, we may be subject to a measure of intellectual excitement, usually followed by a return to previous notions or concepts. For example, following the recent case of the Denisovans (Reich et al., 2010), we might reconsider the idea that *Homo heidelbergensis* may have arisen in eastern Africa (Martín-Torres et al., 2011). If there is one factor that is persistent throughout the literature, it is the over-generalization about the environments of fossil hominins with respect to the description of habitats. In most cases, environmental interpretations lack quantification or a definition of spatial or chronological scales (Foley, 1994; Finlayson et al., 2011). Critically, too, most data are not sufficient to produce a coherent story in *tempo* and *mode* that can satisfactorily explain the available fossil record and thus contribute significantly to evolutionary theory. In this Special Issue we take note of these problems, and recognise that much that is published will be 'reasonable speculation', but we believe that, in the view of the advances presented here, this is an acceptable starting point.

## 2. Taphonomical remarks

Direct observations of the mechanisms of ecology and evolution are difficult or impossible to access, and indeed this problem is made worse by the taphonomic context of most palaeontological evidence. Taphonomical research provides an empirical basis for evaluating the significance and meaning of the palaeontological data, but taphonomic interpretations are themselves open to debate. Fernández-Jalvo et al. (2011) use several case studies to examine the importance of taphonomy of critical evidence that contributes to our understanding of human evolution. They use partial evidence from the faunas of Boxgrove, England, to stress the importance of experiments designed to explain the origin of fossil assemblages in hominin-bearing sites. These authors propose that three major matters need to be addressed when reconstructing past environments: i) habitat complexity arising from mixed faunas and floras; ii) biases arising from both accumulation and preservation processes, and iii) the fact that past habitats may not have a modern counterpart with which they can be compared.

The first problem can be addressed by comparing palaeodata with data provided by a combination of modern assemblages from

differentially weighted and diverse habitat types, in order to determine the effects of the studied organisms on the ecological signal (Andrews, 2006). It should be assumed that the mixing of source habitats is the norm rather than exception.

Challenges presented by preservational biases (problem ii) have been described by Carrión and Scott (1999) using as a model the pollen record from Sterkfontein caves in South Africa. It cannot be stressed enough that 'unsuccessful' results should be communicated along with those considered 'successful'. Without this, a false impression can be given about the nature and quality of the evidence. For instance, Carrión et al. (2009) have reported 'failures' with Quaternary pollen analyses in the Iberian Peninsula, and it is interesting that although archaeological caves and rock shelters represent a majority of the 'failed' studies, these sites can still provide important successes. For instance, Fernández-Jalvo et al. (2011), point out that coprolites remain an insufficiently exploited source of paleoecological information.

## 3. Research background in Africa

Studies that identify causal links between the patterns of biological and cultural evolution of hominins and environmental changes in Africa during the last million years are relatively abundant. As a consequence, it has been postulated that selective pressures in favour of bipedal walking may be related to the depletion of forests in eastern and central Africa as a consequence of climatic changes after 6 Ma (Trauth et al., 2003, 2005). It has been considered that the emergence of the Oldowan industry and the internal diversification of australopithecines took place within the context of the climatic conditions after about 2.8 Ma (Bobe et al., 2002; deMenocal, 2004). The appearance of *Homo erectus* and the associated Acheulian industry in Africa has been correlated with environmental changes since about 1.8 Ma (deMenocal and Bloemendal, 1995). The earliest geographical expansions of *Homo* towards southern Africa and Asia (Out of Africa 1 hypothesis) have been correlated with both the extinction of *Paranthropus*, and climatic changes provoking desertification within a large part of the savannah biome of the Rift Valley and the southern Africa highveld (Ségalen et al., 2007).

The characteristics of the physical environment have been taken as forcing factors in the evolution of *Sahelanthropus tchadensis* at 7–6 Ma (Brunet et al., 2002), *Ardipithecus ramidus* at 5.8–5.2 Ma (WoldeGabriel et al., 2009), *Australopithecus anamensis* at 4.2–3.9 Ma (White, 2003), *A. afarensis* at 4–3 Ma (Radosevich et al., 1992; Bonnefille et al., 2004; Haile-Selassie et al., 2010), *Australopithecus bahrelghazali* at 3.4–3 Ma (Brunet et al., 1996), *Paranthropus robustus* (de Ruiter et al., 2009), *Kenyanthropus platyops* at 3.5–3.2 Ma (Leakey et al., 2001), *Australopithecus garhi* at 2.5 Ma (Asfaw et al., 1999; de Heinzelin et al., 1999), and *Homo habilis* at 2.3 Ma (deMenocal, 2004; Wood and Strait, 2004). The earliest dispersal from Africa of *Homo sapiens* has also been interpreted as associated with abrupt dry spells that occurred between 135 and 75 ka (Carto et al., 2008).

Overall, studies of past environments have suggested that *Australopithecus* lived in a more forested habitat than *Paranthropus*, while *Homo* would have been the first genus adapted to savannah-grassland, grassland and steppe (Jacobs, 2004). Traditionally, the preferred hypotheses were habitat-specific and stated that human adaptations, including upright walking, arose on the African savannah, or were influenced by the environmental pressure of an expanding dry savannah. More recently, the variability selection hypothesis formulated by Potts (1998) has been gaining popularity. In this hypothesis the emphasis is put on the ability of hominins to withstand or to respond environmental change, and it is argued that they were not restricted to a single type of environment. It

follows that, while coping with shifts in environmental conditions, resource to behaviour versatility, phenotypic plasticity and gene polymorphism would be needed. A pertinent example of this hypothesis can be seen with *A. ramidus*, which occupied both wooded areas and wooded grasslands with intensive grazing. *Australopithecus anamensis* has been found at Kanapoi and Allia Bay (Kenya) in association with another type of mosaic – an open savanna with low trees and shrubs, but with both grasslands and gallery forests nearby.

#### 4. The palaeoanthropological record

The hominin fossil record across the western Palaearctic during the Early Pleistocene and early Middle Pleistocene is very small, especially evidence for the first inhabitants. This limitation has resulted in a proliferation of nomenclatural and taxonomic terms that have been applied, although in different degrees, to all the taxa described, namely *H. habilis*, “*Homo georgicus*”, *Homo erectus*, “*Homo ergaster*”, *Homo antecessor*, “*Homo cepranensis*”, and *H. heidelbergensis* (Table 1). The evolutionary mechanisms invoked to justify this proliferation include gradual trending from one species to another (Cartmill and Smith, 2009; Arsuaga, 2010), punctuated equilibria, and phyletic speciation (Gould, 2002; Vrba, 2006). Other processes that have not always been taken into account are the possibility of variation in levels of sexual dimorphism (Agustí et al., 2009; Rightmire, 2009). Likewise, the concepts that humans are a polytypic species (that is, an interwoven network of populations with varying degrees of gene flow between species [Tattersall, 1996; Finlayson, 2009; Dennell et al., 2011]), and modular evolution and evolutionary changes in ontogeny have not been sufficiently incorporated into current theory (Zollikofer and Ponce de León, 2009).

It is generally accepted that *Homo* evolved in east Africa between 2.5 and 2.0 Ma (Kimbel et al., 1996). Indisputable evidence for the existence of hominins during the Middle Villafranchian (2.6–1.8 Ma) in Eurasia and north Africa is so far lacking. The oldest fossil evidence within Eurasia is from Dmanisi in Georgia (Lordkipanidze et al., 2007), and it seems that some of these earliest Eurasians are morphologically close to both *H. habilis* and *H. erectus* (de Lumley et al., 2006; Agustí and Lordkipanidze, 2011). This first appearance of *Homo* outside Africa is likely to have been achieved via the Levantine Corridor (eastern margin of the Mediterranean) and into Transcaucasia (Agustí et al., 2009). The oldest known humans of eastern Asia may well be from the top of the Sangiran Formation in Java at c. 1.6–1.5 (1.02) Ma (Kaifu et al., 2005; Bettis et al., 2009). The fragmentary remains (incisor teeth associated to stone tools) at Yuanmou in the Yunnan Province of southern China, dated at 1.7 Ma (Zhu et al., 2008), have not been yet deciphered, and there is as yet some debate about their assignation to *Homo* (Dennell, 2009).

With respect to understanding the expansion of *Homo* in western Eurasia, the next significant fossil, although consisting solely of isolated teeth, occurs in Ubeidiya, Israel, around 1.4 Ma, and has been attributed to *H. erectus/ergaster* (Belmaker et al., 2002). For the western part of the Palaearctic, the oldest record is the ~1.2 million year old mandible in the Sima del Elefante, Atapuerca, attributed to *Homo antecessor* (Carbonell et al., 2008; Rodríguez et al., 2011). Other notable *erectus* fossils include the northern China Gongwangling (Lantian) dated at about c. (1.36)–1.15 Ma (An and Ho, 1989), and Zhoukoudian at c. 780–680 ka (Shen et al., 2009). In northern Africa the human fossil sites at Tighenif near Ternifine in Algeria, have been dated at c. 700 ka (Geraads et al., 1986) (Table 1). Within this early *Homo* radiation, the genealogic placement of *H. antecessor* from Atapuerca Gran

Dolina TD-6, dated at 960–780 ka (Berger et al., 2008), remains controversial (García and Arsuaga, 2011).

*H. heidelbergensis* may have evolved from an *erectus* ancestor through a speciation event in Africa or Eurasia prior to 600 ka (Stringer and Andrews, 2005; Mounier et al., 2009; Rightmire, 2009). Although genetic linkages to *H. antecessor* cannot be excluded (Dennell et al., 2011), *H. heidelbergensis* is more likely to be an immigrant reaching Europe after 700 ka, with the Mauer specimen as fundamental evidence. In this volume, new micro-mammal material from Mauer allows Wagner et al. (2011) to place the famous *H. heidelbergensis* mandible of the Lower Sands into either MIS 15 or MIS 13 interglacials, while other stratigraphic and chronological evidence favours a correlation to MIS 15 (between 568 and 621 ka: Wagner et al., 2010). The probable *heidelbergensis* specimens from Caune de l'Arago, France (de Lumley and de Lumley, 1971), Salé, Morocco (Hublin, 1985), Broken Hill (Zambia) and Ceprano, Italy (Manzi et al., 2011) (Table 1) appear to be younger and demonstrate that by 400 ka the Heidelbergers had spread over much of Africa, the Mediterranean Basin and continental and northern Eurasia.

Plausibly, the European populations of *H. heidelbergensis* evolved into the Neanderthal lineage, whereas in Africa they would be ancestors to *H. sapiens* (Stringer, 1983, 2002; Hublin, 1985, 2009). Genetic estimates for this most recent common ancestor of *Homo neanderthalensis* and *H. sapiens* support the notion of a widely-dispersed ancestral species during the middle part of the Middle Pleistocene, which separated into at least two descendent populations prior to the late Middle Pleistocene, perhaps forced by isolation during the MIS 12 climatic crisis at c. 480–425 ka (Endicott et al., 2010). Given its Neanderthal features, it is likely that the population from Sima de los Huesos was a core population for the Neanderthal gene pool (Rosas, 2001; García and Arsuaga, 2011; Dennell et al., 2011). However a conflict arises with its proposed early chronology at c. 530–250 ka (Bischoff et al., 2007; Endicott et al., 2010), which has no counterpart in the palaeoanthropological record of Eurasia. The combination of primitive and derived traits in Eurasian Heidelbergers may seem random (Bermúdez de Castro et al., 2009) and therefore, difficult to sequence chronologically, but recognising the Sima sample as early Neanderthal rather than *heidelbergensis* removes some of these issues (Endicott et al., 2010).

#### 5. The archaeological record

The Oldowan (Mode 1) is first recorded in Africa at around 2.6 Ma at Gona in Ethiopia (Semaw et al., 2003). During the Early Pleistocene, it spreads southwards (from 2.4 to 1.7 Ma) and then outwards to North Africa, eastern Europe and Asia. Thus, it is possibly recorded in Riwayat, Pakistan, at c. 1.9 Ma (Dennell, 2009), at Ain Hanech in North Africa, at 1.8 Ma (Sahnouni et al., 2011), Dmanisi in the Caucasus at c. 1.8 Ma (Agustí and Lordkipanidze, 2011), Yuanmou in southern China at c. 1.7–1.6 Ma (Zhu et al., 2008), and Majuangou in northern China at c. 1.36 Ma (Zhu et al., 2008) (Table 2).

In Europe, the Oldowan occupation was important during the Early and Middle Pleistocene. Thus, fossil terraces of the Middle River Loire tributaries, dated by ESR between 1.7 Ma and 130 ka, embrace around 80 prehistoric localities with Mode 1 industries located at Pont-de-Lavaud in the Creuse Valley, Lunery in the Cher Valley and Saint-Hilaire-la-Gravelle in the Loir Valley (Despriée et al., 2011). Lézignan-la-Cébe at Hérault valley, Languedoc–Roussillon in southern France, is a prominent site with 1.57 Ma dated lithic assemblages of pebble culture type associated with vertebrate fauna (Crochet et al., 2009). The Orce region of south-eastern Spain also provides evidence for Oldowan manufacturers at c. 1.4–1.3 Ma (Martínez-Navarro et al., 1997) (Table 2), and dating of

