Early and Middle Pleistocene Faunal and Hominins Dispersals through Southwestern Asia

The Harvard community has made this article openly available. Please share how this access benefits you. Your story matters.

Citation

Published Version
doi:10.1016/j.quascirev.2010.02.016

Citable link
http://nrs.harvard.edu/urn-3:HUL.InstRepos:4270472

Terms of Use
This article was downloaded from Harvard University’s DASH repository, and is made available under the terms and conditions applicable to Open Access Policy Articles, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#OAP
Early and Middle Pleistocene Faunal and Hominins Dispersals through Southwestern Asia

Ofer Bar-Yosef and Miriam Belmaker

Department of Anthropology
Harvard University
11 Divinity Avenue
Cambridge MA 02138
Phone ++ 1 617 495 1279
Fax ++ 1 617 496 8041
Abstract

This review summarizes the paleoecology of the Early and Middle Pleistocene of southwestern Asia, based on both flora and fauna, retrieved from a series of ‘windows’ provided by the excavated sites. The incomplete chrono-stratigraphy of this vast region does not allow to accept the direct chronological correlation between the available sites and events of faunal and hominin dispersals from Africa. It also demonstrates that hominins survived in a mixed landscape of open parkland with forested surrounding hills. In addition, the prevailing environmental conditions are not sufficient to explain the differences between ‘core and flake’ and the Acheulian industries that probably reflect the learned traditions of different groups of hominins successful adaptations to new ecological niches away from the African savanna. The current distribution of lithic industries across Eurasia is undoubtedly incomplete due to lack of cultural continuities as well as paucity of field research in several sub-regions. This observation supports the contention that what we view as a constant stream of migrants was actually interrupted many times. The continuous occupation of southwestern Asia by the makers of the Acheulian is in contrast with neighboring regions such as the Iranian plateau and Eastern Europe. A more complex model is required to explain the Eurasian archaeological-cultural mosaic recorded in Eurasia.
Introduction

The effect of climate change on the tempo and mode of early hominids dispersals from Africa during the Early and Middle Pleistocene is one of the main interests in paleoanthropology and Paleolithic archaeology (Behrensmeyer, 2006). It has been suggested that the expansion of savanna environments during the Early Pleistocene allowed for the first ‘Out of Africa I’ dispersal (Dennell, 2004; Martínez-Navarro, 2004) and that humans dispersed into Western Europe during warmer periods and that the dispersal was highly influenced by climate rather than culture, which played only a minor role (Agustí et al., 2009a). However, these theories assume as a working hypotheses that the presence of hominins and faunal present in the paleontological and archaeological record is continuous. Here we would like to focus on southwestern Asia that served as the main corridor for hominin dispersal during the Early and Middle Pleistocene and address the assertion that we can test hominids co-dispersed with other taxa and the extent of the response to climatic forcing. We will propose that there is no correlation between hominid and faunal dispersals and suggest that early Homo dispersals were not directly controlled by climatic forcing.

Geological and archaeological investigations in southwestern Asia produced a few “windows” into the geological sequence of the Early and Middle Pleistocene. Most of these “windows” are known from excavations of archaeological sites. Hence, in order to provide a continuous narrative of hominin and faunal dispersals we need to combine the chronologically patchy information with the physiographic variability of this vast region, as well as the incomplete paleo-climatic conditions that determined the distribution of resources in each sub-region.
The sub-regions of southwestern Asia are commonly identified from north to south and west to east as follows: Anatolia, the southern Caucasus, The Zagros mountains and the Iranian plateau, the Levant and the Arabian peninsula. Among these, due to many years of field and laboratory research, the better known is the Levant. It also has the advantage that researchers from various schools and institutions conducted surveys of Quaternary deposits, drilling boreholes for water and pollen, and archaeological excavations of Lower Paleolithic occupations. Thus the accumulated information creates an imbalance between the areas, some of which like the Iranian and the Anatolian plateaus are of larger area than the Levant but yet poorly known. We are therefore forced to base our review on the Levantine sequence and touch upon, in a more cursory fashion, the other sub-regions.

The Levant is a unique biogeographic entity within southwestern Asia. It lies at the crossroads of Africa and Eurasia and has more lush environments compared to the alternative dispersal corridor on the southern fringes of the Arabian Peninsula. This land bridge emerged during the Miocene as a continuous terrestrial belt that allowed various plants and animal taxa to migrate through in either direction (Thomas, 1985; Tchernov, 1988; Bar-Yosef, 1994,1998a). The southern path through the margins of the Arabian Peninsula could be crossed at the Bab el-Mandeb straights during low sea level stands, and along the area that receives the summer Indian Ocean monsoon to be followed by a passageway through the Hormuz straights into the southern coast of Iran (Fig. 1), and a northern path via the Nile river and the Sinai Peninsula.

During the Middle Pleistocene both land and sea bridges were potential dispersal routes for hominins (Derricourt, 2006). However, the available archaeological evidence
was retrieved only from the Levant with a few indications from the southern route (Amirkhanov, 1991). During the Late Pliocene and Early Pleistocene there is no evidence for a land bridge over the Bab el Mandeb straits. Indeed, during this time period, dispersals of most animal and plants seem to have been limited to the terrestrial Northern corridor of the Levant.

It is well-known that dispersals of early *Homo ergaster/ectectus* from Africa across Eurasia during the Early and Middle Pleistocene are interpolated from isolated archaeological and fossil sites (e.g., Gabunia and Vekua, 1995; Larick and Ciochon, 1996; Bar-Yosef, 1998a; Potts, 1998; Arribas and Palmqvist, 1999; Bar-Yosef and Belfer-Cohen, 2001; Potts, 2002; Antón and Swisher, 2004; Martínez-Navarro, 2004; Lordkipanidze et al., 2007). The reasons for these long-range migrations, whether in a form of “leap frog” expansions or gradual diffusion, are formulated as plausible hypotheses, open to alternative interpretations. Moreover, the advantages for leaving Africa are not easily testable (e.g., Bar-Yosef and Belfer-Cohen, 2001). One may use the biogeographic ranges outside Africa, from the Iberian peninsula to East and Southeast Asia, occupied by early hominins, to calculate the rate of movements and the chance for long term survival of early mobile hunter-gatherers. Currently it seems that it took ca. 0.5 Ma to reach Western Europe by ca. 1.3 Ma (Agustí et al., 2000) and much less time to get to ca. 1.66-1.7 Ma to East and Southeast Asia (Zhu et al., 2003; Antón and Swisher, 2004). One of the major questions is how African species adapted to the ecological variability in Eurasia and the role the ‘culture’, as recorded in the stone tools, assisted (or not) in the survival of lineages in the new territories.
For the purpose of making the most parsimonious explanations about hominin adaptations, and indicating where and when continuity is interrupted, probably by the demise of some groups, we provide a brief review of current climatic and vegetation conditions, a survey of the main Lower Paleolithic sites, followed by a summary of the vegetation and faunal records as a basis for environmental reconstruction and long distance correlations with known climatic events, and evaluation of hominin dispersals through this region.

Current Climatic Conditions

The dominant physiographic feature of southwestern Asia is the combination of mountains, plateaus, alluvial plains and desert landscapes including oases. The Anatolia plateau is surrounded by mountains ranges in the north and the south where the Taurus Mountains arching eastward into the Zagros Mountains. The Levant, along the eastern Mediterranean coast has several parallel features. The narrow coastal plain in the north widens in the south, the mountain ranges create the main watershed of this sub-region, the Anuq-Beqa’a-Jordan Rift Valley stretches from north to south, and the Trans-Jordanian or Syro-Arabia desert plateau descends eastward and southward. The Euphrates and the Tigris rivers and their tributaries cross the Mesopotamian plain, which is bordered by the Zagros Mountains and the Iranian plateau. The latter was and is mainly desert strewn by oases.

Today’s climate of the region is dominated by cold winters with the precipitation brought by the westerlies. Snow falls only in the higher mountains, and in particular in eastern Turkey and the northwestern Zagros. Summers are hot and dry. There is a wide
range of variation across the region. Thus, winter temperatures are milder in the coastal belts and more severe inland or at higher elevations and precipitation is effected by distance from the Mediterranean Sea and the local sub-regional altitude.

The East Mediterranean region is located between the more temperate European climatic zone in the north and the hyper arid regions of the Saharo-Arabian desert belt in the south. Since the synoptic hydrological conditions may affect the entire southwestern Asia, the question is whether and how warm to cold and humid to dry oscillations affected the Levant since the Early Pleistocene (Frumkin and Stein, 2004).

Models of Pleistocene climates attempted to explain the paleoclimatic record of the Levant. Earlier Butzer (1958) suggested a high correlation between the local intensification of the westerly circulation of the Mediterranean during glacial periods and the deep Cyprus Lows that would explain the increase in rainfall during glacial times. Similar views were expressed by others (e.g., Horowitz, 1979). Recently, the extent the increase of annual precipitation during North Hemispheric glaciations affected the Levant, and whether it extended into the currently dry desert belt in the south has been a topic of debate (Enzel et al., 2008 and references therein).

The climatic conditions and physiographic conditions determined the distribution of the phytogeographic belts (Zohary, 1973; Danin, 1988), and the most frequently encountered mammals in each region (e.g., Harrison and Bates, 1991; Harrison, 1972):

1. The Pontic province – the ‘Euro-Siberian’ region corresponds to the Palearctic deciduous and coniferous forests. It stretches from the southern edge of the Black Sea in northern Turkey as well as relict enclaves in south in the Anti-Taurus Mountains, the Syrian Amanus range and northern Lebanon. Part of the Pontic includes the Hyrcanian
province of the coastal mountains of the southern Caspian Sea that descends into Iraqi-
Kurdistan and northern Syria. It included deciduous species of maple (Acer), birch
(Bitula), hazelnut (Corylus), beech (Fagus), ash (Fraximus), lime (Tilia) and elm (Ulmus)
that have a clear Arcto-Tertiary origin. Other evergreen species that occur in southern
Europe are present such as the boxwood (Buxus sempervirens), holly (Ilex aquifolium)
and yew (Taxus baccata).

2. Irano-Turanian province – covers the sub-regions of the Anatolian plateau, the
Syrian Desert, the Iranian plateau, and stretches into central Asia and the Gobi Desert.
The climate here is dominated by extremely cold winters and very hot summers with little
to no rain fall in the winter. It is dominated by dwarf scrubland and steppes vegetation.

3. The Saharo-Arabian province stretches south of the Mediterranean basin and
extends from Mauritania to the Red Sea incorporating the Sahara desert. This vegetation
is open xeromorphic dwarf scrubland and desert plant associations.

4. The Mediterranean province spreads around the Mediterranean Sea and
includes a combination of maquis and forests dominated by oak (Quercus), Olive (Olea)
and almonds (Amgydalis communis).

5. The Sudano-Zambesian province is confined to the Jordan Valley and preserves
relicts of typical African subtropical savanna species such as the acacias.

Southwestern Asia was frequented by fauna from three biogeographic provinces:

Palaearctic, Oriental and Ethiopian in different proportions. Here we include a
description of extant fauna, all species dating to the early Holocene that predates the
effects of agriculture, horticulture and hunting. Thus most of the data comes from
archaeological excavations.
Many taxa are similar over two or more provinces giving the entire Near East a coherent faunal community (Harrison and Bate, 1992). Two main regions can be observed: The first includes the Mediterranean, Pontic and Iranian plateau provinces with Palaeartic taxa, and the second includes the mesic Mediterranean, Arabian provinces with Ethiopian elements. Taxa common to all regions include *Hyaena hyaena, Felis silvestris, Felis chaus, Panthera pardus, Acinonyx jubatus, Lepus capensis, Hystrix indica, Rattus rattus, Rattus norvegicus, Mus macedonius*. Palaeartic fauna which are found in the Mesic regions of the Mediterranean, the Pontic and much of the Iranian plateau include *Dama mesopotamica, Capreolus capreolus, Cervus elaphus, Sus scrofa, Canis aureus, Canis lupus, Vulpes vulpes, Panthera pardus, Ursus arctos, Martes foina, Vormela peregusna, Mustela nivalis, Meles meles, Lutra lutra, Sciurus anomalus, Spalax leucodon, Apodemus mystacinus, Apodemus sylvaticus, Cricetulus migratorius, Meriones tristrami* and *Microtus guentheri*. The Ethiopian taxa unique to the Arabian region are *Vulpes rueppellii, Vulpes cana* and *Vulpes zerda, Mellivora capensis, Genetta felina, Felis margarita, Caracal caracal, Procavia capensis, Acomys cahirinus, Eliomys melanurus, Gerbillus nanus, Gerbillus dayurus, Sekeetamys calurus,* and *Psammomys obesus*.

Nonetheless, while some genera are common throughout the entire region, the species within each genus differ across the provinces. Thus, the unique species that appear in each province give its unique affinities. For example, the caprine in the Caucasus is *Capra caucasica* while the dominant *Capra* is the Iranian plateau is *Capra aegagrus* and in the Mediterranean and Arabia is *Capra ibex*. The gazelle in the semi arid regions of the Mediterranean is *Gazella gazelle*, in Arabia it is *Gazella dorcas* and in the
Iranian plateau is *Gazella subgottarossa*. Furthermore, other species are unique to each region. For example, species unique to the Pontic region are *Lynx Lynx*, *Apodemus flavicollis*, and *Mesocricetus auratus*. Species unique to the Iranian plateau are the *Ovis ammon*, *Allactaga euphratica*, *Dryomys nitedula*, *Calomyscus bailwardi*, *Meriones persicus* and *Ellobius fuscocapillius*. Species unique to Arabia are *Oryx leucoryx*, *Tragelaphus imbris*, *Jaculus jaculus*, *Arvicanthis niloticus* and *Gerbillus gerbillus*.

However, it is most important to remember that the home ranges of the species is fluid rather than static, and are constantly changing dependant on climatic and environmental changes and inter and intra species competition. Therefore, the presence-absence of faunal elements correspond to the vegetation conditions, and disperse when resources diminish during worsening climatic conditions that could also result in extinction (Bennett, 1997). Thus in the following sections, we will discuss the changes in the distribution of botanical and faunal compositions across the Early and Middle Pleistocene in relation to the biogeographic provinces of southwestern Asia.

**Lower and Middle Pleistocene sites in Southwestern Asia**

The series of sites briefly described below form the isolated windows we have in southwestern Asia into this long period of the Early and Middle Pleistocene. In the absence of radiometric dating and/or paleomagnetic information the ages of several of the localities rely on faunal correlations within the region including long distance comparisons with European sites. Indeed, most of the Pleistocene data was acquired through archaeological excavations while the number of assemblages derived from natural accumulations is limited to a few Pliocene sites in the Caucasus region such as
Kvabebi (Vekua and Lordkipadinze, 2008; Agustí et al., 2009b) and Bethlehem in the Levant (see below).

There are special localities in the Levant that were thought to provide evidence for early presence of hominins, but a close examination do not stand up to the geochronological criteria. The mammalian fauna of Bethlehem is the oldest Plio-
Pleistocene assemblage known from the Levant. This was an animal bone accumulation incorporated in a deposit of flint fragments and clay discovered when a local farmer was digging a well (Gardner and Bate, 1937). The small collection of flints was originally thought to include human artifacts but they have since been shown to be natural (Hooijer, 1958; Clark, 1961).

Another claim for an Early Pleistocene site named Yiron where core and flakes have been retrieved from the gravels in a major crevice. Unfortunately the Yiron basalt on the plateau did not cover this location and thus the date of the lava flow of 2.4 Ma (Ronen et al., 1980; Ronen, 1991a), is unrelated to the human made lithics.

The ‘Erq el Ahmar Formation (Horowitz, 1979) is located about 14 km south of the Sea of Galilee, in the Jordan Valley and accumulated prior to the ‘Ubeidiya Formation. The polarity sequence is correlated with late Gauss and early Matuyuma chrons, within which the Olduvai subchron was identified (Ron and Levi, 2001). Unfortunately the artifacts mentioned in the different papers were found on the surface, except for a few retrieved from a fluvial conglomerate of an unknown stratigraphic position (Tchernov, 1995). Hence, the attribution of these to the Olduvai subchron is only tentative and cannot serve as a well-established evidence for hominin presence prior to Dmanisi (Bar-Yosef, 1998a).
The subsequent analysis of faunal turnovers in the Levant and the Caucasian region is reported in relation to the cultural definitions, and supplemented by the information from dated archaeological contexts (Table 1). It is followed by information from the more poorly known regions of Anatolia, the Iranian plateau and the Arabian Peninsula; For the sake of clarity, we briefly present the major sites that contain archaeological remains and their cultural attributions in the Caucasian and the Levant regions according to their accepted chronology and regardless of their geographic location (Fig. 1). Numerous prehistoric occurrences were assigned to the Early and Middle Pleistocene that did not yield fossil bones or datable substances or deposits amenable to paleomagnetic readings. On morphological grounds the collected or excavated artifacts were attributed to the Acheulian sequence such as the Early Acheulian occurrences at Nahal Zihor in the Negev (Ginat et al., 2003) or the Late Acheulian in Ma’ayan Baruch in the Upper Jordan Valley. In summarizing the archaeological information we do not describe the faunal and floral remains found in each site in this section, as they will be discussed in length in the following one. The condensed information will allow us to demonstrate below that the assumptions concerning continuous hominin dispersals into Eurasia relies on a series of speculations and that the proposed timing of prehistoric migration is not well tied with the transitions among the faunal assemblages.

**Dmanisi**

The site of Dmanisi is located on a basaltic block bordered by two tributaries of the larger Kura River. The prehistoric deposits were target for systematic excavations
(Vekua, 1987; Dzaporidze et al., 1989; Gabunia and Vekua, 1990, 1995; Liubin and  
Bosinski, 1995; Liubin and Bosinski, 1995; Lordkipanidze et al., 2007; Jöris, 2008;  
Rightmire et al., 2006). The geoarchaeological study concluded that entire sequence at  
Dmanisi could be dated to the Olduvai subchron and immediately after as shown by the  
normal polarity of the lower lava flow (1.8±0.1 Ma) and the infillings of the upper  
deposit that date to 1.77 Ma. Several human skulls and postcranial bones are attributed to  
*Homo erectus/ergaster* (Gabunia and Vekua, 1995; Rightmire et al., 2006; Lordkipanidze  
et al., 2007). The lithics of Dmanisi are identified as core and flake industry sometimes  
called “pre-Oldowan” or Mode 1 (de Lumley et al., 2005; Jöris, 2008). The Dmanisi core  
and flake industry marks the presence of hominins that did not practice the production of  
handaxes (bifaces). It indicates that handaxes were not a necessity for the colonization of  
Eurasia. The Dmanisi faunal assemblage is earlier than the faunas of Sénèze and Le  
Coupet, and thus also earlier than ‘Ubeidiya (Tchernov, 1987).

‘Ubeidiya

‘Ubeidiya is situated on the edge of the western escarpment of the Jordan Rift  
Valley and its geological structure was uncovered through a series of excavations  
(already reported in details) an anticline with several undulations disturbed by a few  
faults (Bar-Yosef and Tchernov, 1972; Bar-Yosef and Goren-Inbar, 1993). The exposed  
tilted layers were numbered from those observed as the earliest to the latest over a total  
thickness of 154m. The sequence was subdivided into four cycles: two mostly limnic (Li  
and Lu) and two essentially terrestrial (Fi and Fu).

The raw materials used for manufacturing artifacts were lava (basalt), flint, and
limestone. The basalt nodules occurred as pebbles, cobbles, boulders, and scree components; the limestone was available as much more sparse cobbles within the beach and wadi deposits; and the flint is found in the same environments as small pebbles and cobbles. The ‘Ubeidiya hominins employed each type of rock to shape a different type of object (Bar-Yosef and Goren-Inbar, 1993). Core-choppers and light-duty tools were made of flint, spheroids mainly of limestone, and the handaxe group from basalt, with a few of flint and limestone. There is a direct correlation between the size of the tool-category and the type of raw material. Although basalt is the most common rock and found in every lithological facies at ‘Ubeidiya the most abundant object is the core-chopper, which is made of flint and its detached pieces (flakes). It seems that the lithic assemblages from the lower most layers in the sequence (K/III-12, III-20-22, II-23-24) contain an abundance of core-choppers, polyhedrons and spheroids but lack bifaces, except for one trihedral. The samples are large enough to suggest that they may indicate the presence of an early group of hominins that did not produce bifaces. The overlying assemblages contain bifaces in varying frequencies and can be called Early Acheulian (Bar-Yosef and Goren-Inbar, 1993). As the presence or absence of bifaces is taken to designate different groups of hominins one may speculate that as in Dmanisi, the first hominins to arrive at ‘Ubeidiya, were not the bearers of the Acheulian.

Among the so-called formal categories the frequencies of bifaces are abundant in gravelly layer K-30 although the underlying layer K-29 of the same wadi fill produced very few bifaces. It seems that certain activities were carried in the hilly-forested areas from which the more abraded assemblage of K-30 was derived. The almost total disappearance of bifaces in the later assemblages at ‘Ubeidiya is noticeable and as yet
unexplained.

Estimated dates for the fossil-bearing strata of the ‘Ubeidiya Formation are between ca. 1.6 - 1.2 Ma. Paleomagnetic analysis of the ‘Ubeidiya Formation indicated a reversed polarity suggesting that it predates the Brunhes - Matuyama reversal (Opdyke et al., 1983; Braun et al., 1991; Verosub and Tchernov, 1991). Two short, normal paleomagnetic episodes have been found in the Fi member layers II-33 and II 23-24.

Layer II-33 has been assigned to the Cobb Mt. (1.215 - 1.190 Ma) and layer II 23-24 has been assigned to the Gilsa (1.575-1.567 Ma) (Sagi, 2005). This correlation fits well with an ESR date of ca. 1.2 Ma for the stratum I 26 which immediately overlays stratum II 33 (Rink et al., 2007).

The dating of these short polarity events was also corroborated by local faunal turnovers (Belmaker, 2009). The ‘Ubeidiya fauna (Table 1) can be assigned to a local mammalian fauna biozone older than the assemblages of Bitzat Ruhama, Evron-Quarry and Latamne (Belmaker, 2009). All these sites have been dated to ca. 1.0-1.2 Ma suggesting that the ‘Ubeidiya normal polarity events in strata II 23-24 and II-33 should both predate the Jaramillo (0.99-1.07 Ma). Further corroboration by long-range biochronological correlations indicates that the large mammalian assemblage of ‘Ubeidiya is similar to the Farneta faunal unit (the sites of Selvella and Pietrafitta, Italy) (Belmaker, 2006; Martínez-Navarro et al., 2009), which has been dated to ca. 1.6-1.2 Ma (Caloi and Palombo, 1997 and references therein). Employing similar approach of long distance comparisons to the lithics of ‘Ubeidiya suggests that the assemblages are similar to those from upper Bed II at Olduvai dated to ca. 1.53-1.27 Ma (Bar-Yosef and Goren-Inbar, 1993; Cerling and Hay, 1986).
**Evron-Quarry**

The excavations at Evron-Quarry, located in the coastal plain of the Western Galilee, exposed a sequence of alternating deposits of sandstone (*kurkar*), sometimes up to three meters thick, and red-brown loams (*hamra*), either as isolated lenses or layers up to about one to four m thick (Ronen, 1991b). The layer that contained the Acheulian industry had two distinct horizons of calcareous concretions, occasional artifacts, and sandy clay lenses with pebbles (two to three meter thick) separated from the dark brown-black clay (two m thick) that contained Late Acheulian artifacts and a few animal bones. The artifacts within the archaeological horizon had a vertical distribution of 15-25 cm deep, a phenomenon interpreted as the result of repeated occupations. The archaeological assemblage contained small pebbles of quartz, limestone, and flint, with most of the artifacts made of the latter raw material. No bifaces were found in the excavated areas probably due to their small surface but earlier searches in the quarry dumps recovered twenty handaxes. These are of large size (140-220 mm in length) and demonstrate a relatively crude workmanship that resembles that of the Latamne site (Ronen, 1991b). Large cobbles from which the bifaces were made were recovered together with a group of hard calcite geodes, the heaviest of which was 580g, were brought to the site by the occupants from about 5 km away. Chronologically, the context of Evron-Quarry is assigned to a post-‘Ubeidiya age, and is perhaps contemporaneous with the Latamne site in Syria (ca 1.0-0.8 Ma). Paleomagnetic and ESR studies of the archaeological bearing strata have suggested a date ca. 1.0 Ma (Porat and Ronen, 2002; Ron et al., 2003).
Bizat Ruhama

The site of Bizat Ruhama is situated in the southern coastal plain and the archaeological horizon is incorporated in a paludine deposit (Ronen et al., 1998; Zaidner, 2003a, b; Zaidner et al., 2003). The retrieved rich lithic industry, generally made of small flint pebbles, falls within the category of “core and flake” assemblage with intensively retouched flakes (small borers, notches and denticulates, etc.) No bifaces were found. Paleomagnetic information and TL dates places the site at 0.99 to 0.85 Ma (Laukhin et al., 2001; Ron and Gvirtzman, 2001).

Latamne

The site of Latamne was excavated by D. Clark (1967) and additional fieldwork was conducted by Sanlaville and his associates (1993). The archaeological horizon of Latamne lay in the mid-sequence of the Latamne Formation. It contained the Latamne “occupation floor,” a silt layer only a few centimeters thick (up to 10cm) capped by sandy-silty bedding with traces of rootlets. The sequence was interrupted by erosion and was overlaid by a fluvial sandy deposit, capped by a lacustrine layer (Sanlaville et al., 1993).

Geomorphological observations indicate that the archaeological horizon of Latamne resulted from a low energy water flow responsible for the deposition of the artifacts and their pattern of spatial distribution. About one-third of the total recorded artifacts, made from local available flint, limestone and basalt, were slightly abraded or fully abraded. Tool classes can be roughly divided into a collection of bifaces, light duty
scraper, heavy-duty tools, and a few limestone and basalt spheroids. Several handaxes are trihedral picks similar to those found at ‘Ubeidiya.

Water activity caused leaching of the sediments as well as diagenesis that destroyed most of the bones. Most of the well-preserved identifiable bones were collected from the gravels underneath the archaeological site (Hooijer, 1962; Guérin et al., 1993). The entire assemblage reflect a great similarity between the faunas from Latamne and ‘Ubeidiya. Originally, the date of the site was estimated as ca. 0.7 Ma based on faunal correlations (Guérin et al., 1993) but the presence of the arvicolid *Lagurodon arankae* and typo-technological affinities of the lithic assemblage suggest a date ca. 1.0 Ma (Tchernov, 1994). However, a single TL date of 560 ka for the Latamne Formation led to the conclusion that the site is 700-500 ka years old (Sanlaville, 1988; Sanlaville et al., 1993) which seem untenable.

**Dursunlu**

The quarry of Dursunlu is 75 km northwest of Konya, western Turkey. It comprises Early Pleistocene lacustrine limestones, marls and clay with lignites. Paleomagnetic analysis has suggested a reverse polarity punctuated by three episodes of normal polarity, consistent with an Early Pleistocene age. A more detailed analysis of the drilled cores suggested that the artifacts were derived from two layers between the Jaramillo and MBB, i.e., 0.99 and 0.78 Ma (Güleç et al., 2009). Most of the small lithic assemblage was made of quartz with rare pieces of flint and an igneous rock. The assemblage falls under the category of core and flake industry and provides a unique point in the presence of early hominins in Anatolia.
Gesher Benot Ya’aqov

The site of Gesher Benot Ya’aqov (GBY) lies in the Jordan Valley, at the eastern edge of a vast, basalt-covered area. The excavations in the 1930s by M. Stekelis, and recently by Goren-Inbar and her associates (Goren-Inbar et al., 1991, 1992a, b, 2000, 2004; Goren-Inbar and Saragusti, 1996; Alperson-Afil et al., 2007) provided an African-type assemblage of cleavers and bifaces that is unlike any of the other known Acheulian occurrences in southwestern Asia including both surface and excavated occurrences (e.g., Hours, 1975, 1981; Bar-Yosef, 1987; Goren-Inbar, 1995; Liubin, 2002; Taskiran, 1998). The nature of the deposits and the malacological assemblages, dominated by *Viviparus apameae*, indicate that the archaeological assemblages accumulated on the shores of an expanding lake that flooded the gorge (Horowitz, 1979; Goren-Inbar et al., 1991, 1992a, b; Goren-Inbar and Saragusti, 1996; Feibel, 2004).

The complex stratigraphic sequence, first partially exposed by M. Stekelis (1960) and more recently by systematic excavations conducted by N. Goren-Inbar (Goren-Inbar et al., 2004; Feibel, 2004) contains early layers with Acheulian industry dominated by the production of cleavers and bifaces from basalt, as well as flint and limestone objects. Some of the cleavers were fabricated by the Kumbewa technique. Although lava flows cover the area, on both sides of the parts of Jordan River and in particular the large area of the Hauran-Golan no other Acheulian sites with basalt industry were located. On the contrary, in most cases flint nodules derived from isolated limestone and chalky outcrops, often of Eocene age, served as raw material for fabricating handaxes (e.g., Goren, 1979; Goren-Inbar, 1985; Ohel, 1991).
The archaeological horizons of GBY are embedded in a depositional sequence that accumulated above a lava flow with normal polarity. The lava flow, designated as the Yarda Basalt, was first K/Ar dated to 0.68±0.12 Ma (Horowitz, 1979) and later to 0.9±0.15 Ma (Goren-Inbar et al., 1992a). However, the paleomagnetic sequence within the excavated deposits demonstrated that the Matuyama Brunhes Boundary (MBB) was located within the series of deposits and the accumulation of the entire sequence took place during ca. 100,000 years (Feibel, 2004).

**Holon**

The site of Holon is embedded in marshy deposits overlying an abraded kurkar ridge dated by Horowitz (1979) to around 500-400 ka. The site contained more than one level (Chazan and Kolska-Horwitz, 2007). ESR and luminescence dating (Porat et al., 2002) suggested for the archaeological horizon an average date of ca 205 ka based on ESR and TL dates and suggested that is comparable to the ESR readings from teeth from Tabun layer E of Garrod’s excavations (the Acheulo-Yabrudian industry). However, TL dates of burnt flint pieces from Tabun E indicate an age older of 270 ka, considered as the onset of the Mousterian (Mercier et al., 1995) dated also in other sites around 220-250 ka. Unfortunately the dates for Holon were retrieved from another geological exposure as the area of the original site lies below a major factory.

The bifaces of Holon are mostly of pointed and rounded aspects; the flake industry contains side scrapers, denticulates, and notches, along with cores and debitage products This lithic assemblage has been attributed to the Late Acheulean (Chazan and Kolska-Horwitz, 2007) and if the dates are accepted it would mean that either the Holon
Acheulian was contemporary with the early Mousterian, which is untenable, or that there is a systematic difference between the luminescence dates of quartz grains that were retrieved from another location although near the location of the original excavation.

Qesem

Qesem Cave is located 12 km east of Tel Aviv, Israel. Excavation in the cave revealed several meters of deposits with abundant lithic and faunal assemblages and plenty of evidence for systematic use of fire (Karkans et al., 2007). Uranium series dates have suggested an age bracket of 0.4 - 0.2 Ma (Barkai et al., 2003). The rich lithic assemblages, dominated by the production of blades, were assigned to the Amudian culture (Gopher et al., 2005; Barkai et al., 2006; Lemorini et al., 2006).

Revadim

Revadim Quarry is located on the southern coastal plain of Israel, north of Kibbutz Revadim. Paleomagnetic dates suggest a normal polarity indicating an age younger than 0.78 Ma. OSL dates suggest a minimum age bracket of 0.3-0.2 Ma. (Gvirtzman et al., 1999; Marder et al., 1999). The lithic assemblage at the site suggests a high frequency of flake tools and the presence of handaxes. The typo-technological characteristics of the bifacial tools have suggested that it may be attributed to the Late Acheulean culture (Marder et al., 1999, 2006).

Oumm Zinat
The site of Oumm Zinat is situated 500 m east of Kibbutz Evron and was first excavated by Prof. Stekelis in 1950. Subsequent excavations by Gilead and Ronen in 1977 revealed a small to medium size assemblage dominated by hand axes contemporaneous with Late Acheulean such as Oum Qatafa D1 and Tabun E/F (Kolska-Horwitz and Tchernov, 1989)

Tabun E
Tabun Cave in location on the Southwest flanks of Mount Carmel, Israel on the banks of Wadi el Mughara (Nahal Me’arot). The excavation of the cave began in 1930’s under Bate and Garrod and continued with Jelinek (1970-1972) and recently A. Ronen since the 1990’s. Layer E consists of slightly abraded flint over an area of 1.0X1.3 m. The lithic assemblage was characterized as Late Acheulean (Garrod and Bate, 1937).

The TL dates for Tabun Ed to D suggested that they were deposited during MOIS 9 through 8 (Mercier et al., 1995), more recent dates by Mercier and colleagues (2000) suggest that Tabun F and E were deposited during MOIS 9 between 350± 30 and 330± 30 ka. However, ESR dates for Tabun E by Grün et al., (1991) and Grün and Stinger (2000) suggested a date of only 200 ka.

Oumm Qatafa
Oumm Qatafa is situated on the left bank of Wadi Khareiteitun in the Judean Desert, ca. 15 km west of the Dead Sea. The site was excavated by R. Neuville between 1928-1949 (Neuville, 1951) where he identified a sequence which spans the chacolithic
through the Lower Paleolithic. The Upper Acheulian level in D2 is characterized by broad, ovate discoidal and cordiform bifaces. Recent ESR dates obtained from level D2 indicate an upper date of 213±26 ka and thus an end for the late Lower Paleolithic (Porat et al., 2002).

**Early and Late Acheulian in the Levant**

Surveys along the Levantine coast located a few occurrences that appear to be of Early Pleistocene age although dating, in most cases, is rather tenuous due to lack of datable substances. Shorelines were dated on the basis of their elevation above sea level, while the known relative ages of foraminifera and marine shell assemblages were also incorporated into these figures along the western mountainous range along the Levantine coast, a few artifacts were found on terraces as high as 120 m above sea level. We therefore choose to summarize those sites where systematic excavations or surveys were conducted and their dates depend of the geological stratigraphy and its suggested correlation with sea level chronology. Here we add some brief information about the main occurrences, and for a full survey see the available summaries (e.g., Hours 1975, 1981; Muhesen, 1985, 1993; Sanlaville et al., 1993; Bar-Yosef, 1998a).

One of the distinctive sites is Kefar Menachem, situated in the interior part of the coastal plain and was excavated twice (Gilead and Israel, 1975; Barzilai, 2006). The lithic industry is embedded in red loam of an Early Pleistocene age (Horovitz, 1979). The lithic assemblages of both excavated areas are comprised of numerous core and flake products, a few flake-tools (classified as end-scrapers, side scrapers, burins, notches, and denticulates). The use of direct hard hammer percussion is dominant. To date, the rare
bifaces have been found only on the surface and their attribution to the excavated
collections is doubtful. These bifaces are described as irregular ovates, picks, long
lanceolates, and backed bifaces (Gilead and Israel, 1975) who tentatively related this
surface assemblage to the Early Acheulian.

Most of what is known from the areas of Lebanon and Syria was obtained through
the study of the terraces of Nahr el Kebir, the Orontes, and the Middle Euphrates. The
majority of the collections were classified as Early and “Middle Acheulian” first on the
basis of stratigraphic grounds and later upon consideration of their typological
characteristics. Rare finds were retrieved and in several localities in the Beqa’a Valley.

Lithic studies of the so-called “Middle Acheulian” assemblages identified two
geographic facies. The sites along the coast, such as Berzine and Ouadi Aabet, contain
essentially amygdaloid and oval bifaces, while the inland sites (Joub Jannine II and
Latamne) have more lanceolates and trihedral picks, and along the Nizip river (Minzoni-
Déroche and Sanlaville, 1988), a tributary of the Euphrates in Turkey, recognized a
similar distribution of the “Middle Acheulian” artifacts.

The general technological tendency among the Acheulian sites is toward a greater
use of soft hammer percussion and the sporadic appearance of the Levallois technique
(Copeland and Hours, 1981). Typologically, the almost total disappearance of core-
choppers is noticeable. The cordiform and amygdaloid bifaces outnumber the ovates. The
length of the handaxes decreases in general, a tendency that was already noted by D.
Gilead (1970) for the southern Levantine samples.

The sites of Hummal and Nadaouiyeh I were discovered in El-Kowm basin
(Hours et al., 1983; Le Tensorer et al., 1993), and exposed several occupational horizons.
Nadaouiyeh I comprised of an accumulation of alternating clayey layers and by sandy layers near an artesian spring. The stratigraphy is a complex one, marked by slumping and erosion. The systematic excavations demonstrated the presence of in situ Acheulian assemblages. The bifaces, generally amygdaloid, were accompanied by a rich flake industry in every one of the six tested layers. The presence of the Levallois technique was noted in low frequencies. In addition, the both Hummal where a much longer depositional sequence was revealed and Nadaouiyeh contain Yabrudian or Acheiulo-Yabrudian capped by Hummalian (an early Mousterian industry) contexts (LeTensorer 2004).

Subdividing the Late (or Upper Acheulian) into phases or “facies” was and still is not an easy task. On the basis of technological and morphological considerations Gilead (1970) subdivided the Late Acheulian into several groups as follows:

A. The Ma’ayan Barukh group (MB), mostly from open-air sites, is characterized by the dominance of the cordiform aspect (including amygdaloids, cordiforms and subtriangulars) with fewer ovate and a few pointed bifaces and rare cleavers. The assemblage from the excavations of Umm Qatafa D2 is included in this group.

B. The Evron-Kissufim group (EK) is, on the basis of stratigraphic evidence, later than the MB group. It contains a richer flake tool component, up to 30-60%, with clear evidence for the manipulation of the Levallois technique. The bifaces show a decrease in rounded aspects (ovates and discoids) and a slight increase in the pointed forms.

C. The Sahel el-Khoussin-Yiron group (SY) are those assemblages mostly surface collected in the hilly areas and flanks. The bifaces are somewhat cruder than those of the other groups with an occasional dominance of the rounded aspect over the cordiform
aspect (Yiron, Beith Uziel, Baqaa-Rafaim etc.). As in the EK group, the Levallois technique was practiced in some sites. It is worth noting that despite the hilly distribution, these assemblages are not present in the three caves where Late Acheulian layers were uncovered (Tabun F, Abu Sif, Umm Qatafa D).

The frequency of refinement index (thickness/breadth x 100) demonstrates the differences among the sites. The same is probably true when the mean length among Late Acheulian sites is considered. Wherever large cobbles were available, there was a tendency towards larger bifaces. However, a general tendency for decrease in biface length could indicate increasing efficiency of resharpening (perhaps longer curation?) during the Late Acheulian.

The flake industry of most of the Late Acheulian occurrences is not very well known. In some places, the number of flakes cannot account for their manufacture. For instance, the thousands of bifaces found in Ma’ayan Barukh may have been produced in an area further north near the Litani River. The flakes collected from the same surface clusters could indicate some resharpening (although small flakes and chips are not easy to retrieve in the deep red soil of these hills). It seems that the concentration of bifaces near the Hula Lake shores on the interfluves of freshwater creeks may represent repeated butchering activities in a pristine environment.

A unique Late Acheulian site, embedded between a lava flow dated to 233±3 ka and an older lava flow dated to 800 ka, was excavated on the edge of the crater lake known as Berekhat Ram on the Golan plateau (Goren-Inbar, 1985). The rich assemblage contains several thousands of artifacts, mostly in mint condition, with about four hundred of retouched pieces including eight small bifaces. The makers of the industry employed
the Levallois centripetal (radial) technique. A special find is a human figurine (Goren-Inbar, 1986) that recently received much attention in the debate concerning the capacities of Archaic *Homo sapiens* or late *Homo erectus* (e.g., Marshack, 1997; D’Errico, 2000). The actual date of the site is unknown but given the current TL dates of the Acheulo-Yabrudian, it should be placed during the time span of 350-450 ka.

In general, Late Acheulian sites can be found across the southwestern Asia in every environment including the coastal plain, hilly areas, inter-montane valleys, and oases and in desert landscapes. The best example to date from an oasis situation is the series of Late Acheulian assemblages which is characterized by high frequencies of bifacial cleavers, uncovered in the Azraq basin (Copeland and Hours, 1989; Rollefson, 1997). Among these, the sounding at Lion Spring provided stratified lithic assemblages that are characterized by ovate, amygdaloid, and cordiform bifaces, with a rich flake industry. In the absence of precise dating and on the basis of comparisons with the occupations in other location it seems that some Late Acheulian occupations should be correlated with periods of wetter conditions during the time span of ca. 600-400/350 ka.

**The Acheulo-Yabrudian**

The Acheulo-Yabrudian, was renamed as the Mugharan Tradition by Jelinek (1981, 1982a, b), and has a definite geographic distribution from the Taurus foothills to the central Levant (Bar-Yosef, 1998b). It is generally dated to 400/350-250/220 Ka, and is found stratigraphically always under the Early Mousterian (e.g., Tabun, Hayonim, Misliyeh caves; Garrod and Bate, 1937; Weinstein-Evron et al., 2003). We stress that in spite of intensive surveys, none of the typical artifacts by which this entity is defined
were found in the Negev and Sinai or in the desert region of southern Jordan. Three facies that sometimes considered as independent industries were identified on the basis of quantitative studies, as follows (Jelinek, 1982a, b; Copeland and Hours, 1983):

1. The Yabrudian facies contains numerous side-scrapers, often made on thick flakes including canted ones, thus resulting in relatively high frequencies of Quina and demi-Quina retouch with a few Late Paleolithic tools and rare blades. Although typologically, Levallois-type products have sometimes been mentioned, the reconstruction of operational sequences has not yielded a well-identified Levallois method.

2. The Acheulian facies is considered by Jelinek (1982a, b) to consist of up to 15 percent bifaces, with numerous scrapers fashioned in the same manner (Quina type scalar retouch) as the Yabrudian ones.

3. The Amudian facies is characterized by end scrapers, burins, backed knives, and rare bifaces and was therefore originally called ‘Pre-Aurignacian’ in the sense of being blade dominated. Not surprisingly, until the 1940s the term Aurignacian was used to refer to all early Upper Paleolithic industries in Western Eurasia. The Amudian facies, following the Tabun excavations, seems to be closer typologically to the Acheulian than to the Yabrudian and contains evidence for limited practice of the Levallois technique (Jelinek, 1982a, b). The “Pre-Aurignacian” in Yabrud I and Abri Zumoffen are richer in “Upper Paleolithic” elements. The excavations at Qesem cave produced rich assemblages of blades and platy of evidence for the use of fire (Gopher et al., 2005; Barkai et al., 2006; Karkans et al., 2007) and a faunal assemblage dominated by Fallow deer (Stiner et al., 2004).
The Lower Paleolithic of Iraq, Iran and the Caucasian region

The vast geographic area summarized here is generally poorly known. The scant evidence from Turkey on one end of the region and India on the other, including a few recorded find spots from Iran (Smith, 1986) and from the Arabian Peninsula (Zarins et al., 1979, 1980, 1982; Whalen et al., 1983, 1984; Abdul Nayeem, 1990), indicate that bifaces can be found everywhere. The distribution toward the northern edges of the Near East has implications for the reexamination of the “Movius line”.

In Iraq, little is known beyond the site of Barda Balka, located in the Chemchemal valley in Kurdistan, which was collected and excavated by Howe (Braidwood and Howe, 1960). This predominantly flake assemblage may be of Middle Paleolithic age. Iranian finds are also few and are far apart. In Khorasan, on the edge of a dried-up lake, quartzite and andesite core-choppers were collected (Ariai and Thibault, 1975/77). In the absence of dates, the investigators related the assemblage to the Late Pliocene on typological grounds. Isolated bifaces have been collected in various places in Iran (Smith, 1986). The Ladizian industry in Baluchistan (Hume, 1976) to the east should be mentioned briefly. It is defined on the basis of scatters of lithics on old river terraces and it is a core-chopper industry with retouched pieces but no bifaces. Hume (1976) has proposed a late Middle Pleistocene age for the Ladizian.

Early and Late Acheulian sites in Georgia were either surface collected or excavated (Liubin and Bosinski, 1995; Liubin, 2002). Among the surface sites, some of the interesting collections were done in Cikiani, near Paravani in southern Georgia, where cleavers and handaxes were found (Kikodze, 1986). The bifaces were made of andesite
but most of the cores were made of obsidian. Persati, another surface site, which is yet unpublished, is located on top of a volcanic plateau that is apparently the continuation of the Dzavacheti range in southern Georgia, about 2100 m above sea level (Kikodze, personal communication). The artifacts were found at the edge of lacustrine sediments, dated to the Neogene. One of the find spots seems to be eroding from these lake deposits, but radiometric dates are not available.

Acheulian industries were uncovered in four excavated caves: Azych, Kudaro I and III, and Tsona. The lithic industry in Azych, located 800 m above sea level, is subdivided on the basis of the observed stratigraphy into several phases of the Acheulian. The earliest levels produced a few core-choppers but they are without clear attribution to a prehistoric entity (Liubin and Bosinski, 1995; Liubin 2002). The richest assemblages were uncovered in layers VI and V, including mainly Late Acheulian bifaces with distinct use of the Levallois technique. In layer V, a fragment of a hominid mandible was found.

Kudaro I is situated 1600 m above sea level. Layer 5 contained Acheulian artifacts made from local raw material. The entire assemblage is characterized by a high frequency of retouched pieces including numerous side scrapers. Core-choppers and bifaces, mostly of elongated shapes, assign this assemblage to the Late Acheulian. The presence of flake cleavers was noted by the excavator. Three human teeth were also found in this context. Dates suggest a range of 250-300 ka. TL readings indicate a slightly earlier time, 360±90 Ka and 350±70 ka. However, a reversed paleomagnetic situation identified in level 6 immediately below the Acheulian, with the fauna of several Galerian elements, hints that the Acheulian in layer 5 is perhaps of an older age (Liubin and Bosinski, 1995).
Kudaro III produced a more restricted Acheulian collection in layers 6-8 with bifaces and flake tools. A TL date of level 8a was 560±112 ka, while layer 5 produced dates of 252±51 ka and 245±49 ka (Liubin, 2002).

Tsona Cave, at an altitude of 2150 m above sea level, and just about 5-6 km south of Kudaro, is a very large cave. The Acheulian industries were derived from layers 6-7a. Preliminary reports indicate that the lower assemblages (layer 7) that were originally considered as Early Acheulian produced only a small sample. The assemblage of layer 6 assigned to the Late Acheulian contained about 100 artifacts, including 29 bifaces made from local raw material, mostly retrieved in the form of pebbles. The chronological position of this Acheulian is not well-known, however it seems that this cave, like others at high altitudes, could have been occupied only during interglacial times and in most cases were possibly only seasonal hunting camps. At least two other cave sites on the northern flanks of the Caucasus are known to contain Late Acheulian remains.

In sum, the distribution of the Acheulian industries in Western Asia is essentially limited mainly to the Levant with decreasing abundance in the Caucasian region and eastern Anatolia. In spite of the paucity of information from Iran, as mentioned above, there is no evidence for continued distribution of the Acheulian into India. Thus, the “Movius Line,” which distinguishes between the Acheulian and the non-biface industries, separates Anatolia from Eastern Europe and the Iranian plateau and Baluchistan from the Levant.

**Human remains**

While the lithic stratigraphy in the region is rather complete, the hominin remains
are woefully underrepresented. The Lower Paleolithic sequence of Western Asia, apart from Dmanisi, is very poor in human fossils. Dmanisi, as mentioned above, contained several skulls and postcranial bones, demonstrating a large range of morphological variability (Gabunia and Vekua, 1995; Braüer and Schultz, 1996; Gabunia et al., 2000a; Gabunia et al., 2002; Lordkipanidze et al., 2007; Rightmire et al., 2006).

The available human remains from this long period are scanty, and a few are surface finds. The extensive excavations at ‘Ubeidiya (1959-1999) have revealed numerous lithics which attest to hominid presence in the Southern Levant during the Early Pleistocene. Several cranial fragments (UB 1703, 1704, 1705 and 1706), an incisor (UB 1700) and a molar (UB 1701) have been assigned to *Homo* indet. (Tobias, 1966a, 1966b) and as *Homo cf. erectus* (Tchernov and Volokita, 1986). Belmaker et al., (2002) described a new right lateral hominid incisor (UB 335) from stratum I-26a and which was assigns to *Homo cf. eragster*. However, the antiquity of the previous finds has been contested, and UB 335 is the only one that can be securely assigned to the Early Pleistocene deposits.

Two broken femora from GBY (Geraads and Tchernov, 1983), attributed to *Homo erectus*, were identified in the collections of animal bones made at the site when the deepening of the Jordan River channel took place.

A broken femur was uncovered in Tabun cave layer E (McCown and Keith, 1939) within the Acheulo-Yabrudian assemblage. It thus occupies the same stratigraphic and chronological position as the fragmentary skull from Zuttiyeh (Gisis and Bar-Yosef, 1974). The latter is considered as an example of an Archaic *Homo sapiens* (Vandermeersch, 1995) and could have been one of the potential ancestors of the later
Qafzeh-Skhul group. Recently, this fragmentary skull has been compared to the Zhoukoudian human remains and interpreted as belonging to a generalized Middle Pleistocene Asian population (Sohn and Wolpoff, 1993).

Only after MOIS 5 do hominin remains (both of Anatomically modern humans and Neanderthals) become more common in the region and allow to fully discuss aspect of biological adaptability vis-à-vis both environment and culture.

**Early-Middle Pleistocene Environmental changes**

The unique geological-climatological position of the Levant in conjunction with a highly fragmented habitat contributes to creating an extremely varied and complex biotic picture. The great diversity of the Southern Asian biota, both in number of species and in biogeographic origin (Palearctic, Paleotropic and Saharo-Arabian), is primarily the product of the Afro-Eurasian biotic interchanges over the past 25 million years (Miocene through Quaternary).

Since the beginning of the Miocene Southwestern Asia has been situated at the crossroad between African and the Eurasian continent thus forming a wide land bridge between the two regions. During different time periods, tectonic, climatic and sea level changes altered the “permeability” of this land bridge. At times the region would allow for animals to disperse in opposite directions and in other times the land bridge served as a barrier. The Messinian event at the end of the Miocene represents a period of long distance reciprocal biotic exchange due to the dramatic lowering of the Mediterranean Sea level. However, since then the developing Red Sea finally limited this geographic
corridor to the Levant and the southern Arabian Peninsula. Indeed, these two passages functioned as a selective filter for most organisms, through which only specific species could spread or pass (Tchernov, 1988; Tchernov and Belmaker, 2004).

The onset of the Pliocene is marked by an abrupt transgression of the Mediterranean and reestablishment of the barrier between Africa and Eurasia. Thus, Africa became considerably isolated from the rest of the world by the Saharo-Arabian arid belt. North Africa was even further isolated from both sub-Saharan Africa and the eastern Mediterranean region (Thomas, 1985). During this period, the main biotic influences in the region were Asiatic, primarily from the Irano-Turanic region. These are recorded mainly in Anatolian sites, which include many forest dwellers such as the Cervids. The Taurus-Zagros Mountains and the Saharo-Arabian developing desert belt eventually became a biogeographic barrier, particularly for laurophyllous (evergreen broad-leaved) plant species (Jacobs et al., 1999), forest dwellers (Cervidae, Castoridae, Gliridae and Ursidae) and aquatic animals. Hence, the transgression of the Mediterranean increased the isolation of the Southwestern Asia.

Towards the end of the Pliocene and in the Early Pleistocene, the regression of the Mediterranean terminated the quasi-isolation of the region and the increase glacial-interglacial cycles had their impact on the region under discussion.

Vegetation and pollen

The bimodal Mediterranean climate has been shown to appear in Southwest Asia during the late Pliocene ca. 3.2 Ma as part of a global cooling trend and was fully established by 2.8 Ma (Suc, 1984). Unfortunately, long pollen cores that would allow for
a continuous paleobotanical reconstruction throughout the Early and Middle Pleistocene are rare in Western Asia in comparison to marine cores in central from the Western Mediterranean Sea and the Aegean. Nonetheless, these provide a scale to which we can compare results from smaller cores obtained in the region.

A succession scheme has been developed for the Mediterranean vegetation for glacial-interglacial cycles such that glacial steppe vegetation in replaced by sclerophyllous woodland (dominated by *Quercus, Pinus, Betula* and *Juniperus*) and then by deciduous forests (deciduous *Quercus, Carpinus, Ostrya* and later on *Abies* and *Fagus*), followed by a regressive phase of open woodland. Specific regional pattern reflects local climatic conditions but pollen analysis in the Mediterranean basin has shown that the vegetation succession follows the processional insolation cycles (Tzedakis, 2007). Thus during the Early Pleistocene, while the glacial-interglacial cycles were dominated by the obliquity 41 ka cycles, the succession of floral communities followed a cycle roughly every 23 ka.

A long pollen core in Teneghi Philippon, Greece, that spans the last 1.35 million years, allows us to test general trends in vegetation in relation to orbital forcing. Flora reconstruction for the glacial periods were based on the minima of the AP percentage and are reflected during MOIS 22, 16, 12, 10, 8 and 6 with 16 (0.65 Ma) being the most extensive during the past 1.35 Ma. In early periods such as MOIS 38, 40 and 42, *Artemisia* levels were over 90% indicating extreme aridity, however these conditions were not sustained over a period longer than 10 ka (Tzedakis et al., 2006).

The majority of pollen data is derived from late Pleistocene and Holocene sediments and post date the period discussed in this study. A playnostraigraphy of the
Jordan Valley (Horowitz, 2001) provides a generalized Quaternary sequence for the Levant, but unfortunately is not well dated. The sequence records alternations between wet and dry Mediterranean flora. The interglacial flora was poor in arboreal pollen in comparison to modern day conditions. A north–south gradient indicated 3- 5% arboreal pollen in the north associated with steppe elements while southern cores indicate no arboreal pollen but proliferation of desert plants. In comparison, the pluvial periods or the glacial flora was dominated by arboreal pollen, and of interest is the increase of pollen the winter deciduous oak *Quercus ithaburensis* (Horowitz, 1988).

Pollen from archaeological sites, in spite of the time gaps, provides another angle to landscape reconstructions, and the conditions that faced the early hominins. A study in Dmanisi indicated a forested area with *Abias, Pinus, Fagus, Alnus, Castanea, Tilia, Betula, Caprinus* and rarely *Ulmus* and *Salix*. Bushes and shrubs are represented by rhododendron, *Corylus* and myrtle and the herbaceous vegetation is dominated by Cyperaceae, Germinaceae and Polygonaceae (Dzaparidze et al., 1992) consistent with the humid thermophilous broad leaf forest zone which is similar in the region today in the western Caucasus (Zazanashvili et al., 2000).

Only few botanical remains have been retrieved from ‘Ubeidiya, all from the Li cycle. Macrofloral remains of fossilized leaves were discovered in the limnic laminated layer III- 19. These have been identified as *Pistacia lentiscus, Rhus tripratita* and *Myriophyllum* sp. (Lorch, 1966). Pollen spectrum was extracted from layer III-12, analyzed by A. Horowitz (Bar-Yosef and Tchernov, 1972) indicating 82% arboreal species of which the overwhelming majorities are *Quercus* sp. followed by *Juniperus* sp. and *Olea* sp. Non-arboreal families include Gramineae, Cruciferae and Compositae.
Cyperaceae comprise 8.4% of the pollen and attest to the water habitat present at the site suggesting a period more humid than today.

There is a small pollen spectrum from Bitzat Ruhama \((n=114)\) reflecting relatively high frequencies of arboreal pollen including Quercus, Pinus, Olea and Cedrus. (Zaidner, 2003b). Among the non-arboreal pollen we encounter Chenopodiaceae, Palmae, Poaceae and Liliaceae. The presence of cedar is indicative of a colder environment in the region than the present (Zaidner, 2003b).

A pollen sample from the Latamne formation indicates that mountain slopes near the site were forested by board leaf trees such as Quercus, Caprnius, Tilia, Juglans, Ulmuss, Corylus and Betula and coniferous species such as Pinus and Cupressus (Dodonov et al., 1993).

The wood remains of GBY suggest the presence of Mediterranean wood and plant species and that the climate in the Hula valley at the time of deposition resembled the seasonal Mediterranean pattern seen today. Among the dominant species are oak (Quercus sp.), wild pistachio (Pistacia atlantica), wild olive (Olea europaea), plum (Prunus sp.), and jujube (Ziziphus spina-christi) (Goren-Inbar et al., 2004; Werker, 2006).

Immersed or floating freshwater plants are common at the site and include species such as Euryale ferox, Najas foveolata, Nymphoides cf. peltata, Potamogeton coloratus/polygonifolius, the extinct Stratiotes intermedius, Trapa natans and apparently Sagittaria sagittifolia. Bank forest taxa include wild grape (Vitis sylvestris) and ash (Fraxinus syriaca).

Pollen analysis from this site (van Zeist and Bottema, 2009) supports the general landscape reconstruction derived from wood identification specifically the presence of
*Quercus ithaburensis – Pistacia atlantica* woodland or park-forest. Above 400-500m to the west of the valley, this Tabor Oak woodland species was replaced by *Pistacia atlantica- Amgdalus korschinskii* woodland. The overall pattern indicates that the upper Jordan Valley did not undergo any significant vegetation changes as a results of the glacial- interglacial periods as we see in higher latitudes and the overall vegetation as observed in the wood remains as in the pollen reflects comparable environs to those of today. However, oxygen and carbon stable isotope evidence derived from gastropods and ostracods at GBY as well as evidence from mollusk ecology indicate a climatic shift (Rosenfeld et al., 2004; Ashkenazi et al., 2009; Spiro et al., 2009) inline with global climatic forcing throughout the sequence across the MBB, the paleoecological reconstructions based on vegetations (pollen, wood) indicated that climatic forcing may have had a stronger effect on the local hydrological regime and aquatic fauna that on the terrestrial ecosystem and most notably fauna (see Kingston, 2007, for further discussion of this phenomenon).

**Faunal turnovers and dispersal from Africa**

The paucity of sites from the Early and Middle Pleistocene does not allow to track both inter and intra variability within each of the sub-regions during this long period. There are far less sites that preserve well-dated faunal assemblages than lithic localities that can be used for paleontological and paleoecological analysis. The observations made on the basis of fossiliferous sites are generally correlated with the European and South African sequences (Belmaker, 2009). While the actual species composition within each region is different the tempo and mode of change are similar.
across the region and point to a secular trend of cooling through time. Data for this
analysis is derived from archaeological sites (see previous section for detailed description
of the sites) as well as a several paleontological site that yielded only faunal material.

The Late Pliocene is well recorded in the Caucasus such in Kvabebi, (Georgia)
which yielded a large assemblages indicative of a marshy and riverine habitat (Vekua,
1995) surrounded by open woodland environment (Agustí et al, 2009b). Similarly, the
Bethlehem fauna with the small assemblage of 11 mammalian species can be identified
as representing a humid and temperate woodland environment (Gardner and Bate, 1937;
Hooijer, 1958). The presence of Giraffa sp. uncovered in Bethlehem suggests an African
dispersal during the Late Pliocene although the poor preservation of the specimen
precludes identification to species (Robinson and Belmaker, in press). The presence of
the three-toed horse Hipparion (Hooijer, 1958) would indicate a date ca. 2.5 Ma. During
this time period, the Jordan rift had not formed in its current state (Horowitz, 2001),
which may have hindered a large dispersal from Africa. Furthermore, as previously
mentioned, the absence of sites prior to Bethlehem does not allow us to pinpoint the
precise date of this dispersal which may have occurred any time prior to that.

The transition from the Late Pliocene to Early Pleistocene, similarly to the
Olduvai dry event, indicates a shift from a more humid and wet environment to a more
open, partially dry and somewhat cooler conditions. The change is attested when the
faunal assemblages of Bethlehem and Kabevebi are compared to Dmanisi (1.8 – 1.77
Ma) (Gabunia et al., 2000; Agustí et al, 2009b), Kotsakhuri (1.63 – 1.83 Ma) and Tsalka
(Vekua and Lordkipandize, 2008). While the fauna from these sites is characteristic of
Mediterranean temperate woodland indicated by a high proportion of cervids, an
ecological shift to a more open habitat is marked by the first appearance of several taxa such as the Mammoth (*Mammuthus meridionalis*) and the large Stenoid horse (*Equus stenonis*).

A local faunal turnover can be observed between the Early Pleistocene fauna dated to ca. 1.8 – 1.7 Ma as represented by Dmanisi, Kostakhuri and Tsalka, and the younger site of ‘Ubeidiya (1.6 – 1.2 Ma). While all sites have many taxa in common, the older sites exhibit a more archaic suite of species including *Canis etruscus*, *Cervus perrieri* and *Eucladoceros* sp. replaced by the younger *Canis mosbachensis* and late Villafranchian cervids *Praemegaceros obscurus-verticornis* at ‘Ubeidiya. ‘Ubeidiya possibly represents a long sequence spanning ca. 400 Ka and its landscape was essentially Mediterranean woodland similar to that of Dmanisi as shown by the great abundance of cervids and other Eurasian taxa (Belmaker, 2009). However, several new taxa that appear in ‘Ubeidiya are not present in the previous Late Pliocene deposit of Bethlehem (ca. 2.5 Ma) and the Early Pleistocene sites in the Caucasus. These include the unique suite of African taxa such as *Pelorovis oldwayensis*, *Kolpochoerus olduvaiensis* and Cercopithecinae cf. *Theropithecus* sp. (Belmaker, 2010), which coincides with the Aullan dispersal event dated to 1.8 Ma (Arribas and Palmqvist, 1999). This indicates that a dispersal route from East Africa to Eurasia became available during this time or immediately prior to that date.

The comparison between ‘Ubeidiya and Dmanisi is particularly informative. With the exception of the genus *Homo*, the Early Pleistocene sites of the Caucasus are devoid of African taxa (Tappen, 2009 but see Martínez-Navarro and Palmqvist, 1995), and have a high proportion of endemic species such as *Bison georgicus* and *Struthio dmanisiensis*.
This suggests that during the Late Pliocene the Caucasus was isolated and this situation allowed for the evolution of endemic species. However, ‘Ubeidiya and the Georgian sites share several taxa and specifically the jird, *Parameriones obiediensis*. This species was identified as an endemic to ‘Ubeidiya and subsequently found in Dmanisi indicating that the biogeographic route connecting the two regions was open. In addition the path from East Africa into the Levant was also open and led to the influx of African taxa into the latter.

The Epivillafranchian fauna is represented by the sites of Bizat Ruhama, Evron Quarry and Daquara, Latamne in the Levant, Dursunlu in Anatolia and Akhalkalaki in Georgia. The archaic nature of this fauna is maintained by the presence *Hipopotamus behemoth* in Latamne. However, a novel dispersal from Africa is attested by the arrival of the suid *Kolpochoerus evronensis* in Evron Quarry and by *Giraffa camelopardalis* at Latamne (Robinson and Belmaker, in press). Furthermore, the appearance of modern taxa such as *Dama mesopotamica* and *Cervus elaphus* indicates a new and more modern faunal composition.

The increased shift towards a more open, arid habitat, compared to earlier sites dominated by cervids and woodland taxa, is evidenced by the increasing dominance of equids and the steppe mammoth (*Mammuthus trogontherii*). The small faunal assemblage of Bizat Ruhama (ca. 1.0 Ma) in the southern coastal plain has only bovid, equid and hippo remains (Ronen et al., 1998). Evron - Quarry (ca. 1.0 Ma) although situated at the western margins of the Galilee where rainfall is higher than in the south, the cervid sample comprises only of four among a total of 36 (11%) identified specimens, while bovids are represented only by 11 specimens (30%) (Tchernov et al., 1994).
Akhalkalaki (0.9-0.8 Ma) in central Georgia is dominated by megacerids, 

*Stephanorhinus etruscus, Mammutthus trogontherii, Equus suessenbornensis* and *E. altidens* (Vekua, 1986, 1987; Hemmer et al., 2001; Tappen et al., 2002) and Dursunlu in the generally more arid central Anatolia (1.0-0.78 Ma) is characterized by the high frequency of *Equus caballus mosbachensis* and *E. altidens* (Güleç et al., 1999).

A later large faunal turnover is observed between the Epivillafranchian and the Galerian faunas and is date dated to the Matuyama-Brunhes Boundary ca. 0.78 Ma. The best record is derived from GBY. This dated to MOIS 18, is assigned to a wet and humid stage apparent in the high frequency of cervids (*Dama* sp., *Cervus* cf. *Cervus elaphus* and *Megalocerni* sp.) (Rabinovich et al., 2008). A small contribution of African taxa includes *Bos buiaensis* (Martínez Navarro et al., 2009)

The sites of Denizli and Emirkaya-2 in Anatolia and Bear’s cave, Tel Hesi and ‘Ain Soda in the Levant are dated to the early part of the Middle Pleistocene roughly between 0.5-0.43 Ma (Sen et al., 1991; Tchernov and Tsoukala, 1997; Dirks, 1998; Erten et al., 2005). Taxa that appear in the region for the first time include *Panthera leo*, several megacerines and *Capreolus aff. suessenborensis* while the continuation of archaic taxa from earlier time periods include large taxa such as *Stephanorhinus hemitoechus* and *Bos primigenius*. Unfortunately the taphonomic history of these sites precludes a detailed paleoecological analysis. Bear’s cave as its name implies is a carnivore den and presents high frequencies of carnivore taxa and a minimal appearance of herbivore taxa, which precludes an environmental reconstruction. The other sites have only scant remains.

Not surprisingly the assemblage of Yarimburgaz cave, situated in Thrace, the European portion of modern Turkey, includes faunal elements from the Russian plains.
such as *Lagurus transiens* and *Ochotona pusilla* which suggest the expansion of steppe environment in the southern Balkans, consistent with a cold and dry OIS 8 (von Koenigswald, 1998).

The sites of Qesem cave, Revadim and Holon, Hayonim cave layer E, Tabun cave layer E in the southern Levant are dated to the later part of the Middle Pleistocene between 0.43-0.13 Ma and provide a rich faunal assemblage for MOIS 8-6. The layers which dated to the earlier phase of the sequence (MOIS 7) are dominated by cervids most notably *Dama mesopotamica* whereas from MOIS 6, the increase in the mountain gazelle is noted. It has been hypothesized that the increasing frequencies of gazelle may indicate a climatically driven dispersal of an African arid species into the region (Stiner et al., 2004, 2009), which is supported by the presence of a single specimen of *Lycaon pictus* in Hayonim E (Stiner et al., 2001). However, isotopic analysis of teeth of both fallow deer and gazelles from the Mediterranean region from both Middle and Late Pleistocene sites of Qesem, Hayonim and Meged sites did not indicate any significant change in niche utilization between the ungulates, suggesting that the change in abundance may be due to human hunting preferences (Rowland, 2006). During this period there is no sound evidence for an additional dispersal from Africa following the Mid-Brunhes event of 0.43 Ma, represented by extinction of the larger fauna (Belmaker, 2009).

The modern terrestrial ecological signature of both the flora and the fauna of the region developed early in the Pleistocene. While the exact composition of species may have changed throughout the last 2.5 Million years, but the overall biome structure as a Mediterranean region surrounded by a more arid region in the South and East and
temperate region in the north did not alter significantly. The locations and extent of the
borders between the sub-regions may have changed emphasizing the importance of
understanding the role of ecotones in the region.

Discussion - faunal and hominins dispersals

Several trends can be observed in the paleoecological sequence of Western Asia
during the Early and Middle Pleistocene. Within this long sequence, four major
observations are recognized: 1. None of the environmental changes, and particularly in
the Levant, were as dramatic as those recognized in higher latitudes (e.g., temperate
Europe); 2. The climate changed gradually from more humid and closed habitats to more
dry and open ones, through minor fluctuations generally correlated with the marine
isotope data; 3. Punctuated faunal turnovers occurred in rough correlations with Western
and Eastern Europe faunal units and 4. Hominin dispersals at the current state of research
are not positively correlated with faunal turnovers (Table 2).

The evidence presented in this paper indicates that a few faunal dispersals
between African and Eurasia occurred throughout the Late Pliocene through the Middle
Pleistocene. There is a general agreement among scholars that these events were
generally coincident with global climate changes. The main difficulty is attributing each
dispersal event to the time when it took place. The reason is that the known sites and
assemblages, described and discussed above, do not necessarily date these events. We
tend to forget that the discovery of Lower Paleolithic sites is accidental and they cannot
be considered as a continuous chronological sequence. Not surprisingly this is the nature
of windows into the remote past, and one can argue that the dispersals of large mammals
occurred long before their bones were uncovered in the excavated sites. Relating the
dispersal events to the known or conjectured age of an archaeological site may result in
erroneous conclusions.

It should be stressed that the southwestern Asian fauna was established in this
vast region since the Miocene and consisted of characteristic Palaearctic Eurasian
element. The earliest dispersal from Africa of the generally woodland browser species
(n=2) took place sometimes during the late Pliocene. It is recorded in the undated site of
Bethlehem. The next migration was during the Early Pleistocene by several species
marked by their adaptation to open grasslands (n=5). Their representation in the
‘Ubeidiya assemblages does not necessarily indicate the date of the first arrival of these
taxa. A few additional browsers arrived at the time of the Jaramillo Event (n=2), and an
additional grassland species at the Brunhes-Matuyama (n=1) as well as one taxon in the
Mid-Brunhes (ca. 0.43 Ma; Belmaker, 2009).

The attempt to use the evidence from large mammals as a backdrop to
understanding the tempo and mode of early hominin dispersals is generally unsuccessful.
Contrary to what has been suggested (Martínez-Navarro et al., 2007, in press; Agustí et
al., 2009a) it becomes apparent that hominin migrations into this region do not correlate
with the arrivals of large mammals or specific climatic regimes. The earliest dated
hominin dispersal is at the time of the Dmanisi (ca. 1.77 Ma) by bearers of a core and
flake industry. The second, as no other Early Acheulian site was found and dated in
southwestern Asia, is at ‘Ubeidiya (1.6-1.2 Ma).

During the Epivillafranchian, ca. 1.1 Ma, large mammalian fauna arrived in the
Levant from Africa as attested by the fauna of Evron and Latamne. However, the lithic
industry of these sites does not differ from other Early Acheulian assemblages, and in the lack of specific tool-types or new knapping techniques, we see no evidence for additional migration of African hominins into southwestern Asia.

The site of GBY is interpreted to be the archaeological remains of a group of hominids that migrated from Africa (Bar-Yosef, 1987; Goren-Inbar and Saragusti, 1996). The lithic industry at GBY bears an African stamp and is still a rare occurrence in the Levant in spite of large surveys (e.g. Hours, 1981). The hominins had a definite preference for employing basalt as the main raw material although flint and limestone were present in the immediate vicinity. This choice, clearly expressed in high frequencies of cleavers, indicates the African origins of this group. It has been suggested (Bar-Yosef, 1994, 1995) that this move was triggered by environmental change in East Africa that occurred around the Jaramillo subchron or the BMM. Interestingly, the makers of the GBY industry, either passed away after a time span of several dozens of millennia, or simply adopted the making of bifaces from flint with similar shapes to the common ones in the Levant.

Human migrations occurred along the “Levantine Corridor” as defined by the paleontologists (e.g., Thomas, 1985). The Lower Paleolithic assemblages from el-Abassieh in Cairo (Bovier-Lapierre, 1926) may indicate that the Nile Valley was a possible segment of this route. The interior of the Arabian Peninsula was not an option due to the existence of the Saharan desert belt, since the end of the Miocene. Under interglacial conditions the northern penetration of the monsoonal system drastically changed the potentials for increasing amounts of resources in eastern Sahara (e.g.,
Neumann, 1989) and could have facilitated an alternative path for hominins and later Archaic *Homo sapiens* groups along the western shores of the Red Sea.

Thus, the absence of correlation between hominin and faunal dispersals is apparent and points to different underlying mechanisms for the two phenomenon. To reiterate the point we can discuss the situation in Arabia, which is beyond the scope of this paper. Regional surveys in the Arabian Peninsula have led to the identification of find spots and the collection of lithic assemblages with and without bifaces. