



On the Ecological Connection Between Sabre-tooths and Hominids: Faunal Dispersal Events in the Lower Pleistocene and a Review of the Evidence for the First Human Arrival in Europe

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(Received 25 May 1998, revised manuscript accepted 27 August 1998)

The chronology of the first colonization of Europe by hominids has been a rather controversial issue until this decade, with most palaeoanthropologists claiming that there was no significant habitation until Middle Pleistocene times. However, recent findings in Spain, Italy, Georgia and China, as well as the re-evaluation of the evidence from Java and Israel, indicate an earlier arrival of *Homo* in Eurasia, during the Lower Pleistocene. The systematic revision of European assemblages of large mammals has shown a faunal break at the Plio–Pleistocene boundary, marked by the arrival of African and Asian species, which allows the tracing of the ecological and biogeographical scenario in which the first dispersal of hominids out of Africa took place. African immigrants include among others two carnivore species, the giant hyaena *Pachycrocuta brevirostris* and the sabre-tooth *Megantereon whitei*. Sabre-tooth cats were extinct in East Africa by 1.5 Ma, which coincides with the emergence of the Acheulean Industrial Complex, but inhabited Eurasia until 0.5 Ma. Given that *M. whitei* was a hypercarnivorous predator that presumably left, on the carcasses of the ungulates hunted, large amounts of flesh and bone nutrients within, its arrival in Eurasia opened broad opportunities for scavenging by hominids and helps to explain the success of the Oldowan tools until 0.5 Ma.

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Keywords: DISPERSAL OF *HOMO* TO EUROPE, *MEGANTEREON*, *PACHYCROCUTA*, LOWER PLEISTOCENE, OLDOWAN TOOLS.

Introduction

Until this decade most palaeoanthropologists believed that there was no significant habitation in Europe before Middle Pleistocene times (Carbonell & Rodríguez, 1994; Roebroeks & Kolfshoten, 1994, 1995). However, new findings suggest that the first arrival of hominids in Java and Southern Asia took place during the Late Pliocene, and recent discoveries in Spain, Italy and Georgia are providing increasing evidence of an early colonization of Europe in Lower Pleistocene times. Although these findings have forced several researchers to change their understanding of the palaeoanthropological and archaeological record (Carbonell *et al.*, 1995a; Dennell & Roebroeks, 1996), a very restrictive geographic

system of reference (i.e., Europe) still prevails in the analysis of this matter, and the study is usually focused only on the fossil record of the genus *Homo*. In addition, the approach applied in the analysis of the new evidence is rather limited, since the main aim of the majority of prehistorians is to confirm the oldest proposed ages for the earliest human settlements in Europe, and this issue overshadows all others (i.e., the causes and the ecological scenario of this dispersal). The palaeobiological information preserved in the fossil record is not accessed by this restrictive approach, which is strongly biased by our comprehension of what we think human beings are, and even by the extrapolation in time of what we now call Europe.

Has Europe, a political entity defined only by historical attributes, any type of specific meaning 0.1, 0.5 or 1.0 Ma ago? The answer is probably not, but

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what seems clear, and it is thus attested to by the palaeontological record, is that during all of the Quaternary Europe no palaeobiological meaning had been dissociated from Asia. Due to this reason, Eurasia is the geographic unit to which the first human dispersal out of Africa should be referred. However, we should be asking what is more relevant, that humans spread from Africa or that they reached some places in Eurasia? From our point of view the most important issue is to establish the biogeographical scenario and the ecological causes that allowed this dispersal, although this probably may only be addressed by the comparative analysis of the palaeontological and archaeological assemblages preserved in Eurasia. This study will be possible if all the information recorded in both Europe and Asia, although heterogeneous, is considered in an unitary way, as the result of a single cause. Therefore, if we try to establish when the genus *Homo* arrived in Eurasia, the fraction of the record which has been recovered in Europe may be taken to be a first-hand source of information. However, a coherent approach to this issue should take into account not only those aspects related to the chronology or the anatomical features of the Eurasian hominids, but also the climatic and ecological context, the faunal assemblages present in each site, and the role that the technological acquisitions may have played in facilitating the first dispersal of *Homo* outside Africa. We must emphasize here that the lithic artefacts are objects which must be understood by palaeontologists as ethological structures in *sensu stricto* when interpreting their presence in the geological record, i.e., as ichnofossils or indirect evidence of the presence of the organism which produced them (in this case, the object is owing to a specific biological activity, the cultural one).

The Palaeoanthropological and Archaeological Record in Eurasia

Only a few, scattered archaeological sites or hominid remains have yet been found in early Pleistocene

deposits from Europe, and until very recently most European prehistorians believed that there were no significant human settlements in Europe before 0.5 Ma (Bilzingsleben, Boxgrove, Mauer, Schönningen), with most evidences concentrating on <0.3 Ma (Arago, Tautavel, Petralona, La Sima de los Huesos at Atapuerca, Swanscombe, Steinheim) (Arsuaga *et al.*, 1993; Carbonell & Rodríguez, 1994; Roebroeks & Kolfshoten, 1994, 1995). Introducing a note of discord, some archaeological sites (but without human remains) in Europe like Le Vallonet Cave and the Soleilhac open air site, which are placed within the Jaramillo Normal Subchron, have been known from several decades.

However, recent findings in Spain, Italy, Georgia and China, as well as the re-evaluation of the evidence from Java and Israel, indicate an earlier arrival of *Homo* in Eurasia, during lower Pleistocene times. If we evaluate the palaeoanthropological and archaeological record available and its most likely interpretation (Figure 1), we have then a history which is constituted by complementary information from the three geographical fringes into which Eurasia can be divided. As the most significant examples, we can mention the following ones:

In East Eurasia:

- (1) Until very recently, the ages currently accepted for the specimens of *Homo erectus* from Java ranged between 1.2 and 0.7 Ma (Leinders *et al.*, 1985). However, the radiometric ages of several human remains (Mojokerto cranium, Sangiran 27 and 31) obtained using the single-crystal Ar/Ar method (Swisher *et al.*, 1994) indicate 1.6–1.8 Ma for them, thus suggesting that the first occupation of this area may have been latest Pliocene, which coincides with the arrival to Java of several species of mammals originating in Asia (Satir fauna, 1.7 Ma; Semah, 1997). The ages proposed by Swisher *et al.* (1994) are somewhat controversial, since the provenance of the Mojokerto child (the best documented specimen) and even the

Figure 1. Synthesis of the most significant palaeobiological information on the Plio–Pleistocene faunal replacement in Western Europe. The figure includes the micromammalian biozones for the period of time considered (A.c.: *Arvicola cantiana*), the distribution by sites and faunal units of those species of large mammals which are relevant for this study, the relative chronostratigraphical positions of the Javanese sites, and the chronological position of Dmanisi as modern as deduced from biostratigraphy. The palaeontological and archaeological sites from Orce (BL: Barranco León, FN: Fuente Nueva, VM: Venta Micena) have been placed according with the lithostratigraphic sequence in the Orce-Venta Micena sector within the Guadix-Baza Basin, and also as a function of the micro-mammalian assemblages found in them. A faunal replacement which affects many mammalian genera (both micro- and macro-mammals) took place between 1.8 and 1.6 Ma. It was characterized by the extinction of several Pliocene species and by the arrival of new African immigrants, which seem to have been stabilized in Western Europe during the first third of the Lower Pleistocene. Most of them became extinct shortly before the transition between the Lower Pleistocene and the Middle Pleistocene. A new faunal replacement is found above this limit, with species originating in Eastern Eurasia. The Oldowan technological complex is found in Western Europe during the 1.6–0.78 Ma time interval, which coincides with the incomplete record of hominid fossils showing affinities with *H. ergaster*. (See references: 1. Swisher *et al.*, 1994; 2. Gabunia & Vekua, 1995a, b; 3. Dzaparidze *et al.*, 1989; 4. Turner, 1987; 5. Martínez-Navarro & Palmqvist, 1995; 6. Turq *et al.*, 1996; 7. Palmqvist *et al.*, 1996a; 8. Martínez-Navarro *et al.*, 1997; 9. Gibert *et al.*, 1995; 10. Palmqvist, Martínez-Navarro & Arribas, 1996b; 11. Tixier *et al.*, 1995; 12. Carbonell & Rodríguez, 1994; 13. Palmqvist, 1997; 14. Carbonell *et al.*, 1995b; 15. Bermúdez de Castro *et al.*, 1997; 16. Beinhaüer & Wagner, 1992; 17. Roberts, Stranger & Parfitt, 1994; 18. Ascenzi *et al.*, 1996; 19. Torre *et al.*, 1996.) Note: in Cueva Victoria the genus *Megantereon* is marked twice, since the species present has not yet been determined.