**Table 1**  
Chronology of the oldest dated specimens and taxa in the hominin fossil record.

Specimen/s	Taxon	Cronology	Site, region	Reference/s
TM266-01-060-1	<i>Sahelanthropus tchadensis</i>	7–6 Ma	Djurab, N Chad	Brunet et al. (2002)
BAR 1000'00	<i>Orrorin tugenensis</i>	6.1–5.72 Ma	Tugen Hills, W Kenya	Sénut et al. (2001)
ASK-VP-3 (400-405)	<i>Ardipithecus kadabba</i>	5.77–5.54 Ma	Middle Awash, Ethiopia	Haile-Selassie et al. (2004)
ARA-VP, Sites 1, 6 & 7, ARA-VP 6/500	<i>Ardipithecus ramidus</i>	4.51–4.32 Ma	Middle Awash, Ethiopia	White et al. (2009)
KP-29285	<i>Australopithecus anamensis</i>	4.2–3.9 Ma	Kanapoi and Allia Bay, N Kenya	White (2003)
KSD-VP-1/1	<i>Australopithecus afarensis</i>	3.6–2.9 Ma	Korsi-Dora, Afar, Etiopía	Haile-Selassie et al. (2010)
KNM-WT 40000	<i>Kenyanthropus platyops</i>	3.5–3.2 Ma	Lomekwi, Lake Turkana, Kenya	Leakey et al. (2001)
K12	<i>Australopithecus bahrelghazali</i>	3.5–3.0 Ma	Koro Toro, Chad	Brunet et al. (1996)
STS 14, STS 5	<i>Australopithecus africanus</i>	3.5–2.0 Ma	Sterkfontein & Taung, South Africa	Dart (1925)
BOU-VP-12/130	<i>Australopithecus garhi</i>	2.7–2.3 Ma	Bouri, Middle Awash, Ethiopia	Asfaw et al. (1999)
KNM-WT 17000	<i>Paranthropus aethiopicus</i>	2.7–2.3 Ma	Lake Turkana (Kenya), Shungura–Omo (Ethiopia)	Leakey and Lewin (1992)
OH 4,5	<i>Paranthropus boisei</i>	2.3–1.0 Ma	Olduvai Gorge, Tanzania	Leakey (1959)
TM 1517	<i>Paranthropus robustus</i>	2.0–1.0 Ma	Drimolen, S Africa	Keyser (2000)
UW 88-50 (MH1)	<i>Australopithecus sediba</i>	1.95 Ma	Malapa, S Africa	Berger et al. (2010), Dirks et al. (2010)
Several samples	Early <i>Homo</i>	2.4–2.3 Ma	Omo-Shungura, Ethiopia	Howell et al. (1987)
KNM-BC 1	Early <i>Homo</i>	2.4 Ma	Chemeron, Kenya	Hill et al. (1992)
AL 666-1	Early <i>Homo</i> (cf. <i>H. habilis</i> )	2.33 Ma	Hadar, Ethiopia	Kimbell et al. (1996)
KNM-ER 1813 and 1805	<i>Homo habilis</i>	1.9–1.5 Ma	Koobi Fora, Kenya	Leakey (1974)
OH 24	<i>Homo habilis</i>	1.87 Ma	Olduvai Gorge, Tanzania	Blumenscheine et al. (2003)
KNM-ER 1470	<i>Homo rudolfensis</i>	1.9–1.8 Ma	Koobi Fora, Kenya	Leakey (1973)
KNM-ER 2598, 992	<i>Homo erectus</i>	1.9–1.5 Ma	Koobi Fora, Kenya	Leakey and Wood (1973)
D 2700	" <i>Homo georgicus</i> "	1.8–1.7 Ma	Dmanisi, Georgia	Vekua et al. (2002)
KNM-ER 3733	<i>Homo erectus</i>	1.8–1.4 Ma	Koobi Fora, Kenya	Feibel et al. (1989)
Sangiran 1b, 2, 9, 22	<i>Homo erectus</i>	>1.51–1.02 Ma	Java, Indonesia	Kaifu et al. (2005)
Ubeidiya	Erectine	1.4 Ma	Ubeidiya, Jordan Valley, Israel	Belmaker et al. (2002)
TE9-1	<i>Homo antecessor</i>	1.22 Ma	Sima del Elefante, Atapuerca, Spain	Carbonell et al. (2008), Rodríguez et al. (2011)
TD-6	<i>Homo antecessor</i>	960–780 ka	Gran Dolina, Atapuerca, Spain	Berger et al. (2008)
Gongwangling	Erectine	(1.36)–1.15 Ma	Lantian, N China	An and Ho (1989)
Zhoukoudian	<i>Homo erectus</i>	780–680 ka	N China	Shen et al. (2009)
V1519	Erectine? <i>Homo</i> ?	700 ka	Yuanmou, Yunnan, SW China	Zhu et al. (2008)
Tighenif1–3	<i>Homo erectus</i> or <i>heidelbergensis</i>	800 ka	Ternifine, Algeria	Geraads et al. (1986)
Gesher Benot Ya'aqov	<i>Homo heidelbergensis</i> ?	780 ka	N Jordan Valley, Israel	Verosub et al. (1998), Goren–Inbar et al. (2000)
Bodo	<i>Homo heidelbergensis</i>	600 ka	Middle Awash, Ethiopia	Clark et al. (1994)
Mauer	<i>Homo heidelbergensis</i>	600 ka	Graferain Quarry, Mauer, Germany	Wagner et al. (2011)
AT-SH 888, 950	Archaic Neanderthal	530–250 ka	Sima de los Huesos, Atapuerca, Spain	Bischoff et al. (2007)
Boxgrove	<i>Homo</i>	512–478 ka	West Sussex, England	Stringer et al. (1998)
TG IIa–IIb	<i>Homo heidelbergensis</i>	500–250 ka	Galería, Atapuerca, Spain	Rodríguez et al. (2011)
Saldanha	<i>Homo heidelbergensis</i>	500 ka	Elandsfontein, South Africa	Churchill et al. (1996)
Ndutu	<i>Homo heidelbergensis</i>	>400 ka	Olduvai, Tanzania	Clarke (1976)
Salé	<i>Homo heidelbergensis</i>	455–389 ka	Rabat, Morocco	Hublin (1985)
AR II, AR XIII	<i>Homo heidelbergensis</i>	450–400 ka	Arago Cave, France	de Lumley and de Lumley (1971)
Ceprano	" <i>Homo cepranensis</i> "	400 ka	C Italy	Manzi et al. (2011)
Steinheim	Archaic Neanderthal	400–200 (c. 350) ka	Steinheim, Germany	Cartmill and Smith (2009)
Swanscombe	Archaic Neanderthal	400 ka	Swanscombe, England	Stringer and Hublin (1999)
Zuttiyeh	Heidelberg	350–250 ka	Mugharet El-Zuttiyeh, Israel	Bar Yosef and Pilbean (1993)
Kabwe 1	" <i>Homo rhodesiensis</i> "	400–350 ka	Broken Hill Mine, Kabwe, N Zambia	Klein (1999)
Cave of Hearths	Heidelberg	350–250 ka	Cave of Hearths, South Africa	McNabb and Sinclair (2009)
Petralona	Heidelberg	350–200 ka	Clemontsi Cave, Greece	Grün (1996), Delson et al. (2000)
Azokh V	<i>Homo heidelbergensis</i>	>300 ka	Azokh Cave, Nagorno–Karabagh, SE Caucasus	Fernández-Jalvo et al. (2011)
Florisbad	Archaic <i>Homo sapiens</i>	260 ka	Free State, South Africa	Scott and Rossouw (2005)
Biache-Saint-Vaast	<i>Homo neanderthalensis</i>	250–159 ka	Vitry-en-Artois, France	Guipert et al. (2007)
Ehringsdorf	<i>Homo neanderthalensis</i>	205 ka	Weimar, Germany	Grün and Stringer (1991)
Pontnewydd (teeth)	<i>Homo neanderthalensis</i>	200 ka	Denbighshire, Wales, UK	Delson et al. (2000)
Omo Kibish	<i>Homo sapiens</i>	195 ka	Kibish Formation, Ethiopia	Rightmire (2009)
Jebel Irhoud	Archaic <i>Homo sapiens</i>	160 ka	Sidi Moktar, Morocco	Smith et al. (2007)
Herto BOU-VP-16/1	<i>Homo sapiens</i>	160–154 ka	Middle Awash, Ethiopia	Clark et al. (2003)
Krapina J, H, G	Neanderthal	140–120 ka	Krapina, Croatia	Rink et al. (1995)
Skhul V	<i>Homo sapiens</i>	130–100 ka	Haifa, Israel	Grün et al. (2005)
Qafzeh 9	<i>Homo sapiens</i>	130–90 ka	South of Nazareth, Israel	Grün and Stringer (1991)
Ngaloba	Archaic <i>Homo sapiens</i>	129–108 ka	Laetoli, Tanzania	Hay (1987)
Hortus	<i>Homo neanderthalensis</i>	120–110 ka	L'Hortus Cave, France	de Lumley (1973)
Liang Bua Cave	<i>Homo floresiensis</i>	95–12 ka	Liang Bua, Flores, Indonesia	Morwood et al. (2005)

Italian sites also suggest relatively early colonisation, with Pirro Nord (c. 1.6–1.3 Ma) (Arzarello and Peretto, 2010) as the most ancient known settlement. The evidence of human presence is substantiated in such sites like Atapuerca, as the Mode 1 lithics

assemble with human remains dated at c. 1.2 Ma (Carbonell et al., 2008; Rodríguez et al., 2011).

The Acheulean (Mode 2 technology) has been recorded in Africa since c. 1.6 Ma (Konso Gandula, Ethiopia: Asfaw et al., 1992; Roche

**Table 2**  
Chronology for some of the earliest Oldowan (Mode 1) and Acheulian (Mode 2) technologies in Africa, Asia, and Europe.

Industry	Continent	Chronology	Site, Region	Reference
Mode 1	E Africa	2.6 Ma	Awash, Ethiopia	Semaw et al. (2003)
Mode 1	C Asia	1.9 Ma	Riwat, Pakistan	Dennell (2009)
Mode 1	N Africa	1.8 Ma	Ain Hanech, Algeria	Sahnouni et al. (2011)
Mode 1	W Asia	1.8 Ma	Dmanisi, Georgia	Agustí and Lordkipanidze (2011)
Mode 1	S Europe	1.6–1.3 Ma	Pirro Nord, Apulia, Italy	Arzarello and Peretto (2010)
Mode 1	W Europe	1.57 Ma	Lézignan-la-Cébe, France	Crochet et al. (2009)
Mode 1	E Asia	1.36–1.27 Ma	Nihewan-Majuangou, N China	Zhu et al. (2008)
Mode 1	S Europe	1.4–1.3 Ma	Fuente Nueva–3, Barranco León–5, SE Spain	Martínez-Navarro et al. (1997)
Mode 1	N. Europe	950 850 ka	Happisburgh 3	Parfitt et al. (2010)
Mode 2	E Africa	1.6–1.4 Ma	West Turkana, Kenya and Korso Gandula, Ethiopia	Roche and Kibunjia (1994)
Mode 2	W Asia	1.53 Ma	Ubeidiya, Israel	Bar-Yosef and Belmaker (2011)
Mode 2	W Asia	1.0 Ma	Evron–Quarry, Israel	Bar-Yosef and Belmaker (2011)
Mode 2	W Asia	900 ka	Gesher Benot Ya'aqov, Israel	Bar-Yosef and Belmaker (2011)
Mode 2	S Europe	900 ka	Cueva Negra del Estrecho del Río Quípar, SE Spain	Scott and Gibert (2009)
Mode 2	E Asia	800 ka	Bose, S China	Zhang et al. (2010)
Mode 2	N Europe	750 ka	Pakefield, UK	Parfitt et al. (2005), Rose (2009)
Mode 2	N Europe	500 ka	Happisburgh 1	Ashton et al. (2008), Rose (2009)

and Kibunjia, 1994) and then appears in Ubeidiya at c. 1.5 Ma (Bar-Yosef and Belmaker, 2011). After this there is abundant evidence for Mode 2 artefacts that were made during the Middle Pleistocene of Eurasia and north Africa, with early sites such as Gesher Benot Ya'aqov in Israel (Geraads and Tchernov, 1983; Verosub et al., 1998; Alpersen-Afil et al., 2009; Goren-Inbar et al., 2000), and Cueva Negra del Estrecho del Río Quípar in southern Spain (Scott and Gibert, 2009), both dated at c. 900 ka (Table 2). The Cromer Forest-bed Formation at Happisburgh 1 provides early evidence for the Acheulean in Britain at c. 500 ka (Ashton et al., 2008). At the same time Mode 2 technology is widespread in the Brinay and Gievres sites in France, with lithic assemblages being increasingly rich in handaxes after 500 ka along the middle Loire Basin (Despriée et al., 2011).

The early Middle Pleistocene archaeological sites in eastern and southern Britain have yielded remarkable archaeological evidence in recent years and involve a landscape that has been subjected to lowland glaciation on a number of occasions. There is no evidence that early humans survived in Britain during severe glacial or periglacial climates: brief periods of human occupation were separated by lowland glaciation in midland and eastern England. The glacial deposits which overlie the sites of Happisburgh 1 (Ashton et al., 2008) and High Lodge (Ashton et al., 1992), and the periglacial deposits that overlie Boxgrove also preserve the archaeological remains in almost pristine conditions. Elsewhere preservation is provided by river (Parfitt et al., 2005) or estuarine deposits (Happisburgh 3, Parfitt et al., 2010), and even at these sites a capping of glacial deposits has preserved the archaeological sediments and context from erosion (Stringer et al., 1998; Rose, 2009). The presence of glacial deposits provides potential for stratigraphic control and possibly reliable dating of the archaeology. However, as yet, the dating of the glacial episodes is a matter of debate, due to conflicting results from a number of dating methods (geochronometry (amino-acid racemisation), first and last appearance biostratigraphy, and climatic forced geomorphology/lithostratigraphy). For a review of this problem see Rose (2009) and Preece et al. (2009). In this issue, Hosfield (2011) gives convincing proofs for the sporadic existence of humans prior to 500–600 ka (possibly from 1.0 Ma onwards), with Mode 2 technology observed at sites that have been dated to around 600 ka and younger. The British evidence supports the “modified short chronology” model for the occupation of northern Europe (Dennell and Roebroeks, 1996). In total, Britain was habited by humans for less than 20% of the last 500,000 years (Stringer, 2006).

## 6. The palaeoecological record and biogeographical patterns

### 6.1. Reaching and leaving northern Africa: an old story of cultural collapse

The faunal context of the Algerian sites of Ain Boucherit (2.6–1.9 Ma), Ain Hanech and El-Kherba (1.95–1.77 Ma) is examined by Sahnouni et al. (2011) with the goal of reconstructing the palaeoenvironments of Plio-Pleistocene and Early Pleistocene humans in northern Africa. The record of Oldowan stone tools here precedes the European, being as old as 1.8 Ma. It may have been possible to reach northern Africa during the warm stages of the Early Pleistocene by several routes. Recently, zoogeographical and palaeohydrological analyses from the Sahara have shown that animals, and eventually humans, reached northern Africa via this region in preference to the Nile Corridor (Drake et al., 2011). Thus, the “green Sahara”, with its extensive interconnected hydrological systems, would have existed during the Last Interglacial (c. 125 ka), and probably on many earlier occasions during the Quaternary. Drake et al. (2011) also compiled archaeological data in support of this model, showing that stone tools from Oldowan to Neolithic can be mapped within all the mega-lake basins that would form corridors across the Sahara during the wet phases.

It is therefore fascinating that Sahnouni et al. (2011) provide palaeoecological data from the Early Pleistocene to test and support the model of Drake et al. (2011). The local occurrence of permanent water bodies in Algeria from 2.6 to 1.7 Ma is indicated by bone remains of hippopotamus, crocodiles, fishes, and turtles (*Mauremys*). In Ain Boucherit, the faunal composition suggests dry woodland and savannahs, while at Ain Hanech and El-Kherba the vegetation structure is inferred as comprising more open woodland. An overall trend towards increased opening of the landscape is inferred from the presence of hypsodont bovines and equids, a tendency that is also substantiated at El-Kherba by the carbon and oxygen isotope records of pedogenic carbonates between levels C, B and A.

The isotopic signal at these sites also points to the prevalence of C<sub>3</sub> plants, both woody and graminoids, with a progressive increase of C<sub>4</sub> vegetation, suggesting heliophytization. It seems reasonable that these landscapes favoured the foraging activities of early humans in North Africa. Sahnouni et al. (2011) suggest that the closer habitat of Level B at Ain Hanech, and the abundance of tools and fossils at this site, is due to access to edible plants and the success of hunting. In contrast, the most recent Level A, with a lower density of archaeological and fossil finds, may suggest a reduced level of human occupation, all associated with dryness,

forest depletion, extended grasslands, and perhaps higher exposure to carnivore predators. Combining the highly sensitive boundary of the Sahara Desert with the most habitable Mediterranean region, northern Africa provides a model geographical system in which to test ecological hypotheses about how, in the past, humans have responded to climatic changes by adaptation and migration (Plummer et al., 2009). This paper by Sahnouni et al. (2011) may provide one of the oldest stories of cultural collapse.

## 6.2. From Africa to the Caucasus and across Eurasia

As with northern Africa, western Asia may have been occupied by streams of migrants on a number of separate occasions. So far, studies have focused on what might have been climatically-forced extinctions of *H. sapiens* and *H. neanderthalensis* in the East Mediterranean Levant (Shea, 2008). For the Early and early Middle Pleistocene, Bar-Yosef and Belmaker (2011) draw attention to the lack of correlation between hominin dispersals and faunal turnovers, and emphasize the difficulties in establishing models of environmental control due to the fragmentary character of the palaeoanthropological record, a factor that may be due partially to the paucity of field research in some regions. It is notable, however, that the Levant has a quasi-continuous record of Acheulean occupation whereas this is lacking for most of the time in the nearby Iranian Plateau and eastern Europe.

Early and Middle Pleistocene humans of western Asia are associated with landscapes that combine open parkland and forest. The paper of Bar-Yosef and Belmaker (2011) discusses the conventional wisdom that the first “Out of Africa” dispersal was associated with the expansion of savannah environments (e.g. Bobe et al., 2002) and demonstrates that this hypothesis is not validated by the evidence, thus hominins and other faunas had a continuous presence. Indeed, Bar-Yosef and Belmaker (2011) take the argument that early *Homo* dispersals were not directly controlled by climatic forcing. In addition, they suggest that the observed differences in knapping and secondary shaping of stone artefacts in the region may reflect the learned traditions of different groups of hominins.

The uniqueness of “*Homo georgicus*” at Dmanisi as an African component within a Eurasian palaeontological assemblage is put forward by Agustí and Lordkipanidze (2011). It would appear, on the basis of a microfauna dominated by gerbils such as *Parameriones* aff. *obeidiensis*, that the Georgian environments during the time of the Dmanisi occupation were warm and dry. Palaeoecological data provided by Messager et al. (2011) through the analysis of pollen, seeds, and phytoliths reinforce the microfaunal records, and show that humid, subtropical woodlands became more heliophytic with grassland at the time of the first human presence at Dmanisi. General climatic trends in western Asia and northern Africa around 1.8 Ma show increased aridity and decreasing temperatures, with associated steppe-like formations. This scenario, according to Agustí and Lordkipanidze (2011), would have not been favourable to the movement of hominins through the Levantine Corridor, and they propose that the expansion to the southern Caucasus would have been more effective during interglacial episodes sometime between 2.4 and 1.9 Ma, which are likely to have been accompanied by the development of forests in the region (Leroy et al., 2011). This hypothesis tackles the long-standing notion that the increase in the brain and body size of early *H. erectus* is due to a migratory capability/tendency (the so-called “brain expansion scenario”) (Ash and Gallup, 2007).

The work of Agustí and Lordkipanidze (2011) gives support to the view that the exit of the first *Homo* species out of Africa cannot be linked to any sort of animal migratory wave, being more likely the result of behavioural particularities by hominins; for instance a definitive and successful tendency to expand their territory. This

point of view is reinforced by O'Regan et al. (2011), who have scrutinized land mammal faunas for 1335 Pliocene and Pleistocene Afro-Eurasian sites, quoting the first appearances of species, genera, and tribes outside and into Africa, and outside Asia, between 3.0 and 0.5 Ma. Only seven “African” genera are recorded in both Europe and Asia, namely *Pachycrocuta*, *Crocuta*, *Panthera*, *Palaeoloxodon*, *Homo*, *Theropithecus* and *Megantereon*, with the plausible addition of *Potamochoerus* and *Hippopotamus*. The majority of these movements happened prior to 3 Ma or between 1.8 Ma and 1.3 Ma. In the case of *Panthera*, *Crocuta*, *Palaeoloxodon* and *Homo*, it must be remarked that they are all found in Asia prior to their first appearance in Europe. Comparatively few taxa moved into Africa during this time period (*Equus*, *Lycan, Antelope, Nyctereutes*), whereas there is instead much more movement between Asia and Europe (e.g. many bovids and cervids) than between Africa and Europe. Thus, the prevailing pattern of dispersal in the Afro–Eurasian Pliocene and Pleistocene was east–west rather than north–south. It is nevertheless not implausible that *H. erectus* could have moved back into Africa, since it is only after 1.3 Ma that Eurasian mammals seem to stop appearing in the African record. A crucial outcome of this large-scale analysis by O'Regan et al. (2011) is that mammal species (including humans), moved individually, rather than in concert, when the environmental conditions were suitable. This is in agreement with Agustí and Lordkipanidze (2011) and it strengthens the notion that humans were not a component of multi-species waves of dispersal.

The veracity of dispersals through the Levantine Corridor does not diminish the plausibility of alternative routes. A southern route for “Out of Africa 2” through the Persian Gulf has been supported at the Palaeolithic site of Jebel Faya in the Arab Emirates. Here, archaeological and palaeohydrological data point to the early presence of modern humans during the MIS 6–5 glacial–interglacial transition, coinciding with low eustatic sea levels and increased rainfall. The implications are, firstly, that the dispersals would have taken place through relatively rapid coastal movements (Stringer, 2000; Bailey et al., 2008), and secondly, that the route from southeastern Arabia to the Persian Gulf followed wadi channels that would have permitted access to fresh water (Armitage et al., 2011). This model for the MIS 6–5 glacial–interglacial transition may well be applicable to the first dispersals out of Africa during similarly favourable episodes of the Early Pleistocene.

The ecological scenario for the first human colonization of Eurasia is examined from a different perspective by van der Made (2011) using evidence of large mammals. This author compiles information for the Levantine Corridor, western Europe and Java, and fails to see evidence of faunal change around or shortly before 1.8 Ma, while the record thereafter of decreasing faunal exchange through the Corridor is indicative of increasing aridity in parallel with the first evidence for social cohesion at Dmanisi (Agustí and Lordkipanidze, 2011). In handling these data, van der Made (2011) postulates that biological evolution and social organisation would have triggered the initial human dispersal rather than environmental change. Examination of trends, rhythms and events in representative dust flux records from the subtropical Atlantic, the eastern Mediterranean Sea, and the Arabian Sea, many of which have high resolution, demonstrates that the first out of Africa event coincides, not with an increase in aridity but climate variability (Trauth et al., 2007). The date of 1.8 Ma, coinciding with a 400 kyr eccentricity maximum, seems to be a key juncture in hominin evolution.

For the period between 1.8 and 1.2 Ma, Van der Made (2011) considers that the forest landscape of central and western European represented a barrier for the westwards dispersal of *Homo*. Like bison and other mammals, *Homo* and its Mode 1 technology appear to have responded to the orbitally-induced climatic change occurring about 1.2 Ma (MIS 37 and 36), which resulted in the

opening of the European woodlands, enabling the spread of humans towards western Europe. Another important physical barrier would have been the aridity of western Asia until around 0.9 Ma, which would have obstructed the dispersal of Acheulean technology from Africa. According to this scenario, the arrival of Acheulean technology to the extreme west (Iberia) would have taken place soon after this climatic change had occurred, and this is supported by bifaces apparently recorded in Cueva Negra around 900 ka (Scott and Gibert, 2009) (Table 2). There were probably many earlier unsuccessful trials, because Acheulean technology is recorded in Israel at c. 1.5 Ma (Bar-Yosef and Belmaker, 2011).

### 6.3. Dispersal and innovation as prompted by environmental variability

A larger spatial scale in combination with a community-level approach is adopted by Kahlke et al. (2011) who present their findings from an impressive mammal record of 221 key sites, and provide a chronicle of the changes recorded in western Palaearctic habitat diversity between 2.6 and 0.4 Ma. These authors discuss the evolutionary trends and long-term consequences of the repeated replacement of extensive woodland by savannah during the period 2.6 to 1.8 Ma, and the alternation of different types of predominantly open habitats between 1.8 and 1.2 Ma. Both of these patterns are climatically controlled by 41 ka temperature periodicity. In contrast, the time span between 0.9 and 0.4 Ma shows longer climatic cycles (100 ka periodicity) and the cyclic replacement of forested landscapes by open landscapes. In contrast, the period from 1.2 to 0.9 Ma is one of increased climatic and habitat instability. Mammal communities responded to these environmental changes, and humans were not an exception.

Kahlke et al. (2011) indicate that human fossil and archaeological sites occur preferentially in situations with a high diversity of habitats and resources, including large river systems. Climate proxies from these sites also provide evidence for mild climates with low seasonality, therefore implying an absence of strong fluctuations in the physical environment. These characteristics are especially visible between 1.7 and 1.3 Ma, when humans spread westward through the Mediterranean region, and subsequently during the early Middle Pleistocene interglacials, when north-western and central Europe are colonized.

Another issue addressed by Kahlke et al. (2011) is related to technological innovation. They argue that more stable environmental conditions would have permitted the low-risk application of proven subsistence strategies, rather than the need to develop new ones. They consider that innovation would have been prompted by high rates of environmental change, such as during the Upper Pleistocene when the western Palaearctic experiences its most unfavourable conditions. This thesis parallels studies of more recent periods. For instance, after examining the distribution of Middle to Upper Palaeolithic transitional industries across Europe from 45 to 30 ka, Finlayson and Carrión (2007) correlated the archaeological location with the presence of sharp physiographical boundaries, suggesting that these industries, made by both Neanderthals and AMHs, were independent responses to rapid climatic changes. These stresses, experienced by human populations across the Palaearctic, would have created a template for innovation that, in the Late Pleistocene, involved trends towards light, portable and projectile technology, able to be carried over long distances, as a means of reducing risk in an unpredictable environment.

### 6.4. Palaeoenvironments of the first human settlement in Europe

Ever since pioneer excavations began under the leadership of Emiliano Aguirre (e.g. Aguirre, 2001), palaeoecological research in

Atapuerca has produced a myriad of publications. However, a synthesis of the environmental proxies was needed, especially in the light of recent dates that have provided a chronological control for the oldest hominin-bearing beds (Carbonell et al., 2008). In this issue, we present two papers from Atapuerca, one for Trinchera del Ferrocarril (Sima del Elefante, Gran Dolina, and Galería) (Rodríguez et al., 2011), and another one for Sima de los Huesos (García and Arsuaga, 2011).

Rodríguez et al. (2011) detail the biotic assemblages at Atapuerca and infer past environments during three time windows defined by cultural and behavioural features. The oldest phase, between 1.2 and 1.0 Ma, corresponds to *H. antecessor* with Mode 1 technology. An intermediate phase, focussed around 800 ka continues the record of *H. antecessor* with Mode 1 technology. The most recent episode, between c. 500 and 200 ka belongs to occupation by *H. heidelbergensis* or early *neanderthalensis* with Mode 2 technology. By using habitat weighting methods as applied to identifications of small vertebrates (amphibians, squamates, and mammals), large mammals, and fossil charcoal and pollen, Rodríguez et al. (2011) fail to detect any relationship between biostratigraphical and palaeoanthropological and cultural changes. Interestingly, although some small-vertebrate communities comprise steppic species such as *Stenocranium gregaloides* and *Allocricetus bursae*, they also coexist with temperate and thermophilous taxa such as *Hystrix refossa* or *Crocidura*. Additionally, a significant woodland component is deduced from herpetofauna analyses, while the macrofaunal assemblages suggest the coexistence of both trees and open landscapes.

Although pollen analyses in the hominin-bearing levels of Atapuerca have been rather unrewarding (García-Antón and Sainz-Ollero, 1991; Burjachs, 2001), such data as are available supports the conclusion of Rodríguez et al. (2011) that Mediterranean and mesothermophilous elements occur continuously throughout the sequence. This is in accord with the concept that a mosaic of landscapes was maintained through the period of occupation including woodlands, open-humid and open-dry meadows, watercourses, rocky habitats and steppe grasslands. This is a refugial scenario in which thermophilous species do not disappear from the assemblages and is of critical importance if due account is given to the long temporal interval (c. one million years) under scrutiny.

In the context of the Iberian Peninsula, this conclusion is thought-provoking. According to Rodríguez et al. (2011), two local faunal changes are detected in the Trinchera sequence: one that peaks at c. 1.0 Ma within the *H. antecessor* stage, and the other one at c. 600–500 ka, thus coinciding with the apparent replacement of *H. antecessor* by *H. heidelbergensis*. It is worth noting that after MIS 36 up to MIS 33, a major extinction of Arctotertiary plants took place in the Iberian Peninsula, including Araliaceae, *Cathaya*, *Elaeagnus*, *Engelhardia*, *Eucommia*, *Liquidambar*, *Keteleeria*, *Nyssa*, *Sciadopitys*, *Symplocos*, *Pretoria*, *Parthenocissus*, *Pterocarya* and *Tsuga* (Postigo et al., 2009). Later, between 800 and 600 ka, others like Mimosaceae, *Carya* and *Ostrya* became extinct. It is clear that the change in glacial cyclicity from 41 ka to 100 ka, which coincided with a fall in temperatures and precipitation, had its effect on the Iberian biota as a whole. The disappearance of Tertiary plant species, which is also discernible in the pollen record of Atapuerca (Rodríguez et al., 2011; Supplementary Information), involved changes in the eco-morphology of the Iberian forests. Certainly, Iberian floras have persisted for a long period of time relative to floras in the rest of Europe, but within the Iberian peninsular the Mid–Pleistocene Transition (MPT) period from 1.4 to 0.7 Ma is, within the last 65 Ma, the period with the highest rates of phytodiversity-loss, even higher than rates measured for the Oligocene and Miocene biodiversity crises (Carrión and Fernández,

2009). It seems that the relationships between the palaeo-anthropological sequence in Atapuerca and the chronology and environmental changes associated with the extinction of plants in the Iberian peninsula, is an issue that merits future research. Recent analyses of the variation in the small vertebrate assemblages of Gran Dolina, in Atapuerca (Cuenca-Bescós et al., 2011) also show changes during the MPT. This study shows a marked biotic shift across the 780 ka boundary, involving a loss of the small vertebrate diversity and leading to the inference that forests were impoverished at the time of that boundary and onwards.

