Longstanding biogeographic patterns and the dispersal of early Homo out of Africa and into Europe

J. van der Made \textsuperscript{a,}\textsuperscript{*}, A. Mateos \textsuperscript{b}

\textsuperscript{a}Museo Nacional de Ciencias Naturales, CSIC, c. José Gutiérrez Abascal 2, 28009 Madrid, Spain
\textsuperscript{b}Centro Nacional de Investigación sobre la Evolución Humana, CENIEH, Avd. La Paz 28, 09004 Burgos, Spain

Abstract

The study of the biogeography of large mammals may contribute to the understanding of human evolution, dispersal and technological or cultural abilities. The dispersal of Homo seems to have been conditioned by the availability of relatively open landscapes. Longstanding biogeographic patterns suggest that such habitats were available in an area extending from the north of Africa and the Middle East to Central Asia. Early Homo dispersed first into the open landscapes of Asia and later, like many other mammals, it dispersed from there into Western Europe, when environmental change allowed it to do so.

1. Introduction

Several attempts have been made to tie human dispersal to environmental change or to the dispersals of other mammals (Rolland, 1992; Turner, 1992, 1999; Martínez Navarro and Palmaqvist, 1996; Hemmer, 2001; Spassov, 2001, 2002, 2003; Holmes, 2007). If the dispersals of humans and other mammals coincide, this could be because of a direct causal relationship or because both reacted to environmental change. Alternatively, human evolution or cultural or technological advances could allow humans to disperse independently of faunal or climatic change (Carbonell et al., 1999; Dorianchey, 2000, 2008; Belmaker et al., 2002; Petraglia, 2005; Ronen, 2006; Dennell, 2007). The study of the context in which human dispersal took place may contribute to the understanding of human biological and cultural evolution.

The oldest record of the genus Homo and the oldest lithic industry is from around 2.5 Ma in Africa, while the first records from Southern Asia and Europe are around 1.8 Ma and 1.2 Ma, respectively (Dennell et al., 1988; Tixier et al., 1995; Semaw et al., 1997; Dennell and Roebroeks, 2005). These dates suggest that the dispersal of Homo from Africa to Asia and Europe is not a single event related to a single cause, but that it consisted of several events which are related to different causes. Dennell and Roebroeks (2005) suggested the possibility of complex scenarios with part of human evolution occurring in Asia. Recent work on human phylogeny points to a scenario, in which humans evolved in SW Asia and dispersed from there to Europe, East Asia and back into Africa (Martinón-Torres et al., 2007).

As possible routes of dispersal have been suggested: the Strait of Gibraltar, Sicily, the Palestine Corridor (or Levantine Corridor) and Bab al Mandeb. For several reasons dispersals to Europe across the Strait of Gibraltar and Sicily are unlikely (Villa, 2001; Van der Made, 2005c,d). Fernandes et al. (2006) argued that a landbridge connecting Africa and the Arabian Peninsula at the place of the Strait of Bab al Mandeb is unlikely. A model of early hominin dispersal (Holmes, 2007) predicts that the most likely dispersal route from Africa would have been through the Levantine region, followed by an expansion through Central Asia to the East. It is the aim of this paper to discuss aspects of the biogeographic background to early human dispersal.

2. The process of dispersal

Some authors prefer to reserve the word “migration” for cyclic (often seasonal) displacements of individuals and use the words expansion or dispersal if a species occupies a new territory, usually by population growth (Simpson, 1940; Tchernov, 1992). A healthy species has a birth surplus, though population size does not increase indefinitely; litter size may decrease and age of maturity increase, excess individuals loose the competition for resources and mates, or are removed by increased predation pressure, etc. This birth surplus allows a population to recover after some disaster like an epidemic or to expand into new areas when these become available. This expansion is fed by the birth surplus in the zone bordering the “empty” territory. Historic dispersals into suitable habitats show that the limit of the populated area may extend at a rate of over 10 or even over 20 km per year (Van der Made, 1992). This has various implications:
1) If humans originated in Africa, they must have occupied the suitable habitats in an instant, geologically speaking. It does not seem likely, that “demographic pressure”, built up during hundreds of thousands of years in different parts of Africa, was the cause of dispersal.

2) When the limits of suitable habitats widened or when evolutionary or cultural adaptation made new habitats accessible, Homo expanded into wider areas till it was again checked by the limits of the habitats in which it could live.

3. A dry belt from Northern Africa to Central Asia

There is a general consensus that early Homo lived in the open environments of Eastern Africa. Dry areas tend to have relatively open landscapes, Areas with arid and open landscapes tend to change gradually to areas with humid and closed environments. Animals, including Homo, are not adapted to just arid/open or humid/closed environments, but their optimal environment may be intermediate.

At present there is an arid belt extending from the Sahara to the Middle East to Central Asia. This belt limits the distribution of various types of animals, such as Talpidae. Talpidae feed mainly on earthworms and these tend to live in humid, slightly acid soils with abundant organic material and temperatures that are not very high (Edwards and Lofty, 1977). This implies that the distribution of Talpidae is limited by desert soils which develop in arid climates (van der Made, 1992; Fig. 2). Though Talpidae lived since the Eocene in Europe and since the Oligocene in Asia and even reached SE Asia, they never entered Africa and only a limited part of Northern India (coming from the east) (Maglio and Cooke, 1978; Ziegler, 1999).

Castoridae lived since the Oligocene in Northern Eurasia, but never made it to Africa or the Indian Subcontinent (Maglio and Cooke, 1978; Flynn et al., 1995; Hugueney, 1999).

Cervidae have existed since at least 20 Ma and lived in an area extending from Europe and Northern Asia to SE Asia (Vislobokova, 1997; Azanza Asensio, 2000), but did not enter the Indian Subcontinent till some 2.5 Ma ago (Colbert, 1935; Hussain et al., 1992) and Africa until some 0.1–0.2 Ma ago (Maglio and Cooke, 1978; van der Made, 2005a). The Indian Subcontinent may have been limited in the north and east by the Himalayas and remnants of he Tethys, but in the Middle East, during some 17 millions of years, the southern limit of distribution of the Cervidae ran through Anatolia.

From the Oligocene till about 2.5 Ma ago Tapiridae existed in Northern and Eastern Eurasia, but they never entered the Indian Subcontinent nor Africa (van der Made and Stefanovic, 2006).

The brachydont equid Anchitherium lived from some 20 to 11 Ma ago in Europe and the north of Asia, it lived in parts of Anatolia, but never reached Africa nor the Indian Subcontinent (Colbert, 1935; Maglio and Cooke, 1978; Abusch-Siewert, 1983; Flynn et al., 1995). All these animals share that they were limited by arid or open environments and the southern most limit of their distribution was during many millions of years somewhere in Anatolia.

Camels are adapted to arid environments and lived since they appeared in the Old World in the arid parts of North Africa, the Middle East and Central Asia (van der Made and Morales, 1999). Giraffidae are also adapted to relatively open environments and during millions of years, they occurred above all in areas which today have open landscapes (Colbert, 1935; Maglio and Cooke, 1978; Montoya and Morales, 1991; Gentry et al., 1999).

Both lines of evidence suggest that:

1) For possibly as much as 20 million years, there may have been relatively dry or open environments in the north of Africa, the Middle East and Central Asia, though the position and degree of dryness of this dry belt may have fluctuated. The marine record suggests arid conditions in North Africa during the Mio-Pliocene and extensive dune sediments in Chad were recorded with an age of 7 Ma (Schuster et al., 2006). Wind blown dust in ocean cores suggest fluctuations and a general increase in aridity in the north of Africa and the Arabian Peninsula during the past 4 Ma (deMenocal, 1995).

2) The presence of open or arid landscapes could be the reason why early Hominini did not make it out of Africa. Once early Homo became adapted to open and relatively dry environments, its dispersal into these areas may have been favoured to some extend, depending on the degree of aridity.

4. Faunal dispersals from SE Europe and SW Asia to Western Europe

The presence of early Homo in the area of SW Asia and SE Europe is indicated by its presence in Dmanisi with an age of about 1.8 Ma (Gabunia and Vekua, 1995; Lumley et al., 2002; Lordkipanidze et al., 2006). The locality of Dealul Mijlociu (Romania) is reported to have lithic industry and an age around 1.8 Ma and the locality of Sandalja 1 (Croatia) is reported to have yielded a human incisor and a chopper; its age is said to be Late Villafranchian and its faunal list indeed suggests such an age, but the anthropic nature of all these remains is not universally accepted (Radulescu and Samson, 1990; Bossinski, 1996; Radulescu et al., 2003; Spassov, 2003). A human tooth and lithic industry is reported from the lower levels at the site of Kozarnika, with biochronologically estimated ages between 1.2 and 1.4 Ma (Guadelli et al., 2005). A skull and mandible of a toothless individual from Dmanisi suggests that at this stage, there may have been considerable social cohesion (Lordkipanidze et al., 2006) and the fauna from Dmanisi has predominantly European affinities (van der Made, 2005b; Fig. 3.2). Both observations might suggest that further dispersal into Europe would be easy. However, this is not confirmed by the paleontological and archaeological record in Central and Western Europe.

The area of SE Europe and SW Asia around the Black Sea (or its predecessor the Paratethys) is the area where the humid faunas of Europe and Northern Asia intergrade with the faunas that live and lived in the arid area that extends from N Africa to Central Asia. Though no attempt was made to be complete, Fig. 1 shows that many species or genera have been living in this area for hundreds of thousands or even for millions of years before they dispersed further into Europe. Several of the mammals in Fig. 1 were of African origin or related to mammals living in Africa. Many of them were adapted to arid or open environments and several of these dispersed to the arid areas of the Iberian Peninsula without even leaving a fossil record in the more humid areas in Central Europe. This pattern has the following implications:

1) It confirms the biogeographic boundary that was described in the previous section.

2) The first appearance dates of such mammals cannot be used in biostratigraphic correlations. In fact, biostratigraphic correlation from this area to Western Europe is often more difficult than from Europe to China, because of the east-west directed climatic and vegetational zones.

3) The occurrence of Homo at Dmanisi with a fauna of predominantly European affinities does not mean that it was part of the European fauna, nor that it was easy to disperse into Europe. Instead, it may have lived at the limit of its preferred habitat,
Fig. 1. Temporal distribution of selected mammals compared in the Iberian Peninsula (solid lines) and in SE Europe and SW Asia (squares indicating presence in the localities indicated on the right). Ages in Ma on the left, Epochs and their subdivisions after Gradstein et al. (2004), MN units after Mein (1975), de Bruijn et al. (1992) and Agustí et al. (2001). Ranges of the mammals in Spain or Western Europe are indicated by Daams et al. (1998) and de Bruijn et al. (1992). For the latest Miocene and early Pliocene the figure is based on van der Made et al. (2006), for the Late Pliocene and Pleistocene on van der Made (2005b), for the Early Miocene rodents on de Bruijn and Saraç (1991) and de Bruijn et al. (1993), and for the remainder on the literature (incl. van der Made, 1999; Güleç et al., 2003; Fortelius et al., 2003).
resembling the mammals in Fig. 1, which were adapted to open or dry environments and which lived for a considerable time together with mammals of European affinities before dispersing into Europe.

5. Human dispersal into Western Europe

The earliest presence of Homo in Western Europe is indicated by lithic industry in Barranco León 5, Fuente Nueva 3 and Pirro Nord and industry and human remains from Atapuerca Sima del Elefante level TE9 (Tixier et al., 1995; Arzarello et al., 2007; Carbonell et al., 2008). Though there is discussion on the age of some of these localities, a conservative estimate is that none of them is older than about 1.2 Ma.

Fig. 2 shows the dispersals of large mammals into Western Europe during the last 4 Ma. In general, the frequency of dispersal events into Western Europe increased, as well as the number of species involved. There were several important events.

One occurred between 3.5 and 3.2 Ma, when a variety of mammals dispersed and when the oxygen isotope curve shows some peaks suggesting relatively cold phases.
A dispersal event around 2.6–2.5 Ma includes few, but very important mammals. Not only does it include mammals that have been used to define the lower border of the Pleistocene and Quaternary, but these mammals became very dominant in the faunas. If one excavates a fauna of this age, it is likely that a large part of the fossils belong to these mammals. This event coincides with the effects of the 40 ka eccentricity cycle becoming more dominant in the global climate, resulting in an increased seasonality at high and mid latitudes (deMenocal, 1995). Around 2.0 Ma there is an event involving several mammals, but these tend to be much less common than those in the event at 2.6–2.5 Ma. After a relatively quiet period, starting some 1.2 Ma ago, there are many dispersal events, often once or twice per climatic cycle. This happened when the 100 ka eccentricity cycle became more dominant forcing global climate and leading to the major glacial cycles (deMenocal, 1995). The alternation of glacial and interglacial environments increased the number of niches for large mammals. Within these 1.2 Ma more dispersals into Western Europe occurred, than in any period of the same duration in the previous 25 Ma. Though due to the previous continuous or repetitive contacts, no new families or orders appeared in Western Europe, but in number of species involved, the cumulative events from 1.2 Ma onwards approach the major events like the Grand Coupure, Proboscidean, and that in any period of the same duration in the previous 25 Ma.

6. Conclusions

1) The majority of Pleistocene species dispersing into Western Europe are of Asian origins, several of them adapted to open or dry environments.

2) The first human record in Europe at about 1.2 Ma coincides with major environmental change and the onset of a series of dispersals of large mammals into Western Europe. It seems to have coincided particularly with the dispersal of bisons, which are highly adapted grazers and their dispersal may be related to an increase in open habitats.

3) A belt of dry habitats seems to have existed during many millions of years, extending from the north of Africa to Central Asia, though its exact extension, position and degree of aridity may have varied. Along its edges this belt graded into more humid habitats. Homo may have dispersed along this belt into areas with a relatively open landscapes.

4) Many mammals, including Homo, dispersed from this habitat into Western Europe when the opportunity arose, which may have taken hundreds of thousands or millions of years.

5) Human dispersal into Western and Central Europe may have occurred from populations living in Southern or Central Asia at a time when several mammals, typical of open or dry landscapes, dispersed from Asia into Europe.

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