location of the findspot is uncertain; however, the chemical analysis of pumiceous materials adhering to this skull shows similarities but not identity to the volcanic pumice dated radiometrically, which opens the possibility that the calvaria may have been transported and then filled with materials including pieces of a tuff older than the specimen. In any case, the disagreement between the results obtained in both geochemical analyses does not justify rejecting this evidence, since the chemical composition of any clastic deposit always shows small differences owing to the compositional gradient present in this type of sediment; although, the human remains were obviously transported, but this transport must have been shorter than some hundred metres, given the good preservational state of several anatomical regions of the skull. It is very significant that the splanocranium was not preserved, since this is the first part which is separated with the movement, in contrast with the complete preservation of the neurocranium, and more specifically the integrity of the squamose regions. The temporal bone is the first which separates from the other bones of the neurocranium in the skull of juvenile humans, given the structural precariousness of the temporoparietal suture. In fact, this bone is always isolated from other neurocranial fragments, and its separation may owe to a simple gravitational transport of some tens of meters, or even following the putrefaction of soft tissues in addition to a slight rolling movement.

- (2) The finding of archaic hominid dental fragments, which are associated with *Gigantopithecus* teeth and primitive Oldowan stone tools in Longgupo Cave (Wushan, Sichuan Province, China) (Wanpo *et al.*, 1995), is another source of significant information about this dispersal event. Palaeomagnetic, biostratigraphical and geochronological (electron spin resonance) analyses indicate that the hominid-bearing levels date to the latest Pliocene, within the normal Olduvai event (1.96–1.78 Ma). Comparative study of hominid teeth revealed affinities with *H. habilis* and *H. ergaster*, thus suggesting that hominids entered in Asia before 2.0 Ma, coincident with the diversification of the genus *Homo* in Africa, and that this immigrant species was other than *H. erectus* (Larick & Ciochon, 1996). However, it has been argued that these teeth resemble those of *Lufengpithecus*, a fossil ape related to *Pongo* (Wolpoff, 1996). Even if the teeth prove to be of this ape, the hypothesis of human presence at this site would stand, because the lithic artefacts (only two pieces) are significant evidence of human activity, and this evidence should not be affirmed or denied only on the basis of its age.
- (3) Additionally, several teeth of *H. erectus* claimed to be of Early Pleistocene times, with ages in

excess of a million years, have been reported from different sites in Northern China (Jianshi, Luonan, Yuanmon), and a cranium from Gongwangling, near the village of Lantian, has been dated to 1.15 Ma (Zhisheng & Chuankun, 1989).

- (4) Two core flake assemblages of Late Pliocene age have been described from the Indian subcontinent, at Pabbi Hills and Riwayat (Pakistan). Palaeomagnetic analyses indicate an age close to 2.0 Ma for the small number of quartzite pieces found at Riwayat, and probably also a similar age for the larger assemblage at Pabbi Hills (Rendell, Hailwood & Dennell, 1987; Dennell, Rendell & Hailwood, 1988). However, there are some reservations about their stratigraphical position (Hemingway & Stapert, 1989).

In Central Eurasia:

- (1) A human mandible associated with pre-Acheulean lithic artefacts in the Plio-Pleistocene site at Dmanisi (East Georgia, Caucasus). The mandible has been determined as *H. erectus* (Gabunia & Vekua, 1995a, b; Bräuer & Schultz, 1996), although it shows some evolved features like the presence of a vertical chin. The site was originally reported to be 1.8–1.6 Ma (Dzaparidze *et al.*, 1989; Gabunia & Vekua, 1995a) as suggested by the date of the basalts below the deposit, which was estimated by the K/Ar method in 1.8 ± 0.1 Ma. It is interesting to note that both the fossiliferous levels and the volcanic tuff show normal polarity, and they have been thus included within the Olduvai Subchron. The age of the deposit which contains the human mandible has been discussed during recent years, and it was subsequently estimated, rather arbitrarily, to be older than 1.0 Ma, owing to uncertainties related to several stratigraphical and taphonomic aspects as the possibility of diachronic deposits, given the presence of burrows. However, the faunal assemblage from this site, which is clearly not re-worked (Dzaparidze *et al.*, 1989; Gabunia & Vekua, 1995b), is of Late Pliocene age, since it comprises several species of rodents, perissodactyls and artiodactyls which are exclusive of the end of the European Pliocene (biozone MN17), which is coherent with the original date proposed for this site (Figure 1). The determination of the mandible as *H. erectus* has probably forced some palaeo-anthropologists to place this specimen at around 1.0 Ma, thus omitting the biostratigraphical information from the site, although it is possible that this determination will be changed in the future, because the fossil shows several anatomical features similar to those of African hominids (*H. ergaster*) like the WT 15000 mandible, such as a mandibular body not particularly tall, with a curved symphyseal surface having a weak

mandibular trigone and lacking a mental eminence, the molar size sequence ($M_1 > M_2 > M_3$) and the elongated shape of the third premolar (P_3), which is similar to that of Olduvai Bed IV specimen OH 22. As indicated above, the presence of burrows has been argued as a way by which the human mandible could have been infilled into older sediments; however, it would be difficult to explain how this process could have affected the mandible but not the other fossils, thousands of teeth and bones of several species of large and small mammals, which represent a biostratigraphically homogeneous assemblage with a composition typical of the Plio–Pleistocene transition.

- (2) In Israel, the site at 'Ubeidiya provides additional evidence of human presence during Lower Pleistocene times, since important assemblages of lithic artefacts and faunal remains have been dated biostratigraphically at around 1.4–1.3 Ma (Tchernov, 1986). The lithic assemblages comprise two sets: the oldest one is clearly pre-Acheulean (i.e., absence of bifacial handaxes), and the youngest one includes typical Acheulean tools. Several isolated human teeth were also recovered, but their precise stratigraphical context is known only for one of them. Bar-Yosef (1994) indicates that the presence of two different techno-complexes is due to the occupation of this region by two distinct human groups, one replacing the other in a very short time span. Also in Israel, two core tools have been recovered in the sites at Yiron and Erq-el-Ahmar; the first assemblage has been dated radiometrically (K/Ar method) in 2.4 Ma, and the second one was dated palaeomagnetically at 1.9–1.8 Ma, although there are some reservations about both their age and stratigraphic position, as well as on the artefacts themselves (Bar-Yosef, 1994).

In Western Eurasia:

- (1) The finding of human remains and pre-Acheulean stone tools in the karstic site at the Gran Dolina of Atapuerca (Burgos, Spain), in stratigraphic levels which according to palaeomagnetic studies are located below the Brunhes-Matuyama reversal, and thus have an age of <0.78 Ma (Carbonell *et al.*, 1995b; Parés & Pérez-González, 1995), suggests a continued human settlement in Europe at the end of the Lower Pleistocene. However, the age obtained using geochronological techniques seems to be incompatible with the relative dating deduced from the assemblage of mammals present in this site (TD-6 Level), which includes several typical Middle Pleistocene taxa originating in Asia (*Equus caballus*, *Sus scrofa*, *Ursus praeartcos/U. deningeri*, *Cervus elaphus*, *Dama*, cf. *clactoniana*, *Capreolus* sp.) (Figure 1) but no species exclusive of the early Galerian (i.e., the arctic ovibovini *Soergelia elisabethae* and

Ovibos sussenbornensis, the microtids *Allophaiomys bourgondiae* and *A. nutienensis*), which should be recorded in a European assemblage with the age proposed for this site (Azzaroli *et al.*, 1988; Sala *et al.*, 1992). However, some genera of large mammals which have their first appearance datums during the Middle Galerian (*Crocota*, *Bos* and *Panthera*) are represented in TD-6; from a biostratigraphical point of view, this assemblage should therefore be included within the Middle Galerian, in the base of the Middle Pleistocene. This conclusion is corroborated by the absence of *Castillomys crusafonti* from the micropaleontological record of Atapuerca, even in stratigraphic levels older than TD-6, since this species is always present in those Spanish sites of Lower Pleistocene age, being extinct shortly before the beginning of the Middle Pleistocene (Sesé, 1994; Sesé & Sevilla, 1996). Finally, the presence of *Mimomys savini* at TD-6 has been claimed to indicate a Lower Pleistocene or early Middle Pleistocene age for this site (Carbonell *et al.*, 1995b); on the one hand this arvicolid presents a wide biostratigraphical distribution, between the end of the Lower Pleistocene and the lower third of the Middle Pleistocene (Sesé, 1994), being its biostratigraphic value clearly insufficient to clarify the age of TD-6. On the other hand, the Asian origin of the fauna preserved in TD-6 contrasts with the phylogenetic link inferred for the hominids, which have been nominated as *H. antecessor* (Bermúdez de Castro *et al.*, 1997), a species supposedly originating in Africa, which it is proposed as the ancestor in Europe of “archaic sapiens” (*H. heidelbergensis*) and Neanderthals. The new species has been erected using a maxilla of a juvenile individual, whose midfacial profile resembles that of modern *H. sapiens*, although the adult specimens show several anatomical features which are exclusive of the oldest East African populations (*H. ergaster*), for example, the particular root morphology of the mandibular premolars (Bermúdez de Castro *et al.*, 1997).

- (2) The finding of a human calvarium in Ceprano (Italy) seems to introduce more complexity into this analysis, since the skullcap shows characteristics of *H. erectus*, but also some distinctive features as the absence of a slight crest along the centre of the skull or its larger brain; the fossil was unearthed in a clay level below sandy volcanoclastic gravels whose age was estimated by the K/Ar method in 0.7 Ma (Ascenzi *et al.*, 1996).
- (3) A human phalanx has been described (Palmqvist *et al.*, 1996a) in the Lower Pleistocene karstic site at Cueva Victoria (Murcia, Southeastern Spain). The specimen was discovered in a rich bone-bearing breccia, associated with fossils of European Villafranchian mammals, which also contained a molar of an African immigrant

in Western Eurasia, the cercopithecoid *Theropithecus oswaldi* (Gibert *et al.*, 1995). Carbonell & Rodríguez (1994) have reported on a manufactured piece of quartz in this locality, but it must be discarded from this analysis, because the artefact was recovered from an exokarstic deposit close to the entry of the cave, which has no fossil content and can not be correlated lithostratigraphically with the inner bone-breccia.

- (4) The discovery in several Lower Pleistocene sites located below the lower limit of the Jaramillo Normal Subchron (>1.07 Ma) within the Orce-Venta Micena sector of the Guadix-Baza Basin (Granada, Spain) of some controversial palaeo-anthropological remains (Orce skull from the Venta Micena site; see review in Palmqvist, 1997) and an important assemblage of lithic artefacts of Developed Oldowan type (Fuente Nueva-3 and Barranco León-5 sites; Turq *et al.*, 1996), contributes new evidence of human presence in this area during the mid third of the Lower Pleistocene. The tool assemblage of Fuente Nueva-3 (more than 100 pieces) is composed of limestone cobbles and knapped flint (Martínez-Navarro *et al.*, 1997), which are associated in the deposits with several species of large mammals originating in Africa (Martínez-Navarro & Palmqvist, 1995).

The Role of Technology in the Spread of *Homo*

One of the most important consequences of the adaptive shift involved in the origin of *Homo* was habitat expansion (Wolpoff, 1996): humans became a colonizing species as populations expanded their ecological range into arid and highland-to-mountainous habitats, and moved out of Africa to spread across the tropical and subtropical regions of the Old World. By Late Pliocene times the revolutionary discovery by hominids of how to make stone tools took place. This industry is the Oldowan, and the earliest artefacts are dated 2.6–2.5 Ma at Gona, Ethiopia (Semaw *et al.*, 1997). Oldowan assemblages comprise manuports, hammerstones, simple cores and unmodified flakes, and their characteristics are crudeness and opportunistic forms. The main cause of artefact shape variation comes from the shape of the initial blank, and not from a pre-existing idea of the tool maker about its final form. In fact, there are no tool types in the Mode I or Oldowan Industry, since the artefacts are crudely made without regular form, thus suggesting that they were mainly the debris left behind from rook-smashing activities whose main focus was to produce sharp flakes. This technology was useful for scavenging activities, since the cores allowed to break long bones for accessing their marrow content, and the juxtaposition of gnawing marks and tool-produced scratches on bones suggests that some of the flakes

were used for dismemberment of carcasses after the bones were gnawed by flesh-eating carnivores (Capaldo, 1997; Selvaggio, 1998).

By the time of the Middle Bed II at Olduvai (1.4 Ma) a more complex, better-made tool set was being manufactured, the Mode II or Acheulean Industrial Complex, which is first recorded at Konso, Ethiopia (Asfaw *et al.*, 1992). These lithic artefacts will span more than a million years, and are ultimately found across all the inhabited world (i.e., from South Africa to Indonesia). Unlike the Oldowan, the forms of Acheulean tools appear to have been preconceived by their makers. One tool type, the symmetric handaxe bifacially flaked, is its defining characteristic. As stated before, important evidence on the presence of this typology has been detected in the 'Ubeidiya site (Israel), one of the gateways to Europe, with an age of 1.4–1.3 Ma. According to Wolpoff (1996), significant adaptive changes associated with the spread of the Acheulean complex include more effective habitat utilization and additional food resources available through organized hunting, confrontational scavenging and improved techniques for collecting and preparing gathered foodstuffs.

However, the archaeological record of the Upper Pliocene and the Lower Pleistocene in Eurasia is composed (with the exception of the upper lithic assemblage from 'Ubeidiya) exclusively by tool assemblages belonging to the Oldowan techno-complex, during a time interval which comprises from 1.8 Ma (China, Java and Georgia) to 0.78 Ma (Atapuerca, Spain), with the intermediate chronological position (1.4–1.0 Ma) well characterized in the archaeological sites from Orce (Spain). Given the fact that during these ages tool-making technologies seem to be linked to human species, this line of discussion (i.e., the technological one) allows us to presuppose that the first human dispersal to Europe must have involved one species that was only capable of making Oldowan tools, as recorded in the European Lower Pleistocene, and not those included in the Acheulean Industrial Complex. By this reason, the most parsimonious hypothesis is that the human populations that first colonized Eurasia, and more specifically Western Europe, made it before the technological change from the Oldowan to the Acheulean took place in Africa, that is, *prior* to 1.4 Ma. The likely new reinterpretation of the Dmanisi mandible as *H. ergaster*, as well as the anatomical affinities between the adult hominids from Atapuerca TD-6 Level and *H. ergaster*, both could corroborate this hypothesis as a second source of evidence (i.e., the palaeo-anthropological one).

African Species in the Lower Pleistocene of Europe

The well-known sea-level fluctuations and climatic shifts evidenced by stable isotopes provide a basis for the study of major vegetational changes in the

Eurasian continent during the Plio–Pleistocene. Three major sea-level drops stand out in this time interval, owing to the wide-ranging environmental changes that accompanied them in the continental area (Azzaroli, 1995): the Aquatransan, the Aullan, and the Cassian erosional phases. The older of these sea-level falls, the Aquatransan or “Elefant–*Equus* event”, took place halfway through the Pliocene (2.6–2.4 Ma) and was accompanied by a marked cooling of ocean waters, by massive extinctions in marine fauna, and by wide-ranging changes in vegetation and faunas on the continents (the transition from the warm Reuverian to the cooler Praetiglian in Western Europe), including the extinction of warm-forest faunal elements such as zygodont mastodon and tapir, and the arrival from Asia of both elephants and monodactyl equids. The second event, the Aullan (1.8–1.6 Ma), corresponds with a relatively minor retreat of the sea-level, and coincides with the arrival of several African immigrants to Europe, including the genus *Homo* (Martínez-Navarro & Palmqvist, 1995), and with the conventional Neogene–Quaternary boundary. This event will be discussed at depth later. Finally, the Cassian sea-level fall (1.2–0.9 Ma) also coincided with a new cooling of the ocean waters, but it did not affect marine faunas to any great extent; however, it deeply affected continental vegetation and faunas, what has been called in Europe the “end-Villafranchian” dispersal event, marking the transition to the new mammalian assemblages of the Middle Pleistocene (these faunal associations have received the name of Galerian in Western Europe). These major climatic changes were accompanied in East Africa by a shift from mesic, closed environments to more xeric, open habitats, which was reflected in the assemblages of large mammals by a significant faunal turnover between 2.5 and 1.6 Ma (Behrensmeyer *et al.*, 1997), by an increase of the percentage of terrestrial grazers, and by a corresponding decline of both frugivores and species with arboreal locomotion (Reed, 1997).

The systematic study of the macrovertebrate assemblages from Orce and Dmanisi has shown a faunal break at the Plio–Pleistocene boundary in at least the western and central fringes of Eurasia. It has been recorded in part in the Villafranchian of Italy, within the Olivola and Tasso faunal units, where the faunal replacement was called “the Wolf event” (Azzaroli, 1983; Azzaroli *et al.*, 1988). This break is marked by the arrival in Europe of both African and Asian species shortly before and during the beginning of the Pleistocene (Martínez-Navarro, 1991; Martínez-Navarro & Palmqvist, 1995, 1996; Gibert *et al.*, 1995). Immigrants originating in Asia are basically ruminant species (four bovids and two cervids), while African ones include a megaherbivorous species, the hippo, an equid similar to modern grevy’s zebra, a large cercopithecoid and several carnivore species, as a giant hyaena, a sabre-tooth, and probably also a wild dog (Figure 1).

However, two general considerations are necessary before starting a discussion in depth on the palaeobiogeographical spread of these taxa in Europe. The first deals with the chronology of most palaeontological and archaeological sites in Europe and Asia, which is rather vague except for a few cases in which magnetostratigraphical data are available, thus relying heavily on the biostratigraphical study of the faunal assemblages; this situation contrasts with that of those hominid-bearing sites from the main sedimentary basins of the Rift Valley in East Africa, where the stratigraphical sequences include ash layers which have been radiometrically dated. The second problem is concerned with the reliability of taxonomic assignments, since the faunal lists from different palaeontological sites are usually made by different teams of palaeontologists working in Asia and Europe, and thus there exists a high potential for inter-analyst discrepancies, which precludes any reasonable analysis of faunal correspondence between different sites. Both limitations hinder any possibility of testing accurately how well the FADs (first appearance datums) and LADs (last appearance datums) of particular taxa within Europe correspond in time (for an application of this methodology to the analysis of patterns of faunal turnover during the Late Pliocene in the Turkana Basin, see Behrensmeyer *et al.*, 1997).

Owing to the limitations and uncertainties cited above, the focus of the following discussion will be centred on those species of large mammals for which detailed systematic comparisons between Eurasian and African assemblages have been carried out.

The genus *Equus* is first recorded in North America (Hagerman Formation, Idaho) at 3.4 Ma by the species *Equus simplicidens*. A comparative multivariate study of both modern and extinct populations of *Equus* in the Old and New World (Guerrero-Alba & Palmqvist, 1997) has shown two main evolutionary lines in the history of horses. The first one is represented by the “*simplicidens* type” equids, with species which have slender metapodials, well adapted to open and dry plains, like African zebra *E. grevyi*, and Asian hemionos *E. kiang* and *E. hemionus*. The second line includes the “*stenonis* type” horses, equids which are characterized by more robust metapodials, as *E. prezevalskii* in Asia, and *E. burchelli*, *E. zebra*, *E. africanus* and *E. asinus* in Africa. The first monodactyl equids arrived to Eurasia at around 2.5 Ma, where they are represented during the Upper Pliocene by the species *E. stenonis* in Russia (Livezovka), Italy (Olivola, Montopoli), France (Saint Vallier, Chilhac) and Spain (Huélago, Rincón, La Puebla de Valverde). Between 2.3 and 1.4 Ma equids of two species of the “*simplicidens* type” are found in East Africa (Omo Shungura, Olduvai, East Turkana), North Africa (Aïn Boucherit, Aïn Hanech) and the Middle East (‘Ubeidiya). The first of these species (*E. numidicus*) had a larger body size, comparable with that of modern grevy’s zebra, while the second (*E. tabeti*) was

of smaller size, similar to that of extant hemionus. During the Plio–Pleistocene transition *E. numidicus* arrived in Europe (where it has been called *E. altidens*) and is found in Spain (Orce, Cúllar de Baza, Cueva Victoria, Huéscar-1), Italy (Pirro Nord, Selvella), France (Sainzelles) and Germany (Süssenborn). The replacement of *E. stenonis* by *E. altidens* at the beginning of the Pleistocene indicates a change from wet, woodland habitats to more open and dry savannas.

The presence of the African cercopithecoid *Theropithecus oswaldi* in the Lower Pleistocene of Southeast Spain (Gibert *et al.*, 1995) constitutes an important faunal event, since it is the second occasion in which fossils of this genus have been found out of Africa. The palaeogeographical distribution of this large species, whose weight has been estimated to be 65 kg, was basically restricted to Africa until it was discovered in the karstic site at Cueva Victoria, although fossils of *Theropithecus* have been found at Mirzapur, India (Delson, 1993).

The arrival in the Old World of the genus *Canis* from North America took place approximately 3.0 Ma ago, as evidenced by the finding of *Canis etruscus*-like forms in deposits of this age in China (Flynn, Tedford & Qiu, 1991). The first record of this coyote-sized species in Europe is in the Olivola faunal unit (Azzaroli, 1983; Azzaroli *et al.*, 1988; Torre *et al.* 1992) and defines the “Wolf event” (Figure 1). *C. (Xenocyon) falconeri* was a hypercarnivorous canid widely distributed during the Late Pliocene and Early Pleistocene in the Old World (Rook, 1994). This species had a large body size, comparable with that of the living northern races of *C. lupus*, and was characterized by a relatively short neural cranium with a strong sagittal crest and a narrow muzzle. The second metacarpal has a very reduced articular facet for the first metacarpal, which indicates that the latter bone was vestigial if not absent, a condition which indicates increased cursoriality, similar to that of African *Lycaon pictus*, the only extant canid with a tetradactyl forelimb. According to the revision made by Rook (1994), *C. falconeri* is first recorded in China, within the Upper Pliocene locality at Fan Tsun (2.5 Ma). The arrival of this species in East Africa is recorded at Olduvai Bed I (1.9 Ma), which chronologically coincides with the earliest evidence of human presence in Asia. *C. falconeri* spread in Africa between 1.5 and 1.4 Ma (Kromdraai A and Olduvai Bed II, respectively). The first record of this species in Western Europe is in the Upper Valdarno, within the Tasso faunal unit, which according to palaeomagnetic data in Torre *et al.* (1996) is tentatively included in the upper part of the Olduvai Subchron (1.8–1.7 Ma). In spite of the Asian origin of this species, we can not rule out the possibility that it reached Europe from Africa, since its first record in Europe is simultaneous with that of other African immigrant, *Hippopotamus antiquus*. However, the arrival of both species also coincides with those of

other Asian immigrants, like *C. arnensis*, *Praeovibos*, and *A. pliocaenicus*.

Pachycrocuta brevirostris was a large, short-faced hyaena relatively common in Lower Pleistocene European assemblages of large mammals. It had a body and skull 10–20% larger than the modern spotted hyaena, *Crocuta crocuta*, and was well adapted for destroying carcasses and consuming bone (Palmqvist, Martínez-Navarro & Arribas, 1996b; Arribas & Palmqvist, 1998). This species differed from other hyaenids in having a relative shortening of the distal limb segments, which suggests a less cursorial life style, although such shortening could provide greater power and more stability for dismembering and carrying large pieces of carcasses obtained from aggressive scavenging (Turner & Antón, 1996). *P. brevirostris* is recorded in China from the end of the Pliocene (Nihowan) to Middle Pleistocene times (Choukoutien Locality I). This hyaenid was present in India (Pinjor Formation) not before 2.5 Ma. Howell & Petter (1980) think that the South African hyaenid *Hyaena bellax* from Kromdraai could be a member of the genus *Pachycrocuta*, and suggest that it would be the direct ancestor of *P. brevirostris*. This species is recorded in South Africa at Kromdraai A (1.5 Ma), Sterkfontein (Members 4 and 5, 2.6–1.0 Ma) and Makapansgat (Member 3, 3.0 Ma) (Howell & Petter, 1980; Turner, 1990). If its presence at Laetoli (3.5–3.2 Ma, East Africa) is confirmed (specimens tentatively identified as *H. bellax* by Leakey & Hay, 1979), the age of the first appearance of this species on the austral continent would be older. The arrival of this hyaenid to Europe was a significant faunal event. *P. brevirostris* is first recorded in upper Pliocene deposits at Olivola (1.8 Ma), and its latest appearances are in early Middle Pleistocene sites from Central Europe, like Süssenborn (Turner & Antón, 1996). In the Iberian Peninsula this species is found exclusively in early Lower Pleistocene sites, and its record during Middle Pleistocene times is not known. It is difficult at present to decide if *P. brevirostris* originated in Asia or in Africa; however, what seems clear is the presence of this hyaenid in Africa when it spread in Europe during the beginning of the Eburonian event. The extinction in Europe of *P. brevirostris* seems to have been linked to the decline and subsequent disappearance of machairodonts at approximately 0.5 Ma (Turner, 1990, 1992), particularly *Megantereon whitei* (Martínez-Navarro & Palmqvist, 1995), which implied the loss of an important source of partly-consumed carcasses, and thus a change in the interactions between flesh-eating and bone-consuming species of the carnivore guild (Turner & Antón, 1996).

The sabre-tooth genus *Megantereon* shares much in common with *Smilodon*, and both genera form the tribe Smilodontini. The earliest presence of *Megantereon* is recorded at 4.5 Ma in the Bone Valley Formation (Florida), where it is represented by *M. cultridens*. This species dispersed from North America

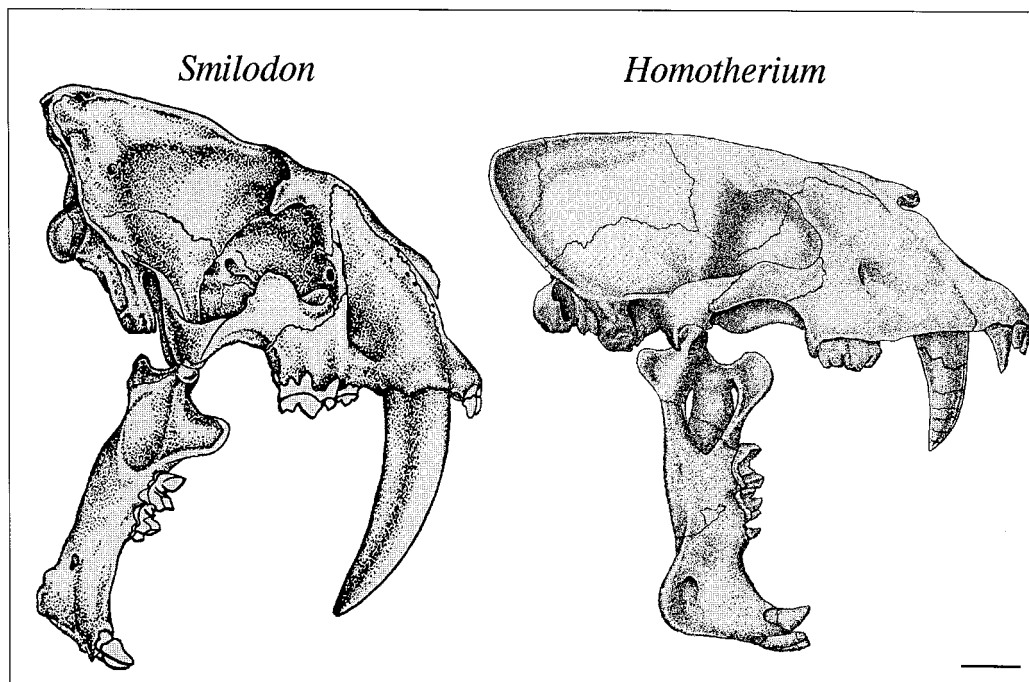


Figure 2. Craniodental morphology of sabre-toothed cats (tribes Smilodontini and Homotherini) (scale bar length represents 50 mm).

between 3.5 and 3.0 Ma, and expanded all over the Old World. Europe was also home to *M. cultridens* until the Lower Pleistocene, and in China it lingered well into the Middle Pleistocene at Choukoutien Locality I (Turner, 1987). In Africa *M. cultridens* gave rise to a new species, *M. whitei*, which is characterized by a reduction in the size of both the maxillary carnassial (P^4) and the mandibular premolars, which is reflected in a diastema between P_3 and P_4 (Martínez-Navarro & Palmqvist, 1995). *M. whitei* replaced *M. cultridens* in Western and Central Eurasia at the Plio-Pleistocene boundary, as recorded at Orce, Apollonia (Mygdonia Basin, Greece) and Dmanisi. The arrival of this carnivore species to Eurasia may have played a very significant role in facilitating the dispersal of *Pachycrocuta* and *Homo* outside Africa, since it was an ambush predator with great killing capability in relation to its flesh requirements, and presumably left large amounts of carrion for both hyaenas and hominids (Palmqvist, Martínez-Navarro & Arribas 1996b; Martínez-Navarro & Palmqvist, 1996).

As we have seen in the above discussion, it seems clear that a flux of African species to Eurasia, mainly to its western fringe, took place during the end of the Pliocene and the beginning of the Pleistocene. The fact that most African species are found in Southern Spain is explained if we consider that the Iberian Peninsula was faunally and climatically a part of Africa during the Neogene, far more than it was a part of Europe, which many palaeontologists consider to begin at the Pyrenees. This is the third approach to the dispersal of hominids to Europe, which allows inclusion of

the genus *Homo* in a faunal set which expanded its palaeogeographical range during these times.

The Role of Sabre-tooths in Facilitating the First Dispersal of *Homo* to Europe

The marked seasonality which characterized temperate Europe for most of the Pleistocene, with cooler and drier conditions than those of tropical Africa, made the availability of large ungulate carcasses for scavenging a key resource for hominids to survive during the cool season (Turner, 1990, 1992). Between 1.5 and 0.5 Ma the composition of the European carnivore guild was quite different from that of East Africa, including two species of sabre-tooth cats (*Homotherium latidens* and *M. whitei*), which presumably maximized the amount of flesh that remained on their kills, thus opening broad opportunities of scavenging for both hyaenas and hominids.

Sabre-tooth cats, which belong to the subfamily Machairodontinae, share among others the following craniodental derived characters (see for review and references: Emerson & Radinsky, 1980; Marean, 1989; Van Valkenburgh & Ruff, 1987; Martin, 1989; Biknevicius, Van Valkenburgh & Walker, 1996; Arribas & Palmqvist, 1998) (Figure 2):

- (1) Elongate and flattened upper canines of two basic types: *Homotherium* (tribe Homotherine) had scimitar-shaped canines relatively short and broad, which were serrated bearing coarse crenulations, while *Megantereon* (tribe Smilodontini)

showed dirk-shaped canines, extremely long, narrow, and without serrations.

- (2) Enlarged upper incisors, which are relatively longer, thicker, more pointed and procumbent than in modern felids, and reduced, incisor-shaped lower canines. The incisor row is long and strongly curved, that suggests for sabre-tooths a functional emphasis on these teeth for tearing and stripping flesh from carcasses, a task that modern felids perform with the assistance of their stout and conically shaped canines; the extremely large upper canines of the sabre-tooths would probably be ineffective at the manipulation of chunks of flesh.
- (3) Upper carnassials (P^4) with a reduced or absent protocone (lingual lobe), which is lowered away from the occlusal surface in *Megantereon*, thus removing it from its role as a hammer for bone crushing (a condition that is present among extant felids in the hypercarnivorous cheetah), and is lost in *Homotherium*, in which there is also an anteriorly added accessory cusp. This tooth forms in sabre-tooths a long thin blade, which is extremely specialized for slicing flesh, and allowed them to deflesh their prey rapidly.
- (4) A lowered glenoid fossa, a reduced height of the coronoid process, a laterally shifted angular process, and a shortened zygomatic arch. All these features allow a wider gape than that of modern felids, but suggest that the temporalis muscle was weaker. However, the temporal fossae were shorter and narrower, which indicates that the temporalis was oriented in sabre-tooths more vertically and perpendicular to the tooth row than in modern felids. This increased the bite force at the carnassial (M_1), which was closer to the mandibular condyle, although it remained significantly lower than in felids.
- (5) An enlarged, lowered and ventrally extended mastoid process, which is enormous relative to modern felids, thus indicating that the cleido- and sterno-mastoid muscles must have been correspondingly large. The occiput in most sabre-tooths is relatively higher and narrower than in felids, and the temporomandibular joint is located more ventrally. The mastoid process is rotated further below the skull joint so that the leverage of the neck muscle is increased, thus suggesting that a head-depressing motion was involved in the penetration of the canines.

The postcranial skeletons of scimitar-toothed and dirk-toothed machairodonts are quite different (Martin, 1989). *Homotherium* was a relatively long legged pursuit predator with the size of a modern lion (150–220 kg, according to regressions of body mass against postcranial measurements in modern carnivores; Anyonge, 1993), which had a comparatively large brain with an enlargement of the optic centre, a condition similar to that of the cheetah (Rawn-

Schatzinger, 1992). The morphology of *Homotherium* is unique among extant and past felids, showing relative limb proportions which indicate increased cursoriality and less prey grappling capabilities than other sabre-tooths. Given the strikingly elongated forelimbs but rather short hindlimbs that characterize the species within this genus, they probably had a sloping back. The brachial index in *Homotherium* (radius length/humerus length) takes values close to or above 100%, which implies that most species of this genus preferred open habitats (Lewis, 1997). According to the results obtained by Anyonge (1996), in a comparative multivariate analysis of the locomotor behaviour of both extinct and modern species of large carnivores, based on cross-sectional geometric properties and linear dimensions of their femora and humeri, the North American species *H. serum* was classified by the discriminant functions in the cursorial category but with a probability of only 0.6; the next group of most likely membership (0.4) was the ambush category. The mean brachial index (103%) is intermediate to that in hyaenids and canids, whereas the mean crural index (tibia length/femur length, 78%) compares with that of the larger living felids; this species therefore had a postural stance that was rather intermediate between cursors and ambushers.

Dirk-toothed machairodonts (*Megantereon*, *Smilodon*) were relatively short limbed ambush hunters, with a comparatively smaller brain, showing olfactory lobes well developed. They had powerfully developed forelimbs, that suggests that a killing bite in the throat may have been coupled with the immobilization of the prey by the front limbs. Comparative multivariate analyses of post-cranial measurements (Lewis, 1997) indicate for *Megantereon* an overall morphology similar to that of extant jaguars, with tree catching and long distance dragging capabilities; the low value for the brachial index (slightly greater than 80% in Eurasian *M. cultridens*; Lewis, 1997) suggests closed habitat preferences. Morphofunctional studies of African *M. whitei* (Palmqvist, Martínez-Navarro & Arribas, 1996b; Martínez-Navarro & Palmqvist, 1996) indicate that this predator generated large amounts of carrion, since it would exploit the carcasses of its prey to a small degree. According to the results obtained by Anyonge (1996) in the multivariate analysis of post-cranial measurements in extant and extinct carnivores cited above, the larger and related New World species *Smilodon fatalis* (350 kg; Anyonge, 1993), a descendant of *M. hesperus*, was placed in the ambush category with a probability of 0.51, and the next most likely category was ambulator (i.e., that of ursids); femoral and humeral cross-sectional properties in *Smilodon* approach those of modern bears. The metapodials of this species were shorter than those of large modern felids and, in addition to slightly smaller brachial and crural indices, the possession of a relatively short tail argues for slower locomotory speeds in this sabre-tooth cat (Anyonge, 1996).

All these craniodental and post-cranial features indicate (1) that sabre-tooth felids were able to hunt very large prey relative to their own size, and (2) that they left on the carcasses of the ungulates hunted large amounts of flesh and all bone nutrients, which were subsequently scavenged by hyaenas and hominids (Marean, 1989). Sabre-tooths became extinct in East Africa 1.5 Ma ago, which coincides with the emergence of the Acheulean Industrial Complex, but inhabited Eurasia until 0.5 Ma (Turner, 1990, 1992). Their persistence may then explain the success of the Oldowan tools in Eurasia, where the Oldowan/Acheulean transition took place much later than in Africa, at approximately 0.5–0.4 Ma (i.e., when sabre-tooths disappeared in this continent), since the sharp flakes characteristic of Oldowan assemblages were fully appropriate for scavenging on partially defleshed carcasses and the cores were used to break bones for their marrow content. In this context, the striding gait for the emergence of the genus *Homo*, the elementary Oldowan stone tools and the expansive pattern of scavenging, also served its initial dispersal from Africa (Larick & Ciochon, 1996), which was facilitated by the availability of ungulate carcasses supplied by sabre-tooth cats.

An opposite interpretation of the ecological opportunities opened by sabre-tooths for the hominids has been argued by Turner (1990, 1992), who considers that the competition with the large and efficient bone-cracking hyaenid *P. brevirostris* made it difficult for hominids to develop an adaptive pattern of scavenging on the carcasses left by sabre-tooth cats, and that a stable and productive niche for the hominids in Europe was only possible after the replacement during Middle Pleistocene times (0.5 Ma) of sabre-tooths and giant hyaenas by modern African carnivores like the lion, the leopard and the spotted hyaena.

However, this argument is contradicted by the results obtained recently in two independent comparative studies (Capaldo, 1997; Selvaggio, 1998) of the incidence and distribution of tool marks and tooth marks on bovid long bone specimens from the FLK 22 assemblage at Olduvai Bed I (“*Zinjanthropus*” site, 1.8–1.76 Ma) and different experimental control samples, which have shown a three stage sequence (carnivore to hominid to carnivore involvement) of site formation. In stage one, flesh-eating carnivores (probably sabre-tooths in most cases) partially defleshed long bones, as deduced from the high frequency of tooth-marks on midshaft fragments; in stage two, hominids processed intact long bones for their marrow content, as inferred from percussion mark percentages,

and the presence of cut-marks indicates that the bones still retained at this stage variable amounts of flesh; finally, in stage three, bone-cracking carnivores consumed long bone epiphyses for grease, as inferred from the underrepresentation of these elements in the assemblage (the abundance of major long bone epiphyses is inversely correlated with their structural density) and the high percentage of tooth-marks on near-epiphyses and surviving epiphyses. Therefore, the results obtained clearly indicate that competition between hominids and bone-cracking carnivores was low at FLK 22, and that hominids had access before hyaenids to those carcasses partially defleshed by sabre-tooths; such a situation was probably the same in Europe during Lower Pleistocene times.

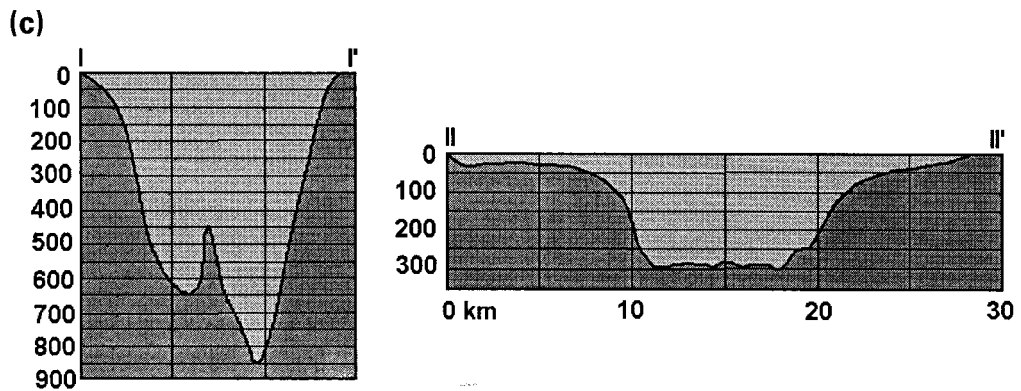
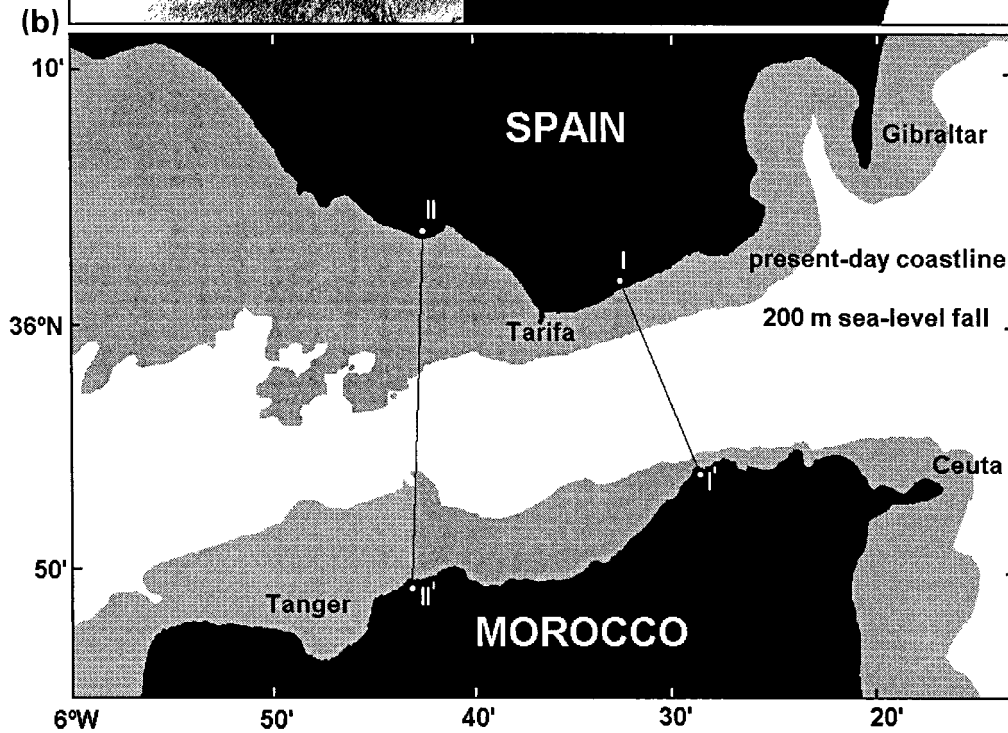
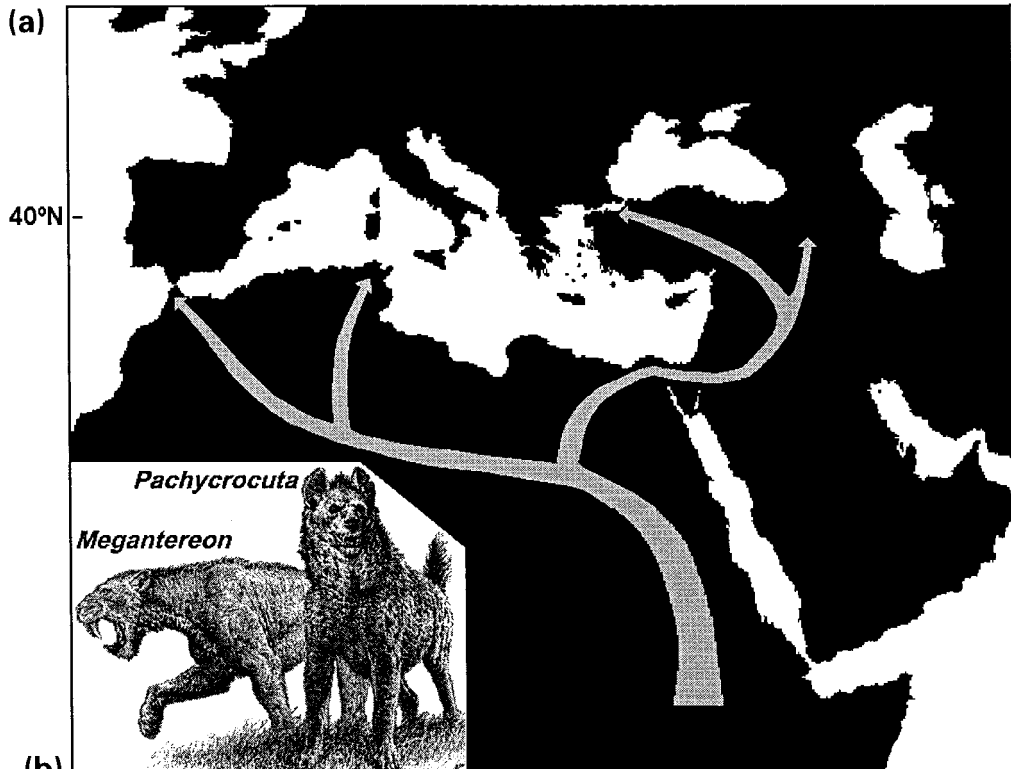
Dispersal Routes to Europe

Most palaeoanthropologists consider that *Homo* spread out of Africa by the Eastern Mediterranean or levantine land corridor (‘Ubeidiyah), reaching Europe through the Straits of Dardanelles (Figure 3(a)), which were closed by low water levels during the glacial cycles. However, it has been suggested that these hominids could have also crossed the Mediterranean via the Gibraltar Strait or even through Sicily (Alimen, 1975; Martínez-Navarro & Palmqvist, 1995, 1996); this possibility would require crossing open waters, even at the lowest sea-levels.

The minimum width of the Strait of Gibraltar is nowadays 14.5 km, but a sea-level fall of 200 m during the Aullan event (1.8–1.6 Ma) would result in the narrowing of this passage up to approximately 6.5 km (Figure 3(b)) and a drop of 300 m would nearly close it (Figure 3(c)). No evidence confirming the ability of *Homo* to cross stretches of open waters has yet been found in Spain or Italy, although the presence of narrow sea stretches does not seem to have represented an effective geographical barrier for human dispersal during the Plio–Pleistocene, as suggested by recent data on the colonization of Flores by *H. erectus* (as well as by other species of continental Southeast Asian fauna), dated at 0.9–0.8 Ma by zircon fission-tracks (Morwood *et al.*, 1998). Even when the sea level was at its lowest, these human populations would have to cross 19 km of water to get to Flores from the closest island of Sumbawa.

There are two additional lines of reasoning that support the possibility of a dispersal through Gibraltar (and perhaps even through the passage between Tunisia and Sicily): (1) the levantine corridor requires longer distance movements to reach Western Europe,

Figure 3. (a) Potential passages for African species to Europe during Lower Pleistocene times, through Gibraltar, Sicily and the Dardanelles. (b) Present-day coastline in the Strait of Gibraltar and hypothesized coastline during the Plio–Pleistocene transition, considering a sea-level fall of 200 m. (c) Topographical profiles of the Strait of Gibraltar between the points I–I’ and II–II’.



crossing large rivers and mountainous chains, with adaptations to different vegetation zones and to broader ranges of temperature and rainfall, and (2) a simultaneous colonization of Europe through Gibraltar, perhaps Sicily, and the Eastern Mediterranean (Figure 3(a)) helps to explain the presence in several north circummediterranean sites of Spain (Orce), Italy (Pirro Nord), Greece (Apollonia) and Georgia (Dmanisi) of certain African species of large mammals which have not been found, at present, in Central Europe during Lower Pleistocene times, such as *M. whitei*, whose dispersal seems to have been limited up to the 40°N parallel (Martínez-Navarro & Palmqvist, 1996).

The Dispersal of *Homo* Out of Africa: Alone or Lonely with Others?

Until now, three chronological hypotheses regarding the first arrival of humans in Europe have been proposed: the Europe of 0.5 Ma (the “Young Europe” of Carbonell *et al.*, 1995a), which was accepted until 1994; the Europe of 1.0 Ma (called the “Mature Europe”), which has been followed since then by most palaeo-anthropologists; and the Europe of 1.5 Ma (the “Old Europe”), which is for us the most reliable chronological scenario, although there are still reservations about this possibility owing to disputes on the human affinities of some controversial fossil remains from Orce (see Palmqvist, 1997), and also owing to uncertainties on the age of Dmanisi. In order to decide in favour of any of them, it is necessary to answer the following question: did humans leave Africa alone or simultaneously as a set of large mammals? This question has fortunately only two possible answers:

- (1) Humans left the austral continent alone. If this hypothesis were correct, the dispersal of *Homo* out of Africa would not depend on any extrinsic factor, but on intrinsic ones (i.e., population “saturation”, technological advances in tool making, etc.) and supposed abilities or attitudes which need to be further established and demonstrated. From this premise, if humans left Africa alone they could do so at any given moment from the time of their origin whenever the geographical and climatic barriers allowed them to disperse. According to the available palaeoanthropological records, the oldest presence of *Homo* in Asia would then be restricted to 1.8–1.6 Ma (Java, Southern China), in the Caucasus to 1.6 Ma (Dmanisi, Georgia), and in Western Europe to approximately 0.8 Ma (Atapuerca, Spain). In this case it would make no sense to consider in this discussion those aspects related with the technological level acquired by the genus *Homo* or with faunal dispersal events during the Plio–Pleistocene. The oldest archaeological and palaeontological evidences recovered in Southeast

Spain (Orce) would not be relevant for this history, since the information supplied by these sites points to a faunal turnover which is not detected in Atapuerca (where the record comprises species originating more recently in Asia, during the Middle Galerian). In this case the arrival of *Homo* to Europe would be independent of other palaeobiological factors, and thus the dispersal would be mono-specific.

- (2) Humans left Africa accompanied by other animals. If this scenario is correct, the fossil record should preserve species originating in Africa within the Eurasian ecosystems of Lower Pleistocene times, and the faunal turnover should concentrate on a restricted chronological interval. This hypothesis is widely corroborated by the fossil records in Europe, as discussed before. If we consider the partial faunal replacement of large mammals which took place in Europe at the Plio–Pleistocene limit (“Wolf event”: Asian species, “*Homo* event”: immigrants from Africa), it is then possible to explain the presence of both African carnivores and Asian ruminants in the Lower Pleistocene of the circummediterranean area, and their coexistence with members of the genus *Homo*, who showed anatomical affinities with *H. ergaster* and possessed the Oldowan Industrial Complex.

The first evidence of this faunal dispersal is recorded at the Plio–Pleistocene transition (1.8–1.6 Ma) in Western Europe, within the Olivola and Tasso faunal units, and in Central Eurasia (Dmanisi), where a complete record of this dispersal event exists, including human remains and evidence of cultural activity. Southeast Spain (Orce-Cueva Victoria, 1.4–1.1 Ma) has an exceptional record of these faunal assemblages, as well as the technological evidence of the first human populations. Finally, the most complete anatomical and cultural evidence of the hominids who could have been the descendant of those directly implied in the first colonization of Eurasia is found at the Gran Dolina of Atapuerca (<0.8 Ma).

Therefore, the recent findings in Atapuerca TD-6 Level do not support the scenario of the mature hypothesis for a colonization of Europe at around 1.0 Ma, given (1) the anatomical features of the hominid remains (which could be better related to *H. ergaster*), (2) the lack of fit between the age proposed for the site, its geographical location and the Oldowan/Acheulean chronology, and (3) the faunal incongruity (i.e., Asian origin of the Middle Galerian species preserved in the assemblage). On the contrary, the record from Atapuerca fills in part the palaeo-anthropological hiatus of the old hypothesis, i.e., the colonization of Europe before 1.5 Ma ago. It is then possible that the hominids from TD-6 represent one of the latest European populations, descended from the ancestor lineage defined by *H. ergaster*, which retained

its initial Oldowan technology and survived in Europe after the extinction that affected other African species of large mammals. It is also possible that this species, which has been called “*Homo antecessor*”, could co-exist in Europe with other populations of hominids originating in Asia, such as *H. erectus* (Ceprano, Italy), which arrived in Western Europe within the Middle Pleistocene faunal set from Asia, but this would be another history.

Acknowledgements

We gratefully acknowledge constructive remarks made by J. Damuth (University of California at Santa Barbara), R. G. Klein (Stanford University, California), R. Potts (Smithsonian Institution, Washington, D.C.) and R. A. Reymont (University of Uppsala). B. Martínez-Navarro (Orce Research Project, Granada) greatly helped us with the revision of the Villafranchian assemblages of large mammals from Europe, and also made very insightful comments which improved the article. This research was supported in part by a general grant from the “Leakey Foundation” and by DGESIT project number PB97–1082 from the Spanish Ministry of Education and Culture.

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