García and Arsuaga (2011) provide palaeoecological information for the interval between 0.9 and 0.4 Ma at Sima de los Huesos (Atapuerca-SH), which represents the best collection of transitional *H. heidelbergensis/neanderthalensis* from anywhere in the world (Arsuaga et al., 1997). Atapuerca-SH comprises a mud-breccia with embedded, well preserved remains of at least 28 human individuals mixed with an assemblage of carnivores (mainly bears (*Ursus deningeri*)) and, to a lesser extent, rodents and insectivores. An overlying speleothem that putatively seals the breccia has been dated by U-series at about 530 ka (Bischoff et al., 2007). To set up the environmental framework for Atapuerca-SH, García and Arsuaga (2011) analyse results from the study of carnivores, ungulates, and stable isotopes, and find that the dominant landscape that existed during this phase was savannah-like open woodland. This conclusion agrees with palynological data obtained from three clay-matrix samples (García-Antón, 1987), which show the prevalence of *Pinus* (40%) and the occurrence of deciduous and evergreen *Quercus*, *Betula* and *Fagus* within a parkland landscape. Additionally, in spite of absence of hyaenas (most likely they were excluded by humans), the diversity of the carnivore assemblage (*Homotherium*, *Ursus*, *Panthera*, *Felis*, *Lynx*, *Vulpes*, *Canis*, *Cuon*, *Meles*, *Mustela*, *Martes*) appears to be the consequence of highly productive ecosystems.

### 6.5. Developments in southern Spain

The human fossil record from Atapuerca represents, to date, the oldest physical evidence of human settlement in Europe, but in the Iberian Peninsula, as in other regions of the circum-Mediterranean, there are open-air archaeological sites with a chronology that has been suggested to be as old as, and even older than Atapuerca. Abundant Mode 1 industry, and possible human remains from the Guadix-Baza Basin sites of Barranco León 5, and Fuente Nueva 3, among other sites of the Orce region, have been dated between 1.4 and 1.1 Ma (Agustí et al., 2009) (Table 2). This chronology is largely established on the basis of magnetostratigraphic studies and micromammal biostratigraphy, and together with the evidence from Atapuerca (Rodríguez et al., 2011), supports the view that the earliest hominins in the Iberian Peninsula occurred in mild, interglacial periods (Agustí et al., 2009; Blain et al., 2009). The localities of the Orce Basin are characterised by the predominance of flakes and debris, cores, and knapped cobbles. Other authors emphasize the uncertainties of the chronological control of the findings (Gibert et al., 2006), pointing out that we can only assert that the sediments that hold the archaeology were deposited during the Matuyama Chron. A similar, but still older palaeontological site in the same region is Fonelas P-1, dated at c. 1.9–1.7 Ma, although so far lacking of human remains (Arribas et al., 2009). A consensus is still needed on the precise chronology of the sites and, in some cases, about the attribution of some bone fragments to hominins (Toro et al., 2009; Martínez-Navarro, 2010). The presence, whether widespread and/or sporadic, of early humans in southeastern Spain at about one million years ago is, however, difficult to deny. In the view of the faunal record and associated ecomorphological and biogeochemical studies (Palmqvist et al., 2008), these early

Europeans may have lived in highly diverse biotopes including open landscapes, but with the prevalence of savannahs, forests, wetlands, and riverine areas. Unfortunately, the vegetational landscapes cannot be reconstructed directly from pollen analyses as this type of study has, so far, proved to be unfruitful (Carrión et al., 2009).

The results from the rockshelter of Cueva Negra del Estrecho del Río Quípar, in the inland part of Murcia province are relevant to this review. A recent study by Scott and Gibert (2009) dates the Acheulean industry of this site at c. 900 ka (Table 2). The human remains (six teeth and two bones attributed to Heidelbergers) are associated with an Acheulean stratigraphical record (Walker et al., 2006) and might be as old as the industry. This new chronological framework leaves open the possibility that these hominins were synchronous with *H. antecessor* of the Gran Dolina and are in fact related to this species. Otherwise the oldest definite Heidelbergers have been found in Ethiopia (Clark et al., 1994) and Germany (Wagner et al., 2010) with ages of about 600 ka. Ongoing excavations in Cueva Negra will hopefully decipher this question. With regard to the ecological scenario, Carrión et al. (2003) have carried out pollen analyses in the site and found a variety of Mediterranean woody species (evergreen and deciduous *Quercus*, *Pinus pinaster*, *Olea*, *Pistacia*, *Phillyrea*, *Arbutus*), and broadleaf trees, some of which are mesothermophilous (*Corylus*, *Fraxinus*), thus suggesting oak-dominated woodlands with pine and juniper, and riparian forests (*Ulmus*, *Salix*), together with a regional pollen signal for steppic areas (*Artemisia*, Poaceae, *Ephedra*), probably in the surrounding highplains. The site is also very rich in faunal remains, including arvicolid rodents, lagomorphs, large mammals (*Stephanorhinus hemitoechus*, *Megaloceros giganteus*, *Bison*, *Macaca sylvanus*), and an impressive avian record with abundance of wetland species (Walker et al., 2006). The general picture is again one of a biodiversity reservoir with access to water bodies and outstanding occurrence of warm-loving species both in vascular plants and vertebrate fauna.

### 6.6. The Italian refugium

Manzi et al. (2011) review the palaeobiological evidence across the Italian Peninsula, making use of pollen and plant macrofossils, large mammals and fossil hominins. These authors organize the discussion into two phases, an initial period of human dispersal during late Early Pleistocene, and a phase of more widespread and stable settlements during the Middle Pleistocene. Although there is no fossil record of humans during the Early Pleistocene in Italy, their presence is inferred from Mode 1 techno-complexes, reported first in the Apulian site of Pirro Nord at c. 1.5–1.3 Ma, in association with faunal remains (Arzarello et al., 2009). Functional turnovers in the mammalian fauna have led to the suggestion that the late Early Pleistocene hominins of sites like Pirro Nord and Colle Curti FU, expanded through the Italian Peninsula during a time of climatic instability which became advantageous for generalist faunas (Manzi et al., 2011). This climatic scenario was accompanied by openings of the woodlands, with a latitudinal pattern that started in the south. Sites such as Monte Poggiolo and Castagnone in the Ceprano Basin, which are dated at about 1 Ma, fall within this pattern. The late Early Pleistocene was also a time when Tertiary floras including genera like *Sequoia*, *Cathaya*, *Liquidambar*, *Eucommia*, *Parrotia*, *Nyssa*, and *Aesculus* became extinct in the Italian peninsula. It is suggested that the small number of archaic hominins living at this time possibly behaved opportunistically as scavengers with poor technological equipment, related to the activities of megahunters like the lion-sized hyaena *Pachycrocuta brevirostris* and the big felids *Homotherium* and *Megantereon*.



The pollen record for the period 1.4–1.07 Ma from Monte Poggiolo (Messager et al., 2011) is described and provides a picture of vegetational developments in the southern Po Plain and Apennine mountains prior to human occupation. These landscapes generally include extensive open grasslands and steppe with *Artemisia* and chenopods. However, there are signs of coniferous (*Pinus*, *Abies*, *Tsuga*, *Picea*, *Cedrus*), and rich angiosperm (e.g. *Quercus*, *Fagus*, *Castanea*, *Carpinus*, *Alnus*, *Betula*, *Juglans*, *Carya*) forests and scrub. Indisputably, the Italian Peninsula behaved at this time as a glacial refugium for temperate trees.

The first fossil record of humans in Italy is in the Middle Pleistocene. These are, however, outstanding for the period between c. 500 to 350 ka, including renowned sites like Visogliano, Fontana Ranuccio, Pofi and the tantalizing Ceprano calvarium, which is now attributed to an ancestral stock of *H. heidelbergensis* dated at about 400 ka (Manzi et al., 2011). This occurrence is probably the final result of the so-called MPR, which involved faunal turnover, decrease in frequency of carnivorous competitor species, landscape fragmentation, and a major change in the vegetation composition of interglacials after MIS 16, with forests becoming dominated by *Quercus* and *Carpinus*. This second wave of human colonisation, lasting until the appearance of the Neanderthals, is characterized by *H. heidelbergensis* and associated Acheulean (Mode 2) technology, involving more efficient hunting and opportunistic omnivory. Neanderthal finds in Italy include the site of Castel di Guido, near Rome, which is dated to between 350 and 125 ka (Manzi et al., 2011). This site and a number of other human fossil sites in Italy, exhibit features suggesting mosaic evolution and gene transfer among peninsular populations.

#### 6.7. The Mediterranean basin: facilitated dispersals during the glacial-interglacial transitions

Early to Middle Pleistocene vegetation changes, leading to the fragmentation of forested landscapes and the development of more open landscapes are not exclusive of the Iberian and Italian peninsulas, but are a general feature of the Mediterranean region. Leroy et al. (2011) develop this concept and its consequences in terms of human palaeogeography during the early Pleistocene, using a 9 ka simulation of the atmospheric general circulation model ECHAM5 coupled with the ocean general circulation MPI-OM, and a dynamic vegetation model. These authors conclude that the best opportunities for the colonisation of the circum-Mediterranean areas by humans and large herbivore herds are during the glacial-interglacial transitions. It is at these times that the landscapes were still open due to uneven rates of colonisation by the tree species that were entering the region during forest development. Since distance and speed of migration are not limiting factors, this situation could hypothetically repeat itself as many as 42 times during the course of the Early Pleistocene. It is clear, however, that at least for some southern regions of the Mediterranean, humans were able to survive the various conditions of a full climatic cycle.

#### 6.8. Northern Europe: occupation during interglacials

To the north of the Mediterranean region, human occupation coincides with interglacials. The case of Mauer is graphic (Wagner et al., 2011). Here, the micromammal fauna includes *Petaurina* and *Myodes*, which suggest forest, while other taxa rather indicate open (*Lepus*, *Cricetus*, *Microtus*), and aquatic habitats (*Drepanosorex*, *Castor*, *Trogontherium*). Large mammal faunas (e.g. *Hippopotamus amphibius*, *Sus*, *Capreolus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus kirchbergensis*, *Cervus*) also point to warm temperate climate conditions with proximity to rivers, openings in the

woodland and open waters, and the absence of permanently frozen water in winter. Cold-adapted species are lacking among both large and small mammals. The putative artefact collection at Mauer suggests that humans manufactured tools from flint pebbles, hunted, and perhaps fished, along these floodplains. This pattern is considered typical of interglacial conditions such as MIS 15 in the regions north of the Alps and the Pyrenees (Wagner et al., 2011).

This scenario may well be extrapolated to Britain for the interglacials of the early Middle Pleistocene (MIS 19–12). Overall, the lithic records of Happisburgh 3 (Parfitt et al., 2010) and Pakefield (Parfitt et al., 2005), Happisburgh 1, High Lodge, Warren Hill, Waverley Wood, Boxgrove, Kent's Cavern, and Westbury-sub-Mendip, are associated with biological and geological indicators of warm and cool temperate climates, as well as a mosaic of open to woodland habitats (Hosfield, 2011). Another general feature is the occurrence of still and flowing water in most settings, and a rich array of plant and animal resources available for exploitation. It is nonetheless worth emphasizing that, in contrast with southern European sites, the British localities are characterised by sub-freezing mean temperatures in the winter months. Subsistence evidence is restricted to a few sites, with Boxgrove providing the strongest suggestion of co-operative hunting in MIS 13. Rose (2009) has provided detailed information on the geological, climatic, and ecological changes associated with human occupation in this period. There is evidence for high biomass production occurring over short intervals coinciding with the temperate part of MIS 19, 17, 15, 13, of the early Middle Pleistocene, and during most of these warmer periods, extending back to at least c. 990–780 ka (MIS 25, MIS 21) there are signs in the region for the brief appearance of humans (Parfitt et al., 2010).

## 7. Processes of evolutionary change forced by environmental changes

### 7.1. A “source-sink dynamics” model for Palaeolithic Europe

Palaeoanthropology needs models of evolutionary change that are consistent with the palaeoecological evidence, the human fossil record, and the archaeological data in order to understand the tantalizing morphological variability of *H. heidelbergensis* in the changing world of the European Middle Pleistocene (Hublin, 2009; Mounier et al., 2009; Arsuaga, 2010). Dennell et al. (2011) develop such a model to explain hominin population dynamics in response to the climatic and environmental disruption of this period. Their reasoning can be summarized as follows: (i) European hominins were distributed in both core (“source”) and peripheral (“sink”) populations, (ii) peripheral populations, which can be viable during interglacials and interstadials, become dead-ends and extinct with climatic deterioration, (iii) core populations often survived in southern European refugia, but occasionally during some coldest episodes, also become extinct. In this case, Europe becomes depopulated and recolonization takes place from western Asian nuclei, (iv) at a continental scale, incessant migration from source to sink habitats would have stabilized the demographic system regardless of low population densities at certain times, and (v) the evolutionary outcome was not allopatric speciation because hominin populations behaved like “tidal islands”, that is, isolation phases were followed by interbreeding phases.

This source-sink model may explain the morphological differences between Heidebergs and early Neanderthals during the Middle Pleistocene, and also the fact that taxonomic similarity, in the form of palaeospecies, was maintained. This model also supports the idea that persistent isolation and repeated genetic bottlenecks led to a drastic reduction in the phenotypic variability and genetic viability of Neanderthals, contributing to their global

extinction (Jiménez-Espejo et al., 2007; Finlayson et al., 2008). This model requires that glacial refugia should be considered as bottlenecks (Bennett and Provan, 2008), that is, areas for survival, rather than locations for retreat. In addition, Dennell et al. (2011) consider that Palaeolithic Europe should not be considered as a closed system, but can be better conceptualized as an open system, as part of the Eurasian landmass. In this context, it would have experienced numerous episodes of immigration throughout the Pleistocene. The arrival and spread of our own species demonstrates this case (Finlayson and Carrión, 2007). Similarly, at a smaller geographical scale, Shea (2008) has shown that the Levant has witnessed turnovers in both Neanderthals and AMHs populations during the Upper Pleistocene, probably forced by decreases in temperature and humidity that would have controlled the capacity of the region to support stable hominin populations. It is also likely that northern Africa, or for Moderns western Asia, would have acted as donor areas.

### 7.2. The selective value of habitat mosaics

Palaeoecological reconstruction for human-bearing sites is often based on qualitative descriptions using fossil mammal and plant proxies. In this Special Issue of QSR, Finlayson et al. (2011) provide a quantitative palaeoecological reconstruction and model by using a database of 79 *Homo* occupation sites with associated bird fossils from the Palaeartic region. An inspection of the relative percentages of major habitat categories supports the view that a close association exists between human occupation sites and wetland sites, including lakes, lagoons and marshes. Another conclusion is that, from Lower to Upper Palaeolithic, there is a shift towards intense seasonal or sporadic habitat occupation of regions such as tundra and the coast, as well as, from Middle Palaeolithic onwards, an increased use of caves during periods of climatic deterioration. In general, single habitat sites have been ignored by humans throughout the Palaeolithic. In contrast, the observed pattern across this wide geographical area and over the entire period of *Homo* occupation indicates a specific and clear association between *Homo* and ecologically rich, semi-open savannah-type ecotonal and mosaic landscapes. Wetlands, coastal and rocky habitats are a regular and prominent component of this landscape.

This conclusion is reinforced by research in Africa and in the western Palaeartic at sites such as Dmanisi, Monte Poggiolo and Pont-de-Lavaud (Messager et al., 2011), Ain Hanech and El-Kherba (Sahnouni et al., 2011), Ubeidiya (Bar-Yosef and Belmaker, 2011), and Atapuerca (García and Arsuaga, 2011; Rodríguez et al., 2011). In the case of Dmanisi, notwithstanding the temporal variation in the pollen frequencies, the long sequence shows the coexistence of heliophytic herbaceous plants with shrubs and arboreal taxa with different ecological requirements, like *Pinus*, *Cedrus*, *Quercus*, *Carpinus*, *Castanea*, *Juglans*, *Platanus*, *Pterocarya*, *Corylus*, *Fraxinus*, *Fagus* and *Tilia* (Messager et al., 2011). Eastwards in Asia, the situation is similar. *H. erectus* in the Solo Basin, central Java (between 1.6 and 1.02 Ma) is associated with low-relief lake margins dominated by moist grasslands with open woodland and savannah in the driest landscape positions (Bettis et al., 2009). At the more humid Javanese site of Trinil (1.5 Ma) the ecological mosaic for *H. erectus* includes grasslands, near-coastal rivers, lakes, swamp forests, lagoons, and marshes (Joordens et al., 2009). As at Dmanisi (Agustí and Lordkipanidze, 2011), all these areas supported a very diverse fauna. It seems that *Homo* was flexible in its habitat use, and therefore active in a wide range of environments, from open grassland and savannahs to riparian forests and mountain woodlands. This flexibility means that *Homo* had increased adaptive capability by which it was possible to draw resources from a miscellany of ecological scenarios.

### 7.3. The role of geological instability combined with topographic complexity

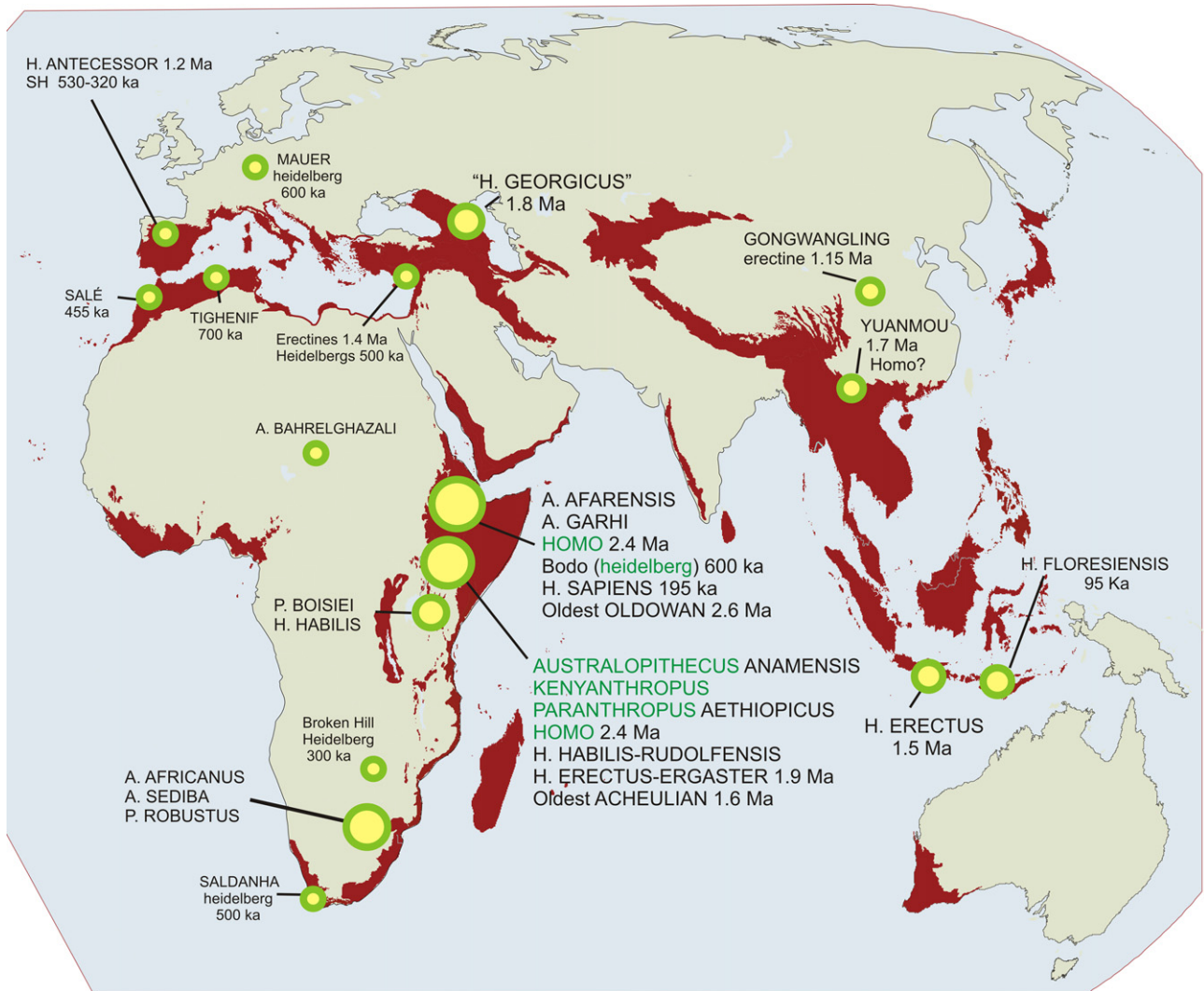
Geological setting is obviously a determinant factor for habitat diversity. While the influence of climatic on human evolution has been widely acknowledged and investigated, the role of topography, especially when linked to the study of geomorphological processes, has seldom been studied. However, these features are of critical importance to understanding evolutionary trajectories. Bailey and King (2011) use field and remote sourced imagery from Africa and the Red Sea region to investigate the relationship of active tectonics and complex topography with archaeological and fossil material. Their methodologies are valid for a broad range of geographical scales, and have potential for future studies of different “Out of Africa” frameworks of human dispersal.

The conclusions of this study are outstanding for hominin ecology: regions that are geologically dynamic will favour the creation and maintenance of mosaic habitats through time. This conclusion exists despite the fact that such regions have intrinsic potential for catastrophic events. It follows that coastlines will be ecologically attractive to humans, and the case studies that have reconstructed past environments along coastal zones support this thesis with a picture of biological disparity and geological complexity (Carrión et al., 2008; Finlayson et al., 2008). The coastal zone has been also been proposed as a corridor for past human expansion (Bailey et al., 2008; Stringer et al., 2008). Coastal environments, especially in tectonically active areas, may also represent refugial territories for European human populations during cold stages of the Pleistocene. Thus, the progressive Neanderthal extinction follows a clear continental to oceanic direction, ending in southern Iberia (Finlayson, 2008).

### 7.4. Was evolutionary change in hominins stimulated within biodiversity hotspots?

We complete this review by addressing the non-debated question of whether the appearance of evolutionary novelties within hominins is concentrated in regions of highest worldwide biological diversity. This question arises from visual inspection of early hominin sites as falling on a map of biodiversity hotspots [http://www.biodiversityhotspots.org/xp/hotspots/Documents/cihotspot\\_map.pdf](http://www.biodiversityhotspots.org/xp/hotspots/Documents/cihotspot_map.pdf) (Fig. 1). Hotspots are regions that contain at least 1500 endemic plant vascular species and have lost at least 70% of their original natural habitat (Spathef and Waite, 2007). Collectively, these areas are endemic to no less than 44% of the world's plants and 35% of terrestrial vertebrates (Brooks et al., 2002). It is assumed that the current areas occupied by hotspots are the remnants of larger territories that have been functioning like engineers of plant and animal diversity over the entire Quaternary and probably long before (Kikvidze and Ohsawa, 2001; Carrión et al., 2006), although it is noted that these regions would shift in focus and extent in response to changes in Quaternary climate (Fig. 1).

The Horn of Africa hotspot and its southern fringes in Kenya and Tanzania embrace the earliest occurrences for genera and most of the earliest for species of fossil hominins. These include *Ardipithecus*, *Orrorin*, *Australopithecus*, *Kenyanthropus*, *Paranthropus*, and *Homo*. At species level they include *Ardipithecus kadabba*, *A. ramidus*, *Australopithecus afarensis*, *A. garhi*, *A. anamensis*, *Kenyanthropus platyops*, *Paranthropus aethiopicus*, *Homo habilis-rudolfensis*, *H. erectus-ergaster* and *H. sapiens* (Fig. 1). This region may also be the place for speciation of Heidelbergers (e.g. Bodo, Middle Awash valley of Ethiopia), and embody the oldest Oldowan and Acheulean tools at 2.6 and 1.6 Ma, respectively. Several other australopithecines (*Australopithecus africanus*, *Australopithecus sediba*, *Paranthropus robustus*) are only known in southern Africa,



**Fig. 1.** Earliest occurrences of hominin fossils, Oldowan (Mode 1) and Acheulian (Mode 2) lithic technologies, and distribution of biodiversity hotspots (in red) (<http://www.biodiversityhotspots.org/xp/hotspots/Documents/cihotspotmap.pdf>), excluding the Americas. For further information on fossil specimens, localities, and references, see Tables 1 and 2.

inland of the Coastal Forests of the Southern Africa hotspot. *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali* do not fit in this geographic frame, being located in the interior of north Africa in the region of Chad.

Within the western Palearctic, the Caucasus includes the first *Homo* occurrences in Eurasia at the site of Dmanisi, dated at ~1.8 Ma (Fig. 1). The Caucasus hotspot is a magnificent example of habitat heterogeneity. This eco-region comprises the Caucasus Ranges, the South Caucasian Uplands, and the Transcaucasian Depression. Climates are extremely variable, with annual rainfall today ranging from as little as 150 mm in the eastern part of the hotspot on the Caspian Coast to more than 4000 mm in the coastal mountains along the Black Sea. The vegetation exhibits high diversity of species (1600 endemics) and communities, including deserts, semi-deserts, grassland steppes, shrublands, arid woodlands, montane coniferous forests, broadleaf forests, swamp forests, together with two refugia of Tertiary flora, the Colchic and the Hyrcanian (Kreuer et al., 2001). These biotopes and characteristics are replicated in the early Pleistocene ecological record (Agustí and Lordkipanidze, 2011; Messager et al., 2011).

*H. antecessor* from Atapuerca, dated at 1.2 Ma is in the Mediterranean hotspot, where important human fossils are also noticed at such sites as the SH-Atapuerca, Ubeidiya, and in northern Jordan (Fig. 1, Table 1). The fossil remains from Yuanmou, dated to c. 1.7 Ma (Zhu et al., 2008), are also allocated in the high biodiversity hotspot of the Mountains of Southwestern China. With the exception of *Sahelanthropus*, the robust southern African australopithecines, and *Homo neanderthalensis* (whose geographic origin is unknown), the remaining fossil human taxa occur first within the context of biodiversity hotspots.

Following from the above discussion the question arises as to why a hotspot should have significance for hominin speciation or morphological innovation? Firstly, the fact that hotspots can be associated with dynamic landscapes (Bailey and King, 2011), are sensitive to climate, and support a wide array of habitats (Sechrest et al., 2002) is likely to enhance species richness, especially in the case of mammals which would be favoured by the appearance of novel configurations (Kingston, 2007). Secondly, hotspots are not only areas of high species richness, but they also contain large amounts of evolutionary history which can be the source of phylogenetic diversity for primates (Spathelf and Waite, 2007).

Thirdly, biodiversity hotspots are regions with high levels of ecological interaction and biotic complexity, which are prime factors affecting diversification by inducing speciation and reducing extinction rates (Ricklefs, 2010). For instance, mutual interactions have been demonstrated to be a potential diversification driver (Yoder and Nuismer, 2010) and co-evolutionary networks can indeed facilitate the maintenance of biodiversity (Bascompte et al., 2006).

In summary, the key factors activating evolutionary change may have been geological instability, and a shifting physiographical heterogeneity in association with high biodiversity and ecological interaction. In this model, climate change is a general driving force. In the construction of palaeoecological theses for human evolution, Kingston (2007) suggests that orbital forcing is a principal organizational factor that determines the assemblage of high resolution environmental proxies that will, in time, provide the evidence for the patterns of heterogeneity through time.

It is proposed that most hominin species may have been derived from small, speciating populations in Africa, which may have developed in geographical isolation from an ancestral stock. Hominin evolution in Africa can be seen as a number of speciation events, and these would have operated as drivers of human phylogeny (Vrba et al., 1995; Gould, 2002; Vrba, 2005, 2006). From these, new species would have migrated out of the original region and, in some cases like *H. erectus*, *H. heidelbergensis* and *H. sapiens*, spread throughout the habitable world focussing, where convenient, on particular biodiversity hotspots. According to this model the western Palaearctic is a territory that has received the products of long distance dispersal and has experienced minor evolutionary changes when compared to eastern Africa, although intra-Asiatic speciation is certainly also plausible (Dennell and Roebroeks, 2005).

Allopatric speciation should not be considered exclusive. It is likely that different species were able to live within the same region for long periods of time as in the case of *H. habilis* and *H. erectus* in the region of Lake Turkana (for perhaps 500 ka, Spoor et al., 2007). Similar situations can be conceived in Dmanisi (Lordkipanidze et al., 2007) and in other Eurasian contexts (Finlayson, 2009). It is now well-known that rapid sympatric speciation, which is identified by high levels of genomic differentiation in the early stages, can occur when the incipient species coexist and interbreed (Andrew et al., 2010). In fact, genes subject to strong divergent selection between incipient species, such as those relevant for habitat choice, can create differentiated regions in the genome (Kelleher and Barbash, 2010).

These are working hypotheses. For while the idea of ecological attractiveness has explanatory power, we do not yet understand how the described sets of physical and biotic impacts operate and interact to produce evolutionary novelties. Modular evolution associated with taxon-specific evolutionary changes in developmental patterns (Zollikofer and Ponce de León, 2009), and the role of highly improbable events (Whitten, 2010) may have been dramatically underrated. Paraphrasing Stephen Jay Gould (Gould, 1995, p. 103): “a species will arise in a single place and then move along an unexpected pathway. In short, all my non-surprises are coordinated by a worldview that celebrates quick and unpredictable changes in a fossil record featuring lineages construed as largely independent historical entities. I should add that I find such a world stunning and fascinating in its chaotic complexity and historical genesis.”

## Acknowledgements

We thank our contributor authors for their dedication to this Special Issue of QSR. This issue has been produced under the

auspices of several research projects funded by the National Plan of Research and Development of the Spanish Ministry of Science, and the Séneca Foundation (Murcia). Among these, the IBERIAN PALAEOFORAS I and II (CGL-2006-2956-BOS, CGL-2009-6988), PALEODIVERSITAS network, and ECOCHANCE Séneca projects have become of crucial importance. Chris Stringer is a Member, and James Rose an Associate Member, of the Ancient Human Occupation of Britain project, funded by the Leverhulme Trust. The Editor-in-Chief, Colin Murray-Wallace is greatly acknowledged for his continuous advice and we are indebted to Debbie Barrett who has solved all our problems from the Elsevier Editorial Office.

## References

- Aguirre, E., 2001. Early human expansions into Eurasia: the Atapuerca evidence. *Quaternary International* 75, 11–18.
- Aguirre, E., 2008. Homo Hispánico. Espasa Calpe. Espasa Forum, Madrid.
- Agustí, J., Blain, H.A., Cuenca-Bescos, G., Ballon, S., 2009. Climate forcing of first hominid dispersal in Western Europe. *Journal of Human Evolution* 57, 815–821.
- Agustí, J., Lordkipanidze, D., 2011. How “African” was the early human dispersal out of Africa. *Quaternary Science Reviews* 30, 1338–1342.
- Alpers-Afil, N., Sharon, G., Kislev, M., Melamed, Y., Zohar, I., Ashkenazi, S., Rabinovich, R., Biton, R., Werker, E., Hartman, G., Feibel, C., Goren-Inbar, N., 2009. Spatial organization of hominin activities at Gesher Benot Ya'aqov, Israel. *Science* 326, 1677–1680.
- An, Z., Ho, C.K., 1989. New magnetostratigraphic dates of Lantian *Homo erectus*. *Quaternary Research* 32, 213–221.
- Andrew, P.M., Sim, S., Powell, T.H.Q., Taylor, M.S., Nosil, P., Feder, J.L., 2010. Widespread genomic divergence during sympatric speciation. *Proceedings of the National Academy of Sciences USA* 107, 9724–9729.
- Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing. *Palaeogeography, Palaeoclimatology, Palaeoecology* 241, 572–589.
- Armitage, S.J., Jasim, S.A., Marks, A.E., Parker, A.G., Usik, V.I., Uerpmann, H.-P., 2011. The southern route “Out of Africa”: evidence for an early expansion of Modern Humans into Arabia. *Science* 331, 453–456.
- Arribas, A., Garrido, G., Viseras, C., Soria, J.M., Pla, S., Solano, J.G., Garcés, M., Beamud, E., Carrión, J.S., 2009. A mammalian lost world in southwest Europe during the late Pliocene. *PLoS ONE* 4, e7127. doi:10.1371/journal.pone.0007127.
- Arsuaga, J.L., 2010. Terrestrial apes and phylogenetic trees. *Proceedings of the National Academy of Sciences USA* 107, 8910–8917.
- Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 1997. The Sima de los Huesos hominid Site. *Journal of Human Evolution* 33, 105–421.
- Arzarello, M., Peretto, C., 2010. Out of Africa: the first evidence of Italian peninsula occupation. *Quaternary International* 224, 65–70.
- Arzarello, M., Marcolini, F., Pavia, G., Pavia, M., Petronio, C., Petrucci, M., Rook, L., Sardella, R., 2009. L'industrie lithique du site Pléistocène inférieur de Pirro Nord (Apricena, Italie du sud): une occupation humaine entre 1,3 et 1,7 Ma. *L'Anthropologie* 113, 47–58.
- Asfaw, B., Beyene, Y., Suwa, G., Walter, R.C., White, T., WoldeGabriel, G., Yemane, T., 1992. The earliest Acheulean from Konso-Gardula. *Nature* 360, 732–735.
- Asfaw, B., White, T., Lovejoy, C.O., Latimer, B., Simpson, S., Suwa, G., 1999. Australopithecus garhi: a new species of early hominid from Ethiopia. *Science* 284, 629–635.
- Ash, J., Gallup, G.G., 2007. Paleoclimatic variation and brain expansion during human evolution. *Human Nature* 18, 109–124.
- Ashton, N.M., Cook, J., Lewis, S.G., Rose, J., 1992. High Lodge: Excavations by G. de G Sieveking, 1962–8, and J. Cook, 1988. British Museum Press, London, pp. 192.
- Ashton, N., Parfitt, S.A., Lewis, S.G., Coope, G.R., Larkin, N., 2008. Happisburgh site 1 (TG388307). In: Candy, I., Lee, J.R., Harrison, A.M. (Eds.), *The Quaternary of Northern East Anglia: Field Guide*. Quaternary Research Association, London, pp. 151–156.
- Bailey, G., King, G.C.P., 2011. Dynamic landscapes and human dispersal patterns: tectonics, coastlines, and the reconstruction of human habitats. *Quaternary Science Reviews* 30, 1533–1553.
- Bailey, G., Carrión, J.S., Fa, A.D., Finlayson, C., Finlayson, G., Rodríguez-Vidal, J., 2008. The coastal shelf of the Mediterranean and beyond: corridor and refugium for human populations in the Pleistocene. *Quaternary Science Reviews* 27, 2095–2099.
- Bar-Yosef, O., Belmaker, M., 2011. Early and middle Pleistocene faunal and hominins dispersals through Southwestern Asia. *Quaternary Science Reviews* 30, 1318–1337.
- Bar-Yosef, O., Pilbeam, D., 1993. Dating hominid remains. *Nature* 366, 415.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Begun, D.R., 2007. Fossil record of Miocene hominoids. In: Henke, W., Tattersall, I. (Eds.), *Handbook of Palaeoanthropology, Primate Evolution and Human Origins*, Vol. 2. Springer, Berlin, pp. 921–977.
- Belmaker, M., Tchernov, E., Condemi, S., Bar-Yosef, O., 2002. New evidence for hominid presence in the Lower Pleistocene of the southern Levant. *Journal of Human Evolution* 43, 43–56.

- Bennett, K.D., Provan, J., 2008. What do we mean by "refugia". *Quaternary Science Reviews* 27, 2449–2455.
- Berger, G.W., Pérez-González, A., Carbonell, E., Arsuaga, J.L., Bermúdez de Castro, J.M., Ku, T.L., 2008. Luminiscence chronology of cave sediments at the Atapuerca paleoanthropological site, Spain. *Journal of Human Evolution* 55, 300–311.
- Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmid, P., Carlson, K.J., Dirks, P.H.G.M., Kibii, J.M., 2010. *Australopithecus sediba*: a new species of Homo-like Australopithecine from South Africa. *Science* 328, 195–204.
- Bermúdez de Castro, J.M., Martínón-Torres, M., Gómez-Robles, A., Margelashvili, A., Sarmiento, S., 2009. Gli Omini dei Atapuerca. Sima de los Huesos e le Origini dei Neandertaliani. In: Facchini, F., Belcastro, G. (Eds.), *La Lunga Storia di Neandertal*. Editoriale Jaca Book Spa, Milan, pp. 61–75.
- Bettis, E.A., Milius, A.K., Carpenter, S.J., Larick, R., Zaim, Y., Rizal, Y., Ciochon, R.L., Tassier-Surine, S.A., Murray, D., Suminto, Bronto, S., 2009. Way out of Africa: early Pleistocene paleoenvironments inhabited by *Homo erectus* in Sangiran, Java. *Journal of Human Evolution* 56, 11–24.
- Bischoff, J.L., Williams, R.W., Rosenbauer, R., Aramburu, A., Arsuaga, J.L., García, N., Cuenca-Bescós, G., 2007. High-resolution U-series dates from the Sima de los Huesos hominids yields: implications for the evolution of the early Neandertal lineage. *Journal of Archaeological Science* 34, 763–770.
- Blain, H.A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from early–middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca, Spain. *Journal of Human Evolution* 56, 55–65.
- Blumenscheine, R., Peters, R., Masao, M., Clarke, R., Deino, A., Hay, R., Swisher, C., Stanistree, I., Ashley, G., McHenry, L., Sikes, N., van der Merwe, N., Tactikos, J., Cushing, A., Deocampo, D., Njau, J., Ebert, J., 2003. Late Pliocene *Homo* and hominid land use of western Olduvai Gorge, Tanzania. *Science* 299, 1217–1221.
- Bobé, R., Behrensmeyer, A.K., Chapman, R.E., 2002. Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* 42, 475–497.
- Bonnefille, R., Potts, R., Chalié, F., Jolly, D., Peyron, O., 2004. High-resolution vegetation and climate change associated with Pliocene *Australopithecus afarensis*. *Proceedings of the National Academy of Sciences USA* 101, 12125–12129.
- Bradley, R.S., 1999. *Paleoclimatology. Reconstructing Climates of the Quaternary*. Academic Press, San Diego.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16, 909–923.
- Brunet, M., Beauvilain, A., Coppens, Y., Heintz, E., Moutaye, A.H.E., Pilbeam, D., 1996. *Australopithecus bahrelghazali* une nouvelle espèce d'hominidé ancien de la région de Koru Toro (Tchad). *Comptes Rendus de l'Académie des Sciences Paris* 322, 907–913.
- Brunet, M., Guy, F., Pilbeam, D., Lieberman, A., Likius, H., Mackaye, M., Ponce de León, M., Zollikofer, C., Vignaud, P., 2002. A new hominid from the Upper Miocene of Chad, Africa. *Nature* 418, 145–152.
- Burjachs, F., 2001. Paleoeología del Homo antecessor: Palinología de las unidades TD5, 6 y 7 de la "Gran Dolina" de Atapuerca (Burgos, España). *Actas del XII Simposio de la Asociación de Palinólogos en Lengua Española (A.P.L.E.)*. Universidad Politécnica de Cartagena. 365–372.
- Candy, I., Coope, G.R., Lee, J.R., Parfitt, S.A., Preece, R.C., Rose, J., Schreve, D.C., 2010. Pronounced warmth during early middle Pleistocene interglacials: Investigating the Mid-Brunhes event in the British terrestrial sequence. *Earth Science Reviews* 103, 183–196.
- Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martínón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergés, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. *Nature* 452, 465–469.
- Carrión, J.S., Scott, L., 1999. The challenge of pollen analysis in palaeoenvironmental studies of hominid beds: the record from Sterkfontein Caves. *Journal of Human Evolution* 36, 401–408.
- Carrión, J.S., Fernández, S., 2009. Taxonomic depletions and ecological disruption of the Iberian flora over 65 million years. *Journal of Biogeography* 36, 2023–2024.
- Carrión, J.S., Fernández, S., González-Sampériz, P., Leroy, S.A.G., López-Sáez, J.A., Burjachs, F., Gil-Romera, G., García-Antón, M., Gil-García, M.J., Parra, I., Santos, L., López-García, P., Yll, E.I., Dupré, M., 2009. Sterility cases and causes in Quaternary pollen analysis in the Iberian Peninsula: the advantages of reporting bad luck. *Internet Archaeology* 25, 1–22.
- Carrión, J.S., Finlayson, C., Finlayson, G., Fernández, S., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations. *Quaternary Science Reviews* 27, 2118–2135.
- Carrión, J.S., Fuentes, N., Fernández, S., 2006. Una perspectiva paleobotánica –y por tanto, heterodoxa, para las grandes extinciones. In: Carrión, J.S., Fernández, S., Fuentes, N. (Eds.), *Paleoambientes Y Cambio Climático*. Quaderna. Fundación Séneca, Agencia Regional de Ciencia y Tecnología, Murcia, pp. 31–53.
- Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A., Chain, C., López, A., 2003. Glacial refugia of temperate, Mediterranean and Ibero North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. *Global Ecology and Biogeography* 12, 119–129.
- Cartmill, M., Smith, F.H., 2009. *The Human Lineage*. Foundations of Human Biology. Wiley-Blackwell, New Jersey.
- Carto, S.L., Weaver, A.J., Lam, Y., Wiebe, E.C., 2008. Out of Africa and into an ice age: on the role of global climate change in the late Pleistocene migration of early modern humans out of Africa. *Journal of Human Evolution* 234, 1–13.
- Churchill, S., Pearson, O., Grine, F., Trinkaus, E., Holliday, T., 1996. Morphological affinities of the proximal ulna from Klasies River Main site: archaic or modern. *Journal of Human Evolution* 31, 213–237.
- Clark, J.D., de Heinzelin, J., Schick, K., Hart, W., White, T., WoldeGabriel, G., Walter, R., Suwa, G., Asfaw, B., Vrba, E., Haile-Selassie, Y., 1994. African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle Awash Valley, Ethiopia. *Nature* 264, 1907–1910.
- Clark, J.D., Beyenne, Y., WoldeGabriel, G., Hart, W., Renne, P., Gilbert, H., Aefluer, A., Suwa, G., Katoh, S., Ludwig, K., Boissérie, J., Asfaw, B., White, T., 2003. Stratigraphic, chronological and behavioural contexts of Pleistocene *Homo sapiens* from middle Awash, Ethiopia. *Nature* 423, 747–752.
- Clarke, R., 1976. New cranium of *Homo erectus* from Lake Ndutu, Tanzania. *Nature* 262, 485–487.
- Crochet, J.Y., Welcomme, J.L., Ivorra, J., Ruffet, G., Boulbes, N., Capdevila, R., Claude, J., Firmat, C., Métais, J., Michaux, J., Pickford, M., 2009. Une nouvelle faune de vertébrés continentaux, associée à des artefacts dans le Pléistocène inférieur de l'Hérault (Sud de la France), vers 1,57 Ma. *Comptes Rendus Palevol* 8, 725–736.
- Cuenca-Bescós, G., Melero-Rubio, M., Rofes, J., Martínez, I., Arsuaga, J.L., Blain, H.A., López-García, J.M., Carbonell, A., Bermúdez de Castro, J.M., 2011. The Early-Middle Pleistocene environmental and climatic change and the human expansion in western Europe: a case study with small vertebrates (Gran Dolina, Atapuerca, Spain). *Journal of Human Evolution* 60, 481–491.
- Dart, R., 1925. *Australopithecus africanus*: the man-ape of South Africa. *Nature* 115, 195–199.
- de Heinzelin, J., Clark, J.D., White, T., Hart, W., Renne, P., WoldeGabriel, G., Beyene, Y., Vrba, E., 1999. Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284, 625–629.
- de Lumley, M.A., 1973. Anténéandertaliens et Néandertaliens du Bassin méditerranéen occidental européen. *Etudes Quaternaires* 2, 1–626.
- de Lumley, H., de Lumley, M.A., 1971. Découverte de restes humains anté-neandertaliens dates du début du Riss à la Caune de l'Arago (Tautavel, Pyrénées Orientales). *Comptes Rendus de l'Académie des Sciences, Paris* 272, 1739–1743.
- de Lumley, M.A., Gabounia, L., Vekua, A., Lordkipanidze, D., 2005. Les restes humains du Pliocène final et du début du Pléistocène inférieur de Dmanisi, Géorgie (1991–2000). *L'Anthropologie* 110, 1–110. I. Les crânes, D 2280, D2282, D2700.
- de Ruiter, D.J., Pickering, R., Steininger, C.M., Kramers, J.D., Hancox, P.J., Churchill, S.E., Berger, L.R., Backwell, L., 2009. New *Australopithecus robustus* fossils and associated U-Pb dates from Cooper's cave (Gauteng, south Africa). *Journal of Human Evolution* 56, 497–513.
- deMenocal, P.B., 2004. African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220, 3–24.
- deMenocal, P.B., Bloemendal, J., 1995. Plio-Pleistocene subtropical African climate variability and the paleoenvironment of hominid evolution: a combined data-model approach. In: Vrba, E., Denton, G., Burckle, L., Partridge, T. (Eds.), *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven, pp. 262–288.
- Delson, E., Tattersall, I., van Couverin, J.A., Brooks, A.S. (Eds.), 2000. *Encyclopedia of Human Evolution and Prehistory*. Garland Publishing.
- Dennell, R.W., 2009. *The Palaeolithic Settlement of Asia*. Cambridge University Press, Cambridge.
- Dennell, R., Roebroeks, W., 1996. The earliest colonization of Europe: the short chronology revisited. *Antiquity* 70, 535–542.
- Dennell, R.W., Roebroeks, W., 2005. An Asian perspective on early human dispersal from Africa. *Nature* 438, 1099–1104.
- Dennell, R.W., Martínón-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. *Quaternary Science Reviews* 30, 1511–1524.
- Despriée, J., Voinchet, P., Tissoux, H., Bahain, J.J., Falguères, C., Courcimault, G., Dépont, J., Moncel, M.H., Robin, S., Arzarello, M., Sala, R., Marquer, L., Messager, E., Puaud, S., Abdessadok, S., 2011. Lower and middle Pleistocene human settlements recorded in the fluvial deposits of the middle Loire River basin, Centre region, France. *Quaternary Science Reviews* 30, 1474–1485.
- Dirks, P.H.G.M., Kibii, J.M., Kuhn, B.F., Steininger, C., Churchill, S.E., Kramers, J.D., Pickering, R., Farber, D.L., Mériaux, A.S., Herries, A.I.R., King, G.C.P., Berger, L.R., 2010. Geological setting and age of *Australopithecus sediba* from Southern Africa. *Science* 328, 205–208.
- Drake, N.A., Blench, R.M., Armitage, S.J., Bristow, C.S., White, K.H., 2011. Ancient watercourses and biogeography of the Sahara explain the peopling of the desert. *Proceedings of the National Academy of Sciences USA* 108, 458–462.
- Endicott, P., Ho, S.Y.W., Stringer, C., 2010. Using genetic evidence to evaluate four palaeoanthropological hypotheses for the timing of Neanderthal and modern human origins. *Journal of Human Evolution* 59, 87–95.
- Feibel, C.S., Brown, F.H., McDougall, I., 1989. Stratigraphic context of fossil hominids from the Omo group deposits: northern Turkana basin, Kenya and Ethiopia. *American Journal of Physical Anthropology* 78, 595–622.
- Fernández-Jalvo, Y., Scott, L., Andrews, P., 2011. Taphonomy in palaeoecological interpretations. *Quaternary Science Reviews* 30, 1296–1302.
- Finlayson, C., 2008. The importance of coastal areas in the survival of Neanderthals populations during the Late Pleistocene. *Quaternary Science Reviews* 27, 2246–2252.

- Finlayson, C., 2009. *The Humans Who Went Extinct*. Oxford University Press, New York.
- Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. *Trends in Ecology and Evolution* 22, 213–222.
- Finlayson, C., Fa, D., Jiménez Espejo, F., Carrión, J.S., Finlayson, G., Giles Pacheco, F., Rodríguez Vidal, J., Stringer, C., Martínez Ruiz, F., 2008. Gorham's Cave, Gibraltar. The persistence of a Neanderthal population. *Quaternary International* 181, 64–71.
- Finlayson, C., Carrión, J.S., Brown, K., Finlayson, G., Sánchez-Marco, A., Fa, D., Rodríguez-Vidal, J., Fernández, S., Fierro, E., Bernal, M., Giles-Pacheco, F., 2011. The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. *Quaternary Science Reviews* 30, 1525–1532.
- Foley, R.A., 1994. Speciation, extinction and climatic change in hominid evolution. *Journal of Human Evolution* 26, 275–289.
- Folinsbee, K.E., Brooks, D.R., 2007. Miocene hominoid biogeography: pulses of dispersal and differentiation. *Journal of Biogeography* 34, 383–397.
- García, N., Arsuaga, J.L., 2011. The Sima de los Huesos (Burgos, northern Spain): palaeoenvironment and habitats of *Homo heidelbergensis* during the Middle Pleistocene. *Quaternary Science Reviews* 30, 1413–1419.
- García-Antón, M., 1987. Estudio polínico preliminar de los yacimientos de la Sierra de Atapuerca (Burgos). In: Aguirre, E., Carbonell, E., Bermúdez de Castro, J.M. (Eds.), *El Hombre fósil de Ibéas y el Pleistoceno de la Sierra de Atapuerca*. Publicaciones de la Junta de Castilla y León. Valladolid, pp. 55–59.
- García-Antón, M., Sainz-Ollero, H., 1991. Pollen record from the middle Pleistocene Atapuerca site (Burgos, Spain). *Palaeoclimatology, palaeogeography, Palaeoecology* 85, 199–206.
- Geraads, D., Tchervov, E., 1983. Femurs humains du Pleistocene Moyen de Geshert Benot Ya'aqov (Israel). *L'Anthropologie* 87, 138–141.
- Geraads, D., Hublin, J., Jaeger, J., Haiyang, T., Sen, S., Toubeau, P., 1986. The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. *Quaternary Research* 25, 380–386.
- Gibert, L., Scott, G., Ferrández-Cañadell, C., 2006. Evaluation of the Olduvai subchron in the Orce ravine (SE Spain). Implications for the Plio-Pleistocene mammal biostratigraphy and the age of Orce archaeological sites. *Quaternary Science Reviews* 25, 507–525.
- Goren-Inbar, N., Feibel, C.S., Verosub, K.L., Melamed, Y., Kislev, M.E., Tchervov, E., Saragusti, I., 2000. Pleistocene milestones on the out-of-Africa corridor at Geshert Benot Ya'aqov, Israel. *Science* 289, 944–974.
- Gould, S.J., 1995. *Dinosaur in a Haystack*. Harmony Books, New York.
- Gould, S.J., 2002. *The Structure of Evolutionary Theory*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.
- Grün, R., 1996. A re-analysis of electron spin resonance dating results associated with the Petralona hominid. *Journal of Human Evolution* 30, 227–241.
- Grün, R., Stringer, C.B., 1991. Electron spin resonance dating and the evolution of modern humans. *Archaeometry* 33, 153–199.
- Grün, R., Stringer, C., McDermott, F., Nathan, R., Porat, N., Robertson, S., Taylor, L., Mortimer, G., Eggins, S., McCulloch, M., 2005. U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. *Journal of Human Evolution* 49, 316–334.
- Guipeit, G., Mafart, B., Tuffreau, A., de Lumley, M.A., 2007. 3D reconstruction and study of a new late middle Pleistocene hominid: Biache-Saint Vaast 2, Nord France. *American Journal of Physical Anthropology* 44, 121–122.
- Haile-Selassie, Y., Asfaw, B., White, T., 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* 303, 1503–1505.
- Haile-Selassie, Y., Latimer, B.M., Alene, M., Deino, A.L., Gibert, L., Melillo, S.M., Saylor, B.Z., Scott, G.R., Lovejoy, C.O., 2010. An early *Australopithecus afarensis* postcranium from Woranso-Mille, Ethiopia. *Proceedings of the National Academy of Sciences, USA*. doi:10.1073/pnas.1004527107.
- Hay, R., 1987. *Geology of the Laetoli area*. In: Leakey, M., Harris, J. (Eds.), *Results of the Laetoli Expeditions 1975–1981*. Oxford University Press, Oxford, pp. 23–47.
- Hill, A., Ward, S., Deino, A., Curtis, G., Drake, R., 1992. Earliest *Homo*. *Nature* 355, 719–722.
- Hosfield, R., 2011. The British lower Palaeolithic of the early middle Pleistocene. *Quaternary Science Reviews* 30, 1486–1510.
- Howell, F.C., Haesaerts, P., de Heinzelin, J., 1987. Depositional environments, archaeological occurrences and hominids from Members E and F of the Shungura formation (Omo basin, Ethiopia). *Journal of Human Evolution* 16, 665–700.
- Hublin, J.J., 1985. Human fossils from the north African middle Pleistocene and the origin of *Homo sapiens*. In: Delson, E., Liss, A.R. (Eds.), *Ancestors: The Hard Evidence*. Alan Liss Inc., New York, pp. 283–288.
- Hublin, J.J., 2009. The origin of Neandertals. *Proceedings of the National Academy of Sciences USA* 106, 16022–16027.
- Jacobs, B.F., 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions. Royal Soc. B. Biol. Sci.* 359, 1573–1583.
- Jiménez-Espejo, F.J., Martínez-Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega-Huertas, M., Finlayson, G., Iijima, K., Gallego-Torres, D., Fa, D., 2007. Climate forcing and Neanderthal extinction in Southern Iberia: insights from a multiproxy marine record. *Quaternary Science Reviews* 26, 836–852.
- Jordans, J.C.A., Wesselingh, F.P., de Vos, J., Vonhof, H.B., Kroon, D., 2009. Relevance of aquatic environments for hominins: a case study from Trinil (Java, Indonesia). *Journal of Human Evolution* 57, 656–671.
- Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombar, F., Lister, A.M., Mazza, P.P.A., Spassov, N., Titov, V.V., 2011. Western Palearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1368–1395.
- Kaifu, Y., Aziz, F., Baba, H., 2005. Hominid mandibular remains from Sangiran: 1952–1986 collection. *American Journal of Physical Anthropology* 128, 497–519.
- Kelleher, E.F., Barbash, D.A., 2010. Expanding islands of speciation. *Nature* 465, 1019–1020.
- Keyser, A.W., 2000. The Drimolen skull: the most complete australopithecine cranium and mandible to date. *South African Journal of Science* 96, 189–193.
- Kikvidze, Z., Ohsawa, M., 2001. Richness of Colchic vegetation: comparison between refugia of south-western and East Asia. *BMC Ecology* 1, 6–16.
- Kimbel, W., Walter, R., Johanson, D., Reed, K.E., Aronson, J.L., Assefa, Z., Marean, C.W., Eck, G.G., Bobe-Quinteros, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evenson, N.M., Smith, P.E., 1996. Late Pleistocene *Homo* and Oldowan tools from the Hadar formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution* 31, 549–561.
- Kingston, J.D., 2007. Shifting adaptive landscapes: progress and challenges in reconstructing early hominid environments. *Yearbook of Physical Anthropology* 50, 20–58.
- Klein, R., 1999. *The Human Career*. Human Biological and Cultural Origins. University of Chicago Press, Chicago.
- Kreuer, V., Zazanashvili, N., Jungius, H., Williams, L., Petelin, D., 2001. Biodiversity of the Caucasus Eco region. *World Wide Fund for Nature, Moscow*.
- Leakey, L.S.B., 1959. A new fossil skull from Olduvai. *Nature* 184, 491–493.
- Leakey, R., 1973. Evidence for an advanced plio-Pleistocene hominid from east Rudolf, Kenya. *Nature* 242, 447–450.
- Leakey, R., 1974. Further evidence of lower Pleistocene hominids from east Rudolf, north Kenya, 1973. *Nature* 248, 653–656.
- Leakey, R., Lewin, R., 1992. *Origins Reconsidered*. Doubleday, New York.
- Leakey, R., Wood, B.A., 1973. New evidence of the genus *Homo* from east Rudolf, Kenya (II). *American Journal of Physical Anthropology* 39, 355–368.
- Leakey, M.G., Spoor, F., Brown, F.H., Gatogo, P.N., Kiarie, C., Leakey, L.N., McDougall, I., 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature* 410, 433–440.
- Leroy, S.A.G., Arpe, K., Mikolajewicz, U., 2011. Vegetation context and climatic limits of the Early Pleistocene hominin dispersal in Europe. *Quaternary Science Reviews* 30, 1448–1463.
- Lordkipanidze, D., Jashashvili, T., Vekua, A., Ponce de León, M.S., Zollikofer, C.P.E., Rightmire, G.P., Pontzer, H., Ferring, R., Oms, O., Tappen, M., Bukhianidze, M., Agustí, J., Kahlke, R., Kiladze, G., Martínez-Navarro, B., Mouskhelishvili, A., Nioradze, M., Rook, L., 2007. Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* 449, 305–310.
- Manzi, G., Magri, D., Palombo, M.R., 2011. Early-Middle Pleistocene environmental changes and human evolution in the Italian peninsula. *Quaternary Science Reviews* 30, 1420–1438.
- Martínez-Navarro, B., 2010. Orce: el hombre fósil. *Garnata* 4, 1–100.
- Martínez-Navarro, B., Turq, A., Agustí, J., Oms, O., 1997. Fuente Nueva -3 (Orce, Granada, Spain) and the first human occupation of Europe. *Journal of Human Evolution* 33, 611–620.
- Martinón-Torres, M., Dennell, R., Bermúdez de Castro, J.M., 2011. The Denisova hominin need not be an out of Africa store. *Journal of Human Evolution* 60, 251–255.
- McNabb, J., Sinclair, A.G.M. (Eds.), 2009. *The Cave of Hearths: Makapan Middle Pleistocene Research Project*. University of Southampton series in archaeology. Archaeopress, Oxford.
- Messenger, E., Lebreton, V., Marquer, L., Russo-Ermolli, E., Orain, R., Renault-Miskovsky, J., Lordkipanidze, D., Despriée, J., Peretto, C., Arzarello, M., 2011. Palaeoenvironments of early hominins in temperate and Mediterranean Eurasia: new palaeobotanical data from Palaeolithic key-sites and synchronous natural sequences. *Quaternary Science Reviews* 30, 1439–1447.
- Moorwood, M.J., Brown, P., Jatmiko, Sutikna, T., Saptomo, E.W., Westaway, K.E., Due, R.A., Roberts, R.G., Maeda, T., Wasisto, S., Djubiantono, T., 2005. Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. *Nature* 437, 1012–1017.
- Mounier, A., Marchal, F., Condemi, S., 2009. Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. *Journal of Human Evolution* 56, 219–246.
- Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., de Esteban-Trivigno, S., Robles, J.M., Galindo, J., Fortuna, J., 2009. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proceedings of the National Academy of Sciences USA* 106, 9601–9606.
- O'Regan, H.J., Turner, A., Bishop, L.C., Elton, S., Lamb, A.L., 2011. Hominins without fellow travellers? First appearances of Afro-Eurasian large-mammals in the Plio-Pleistocene. *Quaternary Science Reviews* 30, 1343–1352.
- Palmqvist, P., Pérez-Claros, J.A., Janis, C.M., Gröcke, D.R., 2008. Tracing the ecophysiology of ungulates and predator-prey relationships in an early Pleistocene large mammal community. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266, 95–111.
- Parfitt, S.A., Barendregt, R.W., Breda, M., Candy, I., Collins, M.J., Coope, G.R., Durbridge, P., Field, M.H., Lee, J.R., Lister, A.M., Mutch, R., Penkman, K.E.H., Preece, R.C., Rose, J., Stringer, C.B., Symmons, R., Whittaker, J.E., Wymer, J.J., Stuart, A.J., 2005. The earliest record of human activity in northern Europe. *Nature* 438, 1008–1012.
- Parfitt, S.A., Ashton, N.M., Lewis, S.G., Abel, R.L., Coope, G.R., Field, M.H., Gale, R., Hoare, P.G., Larkin, N.R., Lewis, M.D., Karloukovski, V., Maher, B.A., Peglar, S.M.,

- Preece, R.C., Whittaker, J.E., Stringer, C.B., 2010. Early Pleistocene human occupation at the edge of the boreal zone in northwest Europe. *Nature* 466, 229–233.
- Plummer, T.W., Ditchfield, P.W., Bishop, L.C., Kingston, J.D., Ferraro, J.V., Braun, D.R., Hertel, F., Potts, R., 2009. Oldest evidence of toolmaking hominins in a grassland-dominated ecosystem. *PLoS ONE* 4, e7199. doi:10.1371/journal.pone.0007199.
- Postigo, J.M., Barrón, E., Gómez-Manzanque, F., Morla, C., 2009. Floristic changes in the Iberian peninsula (SW Europe) during the Cenozoic. *Journal of Biogeography* 36, 2025–2043.
- Potts, R., 1998. Environmental hypotheses of hominin evolution. *American Journal of Physical Anthropology* 27, 93–136.
- Preece, R.C., Parfitt, S.A., Coope, G.R., Penkman, K.E.H., Pönel, P., Whittaker, J.E., 2009. Press. Biostratigraphic and aminostratigraphic constraints on the age of the Middle Pleistocene glacial succession in north Norfolk, UK. *Journal of Quaternary Science* 24, 557–580.
- Radosevich, S.C., Retallack, G.J., Taieb, M., 1992. Reassessment of the paleoenvironment and preservation of hominid fossils from Hadar, Ethiopia. *American Journal of Physical Anthropology* 87, 15–27.
- Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talamo, S., Shunkov, M.V., Dereviianko, A.P., Hublin, J.J., Kelso, J., Slatkin, M., Paabo, S., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. *Nature* 468, 1053–1060.
- Ricklefs, R.E., 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences USA* 107, 1265–1272.
- Rightmire, G.P., 2009. Middle and later Pleistocene hominins in Africa and south-west Asia. *Proceedings of the National Academy of Sciences USA* 106, 10046–10050.
- Rink, W.H., Schwarzc, H., Smith, F., Radovic, J., 1995. ESR ages for Krapina hominids. *Nature* 378, 24.
- Roche, H., Kibunjia, M., 1994. Les sites archéologiques plio-pléistocènes de la formation de Nachukui, West Turkana, Kenya: bilan synthétique 1997–2001. *Comptes Rendus de l'Académie des Sciences, Paris* 318, 1145–1151.
- Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., van der Made, J., Pérez González, A., Blain, H.A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, J., Vallverdú, J., Bennisar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quaternary Science Reviews* 30, 1396–1412.
- Rosas, A., 2001. Occurrence of Neanderthal features in mandibles from the Atapuerca SH-site. *American Journal of Physical Anthropology* 114, 74–91.
- Rose, J., 2009. Early and middle Pleistocene landscapes of eastern England. *Proceedings of the Geologists Association* 120, 3–33.
- Ségalen, L., Lee-Thorp, J.A., Cerling, Th., 2007. Timing of C4 grass expansion across sub-Saharan Africa. *Journal of Human Evolution* 53, 549–559.
- Sénut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., Coppens, Y., 2001. First hominid from the Miocene (Lukoleo formation, Kenya). *Comptes Rendus de l'Académie des Sciences, Paris* 332, 137–144.
- Sahnouni, M., van der Made, J., Everett, M., 2011. Ecological background to plio-pleistocene hominin occupation in north Africa: the vertebrate faunas from Ain Boucherit, Ain Hanech and el-Kherba, and paleosol stable-carbon-isotope studies from el-Kherba, Algeria. *Quaternary Science Reviews* 30, 1303–1317.
- Scott, G.R., Gibert, L., 2009. The oldest hand-axes in Europe. *Nature* 461, 82–85.
- Scott, L., Rossouw, L., 2005. Reassessment of botanical evidence for palaeoenvironments at Florisbad, South Africa. *The South African Archaeological Bulletin* 60, 96–102.
- Sechrest, W., Brooks, T.M., da Fonseca, G.A.B., Konstant, W.R., Mittermeier, R.A., Purvis, A., Rylands, A.B., Gittleman, J.L., 2002. Hotspots and the conservation of evolutionary history. *Proceedings of the National Academy of Sciences USA* 99, 2067–2071.
- Semaw, S., Rogers, M.J., Quade, J., Renne, P.R., Butler, R.F., Domínguez-Rodrigo, M., Stout, D., Hart, W.S., Pickering, T., Simpson, S.W., 2003. 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution* 45, 169–177.
- Shea, J.J., 2008. Transitions or turnovers? Climatically-forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. *Quaternary Science Reviews* 27, 2253–2257.
- Shen, G., Gao, X., Gao, B., Granger, D.E., 2009. Age of Zhoukoudian *Homo erectus* determined with <sup>26</sup>Al/<sup>10</sup>Be burial dating. *Nature* 458, 198–200.
- Smith, T.M., Tafforeau, P., Reid, D.J., Grün, R., Eggins, S., Boutakiout, M., Hublin, J.J., 2007. Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences, USA* 104, 6128–6133.
- Spathelf, M., Waite, T.A., 2007. Will hotspots conserve extra primate and carnivore evolutionary history. *Diversity and Distributions* 13, 746–751.
- Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early *Homo* fossils from Ilkeret, east of Lake Turkana, Kenya. *Nature* 448, 688–691.
- Stringer, C.B., 1983. Some further notes on the morphology and dating of the Petralona hominid. *Journal of Human Evolution* 12, 731–742.
- Stringer, C., 2000. Coasting out of Africa. *Nature* 405, 24–27.
- Stringer, C., 2002. Modern human origins - progress and prospects. *Philosophical Transactions of the Royal Society, London (B)* 357, 563–579.
- Stringer, C., 2006. *Homo Britannicus: The incredible story of human life in Britain*. Allen Lane, London.
- Stringer, C., Andrews, P., 2005. *The Complete World of Human Evolution*. Thames, Hudson Ltd, London.
- Stringer, C., Hublin, J.J., 1999. New age estimates for the Swanscombe hominid, and their significance for human evolution. *Journal of Human Evolution* 37, 873–877.
- Stringer, C., Trinkaus, E., Roberts, M., Parfitt, S., Macphail, R., 1998. The middle Pleistocene human tibia from Boxgrove. *Journal of Human Evolution* 34, 509–547.
- Stringer, C., Finlayson, J.C., Barton, R.N.E., Cáceres, I., Fernández-Jalvo, Y., 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences USA* 105, 14319–14324.
- Tattersall, I., 1996. Paleoanthropology and preconception. In: Meikle, W.E., Howell, F.C., Jablonski, N.G. (Eds.), *Contemporary Issues in Human Evolution*, 21. California Academy of Sciences Memoir, pp. 1–193.
- Toro, I., de Lumley, H., Fajardo, B., Barsky, D., Cauche, D., Celiberti, V., Grégoire, S., Martínez-Navarro, B., Espigares, P., Ros-Montoya, S., 2009. L'industrie lithique des gisements du Pléistocène inférieur de Barranco León et Fuente Nueva 3 à Orce, Grenade, Espagne. *L'Anthropologie* 113, 111–124.
- Trauth, M.H., Deino, A., Bergner, A.G.N., Strecker, M.R., 2003. East African climate change and orbital forcing during the last 175 kyr BP. *Earth and Planetary Science Letters* 206, 297–313.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., 2005. Late Cenozoic moisture history of east Africa. *Science* 309, 2051–2053.
- Trauth, M.H., Maslin, M.A., Deino, A., Strecker, M.R., Bergner, A.G.N., Dühnforth, M., 2007. High- and low-latitude forcing of Plio-Pleistocene African climate and human evolution. *Journal of Human Evolution* 53, 475–486.
- van der Made, J., 2011. Biogeography and climatic change as a context to human dispersal out of Africa and within Eurasia. *Quaternary Science Reviews* 30, 1353–1367.
- Vekua, A., Lordkipanidze, D., Rightmire, G.P., Agustí, J., Ferrer, R., Miasuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de León, M., Tappen, M., Tvalchrelidze, M., Zollikofer, C., 2002. A new skull of early Homo from Dmanisi, Georgia. *Science* 297, 85–89.
- Verosub, K.L., Goren-Inbar, N., Feibel, C.S., Saragusti, I., 1998. Location of the Matuyama/Brunhes boundary in the Geshen Benot Ya'aqov archaeological site. *Journal of Human Evolution* 34 (3), A22.
- Vrba, E.S., 2005. Mass turnover and heterochrony events in response to physical change. *Paleobiology* 31, 157–174.
- Vrba, E.S., 2006. Role of environmental stimuli in hominid origins. In: Henke, W., Rothe, H., Tattersall, I. (Eds.), *Handbook of Palaeoanthropology. Phylogeny of Hominines, Vol. 3*. Springer-Verlag, New York, pp. 1–41.
- Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), 1995. *Paleoclimate and Evolution, with Emphasis on Human Origins*. Yale University Press, New Haven.
- Wagner, G.A., Krbetschek, M., Degering, D., Bahain, J.-J., Shao, Q., Falguères, C., Voinchet, P., Dolo, J.-M., García, T., Rightmire, G.P., 2010. Radiometric dating of the type-site for *Homo heidelbergensis* at Mauer, Germany. *Proceedings of the National Academy of Sciences USA* 107, 19726–19730.
- Wagner, G.A., Maul, L.C., Löscher, M., Schreiber, H.D., 2011. Mauer – the type site of *Homo heidelbergensis*: palaeoenvironment and age. *Quaternary Science Reviews* 30, 1464–1473.
- Walker, M.J., Rodríguez Estrella, T., Carrión, J.S., Mancheño, M.A., López Jiménez, A., Hills, M.D., Walking, T., 2006. Cueva Negra del Estrecho del Río Quípar (Murcia, S.E. Spain): an Acheulian and Levallois-Mousteroid assemblage of Palaeolithic artifacts excavated in a middle Pleistocene faunal context with hominin skeletal remains. *Eurasian Prehistory* 4, 3–43.
- White, T.D., 2003. Early hominids. Diversity or distortion? *Science* 299, 1994–1997.
- White, T.D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C.O., Suwa, G., Wolde Gabriel, G., 2009. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326, 75–86.
- Whitten, E.H.T., 2010. Influence of the improbable in earth sciences. *Proceedings of the Geologists Association* 121, 249–251.
- WoldeGabriel, G., Ambrose, S.H., Barboni, D., Bonnefille, R., Bremond, L., Currie, B., DeGusta, D., Hart, W.K., Murray, A.M., Renne, P.R., Jolly-Saad, M.C., Stewart, K.M., White, T.D., 2009. The geological, isotopic, botanical, invertebrate, and lower vertebrate surroundings of *Ardipithecus ramidus*. *Science* 326, 65e1–65e5.
- Wood, B., Strait, D., 2004. Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution* 46, 119–162.
- Yoder, J.B., Nuismer, S.L., 2010. When does coevolution promote diversification? *American Naturalist* 176, 802–817.
- Zhang, P., Huang, W., Wang, W., 2010. Acheulian handaxes from Fengshudao, Bose sites of south China. *Quaternary International* 223/224, 440–443.
- Zhu, R.X., Potts, R., Pan, Y.X., Yao, H.T., Lü, L.Q., Zhao, X., Gao, X., Chen, L.W., Gao, F., Deng, C.L., 2008. Early evidence of the genus *Homo* in east Asia. *Journal of Human Evolution* 55, 1075–1085.
- Zollikofer, C.P.E., Ponce de León, M., 2009. The evolution of hominin ontogenies. *Seminars in Cell and Developmental Biology* 21, 441–452.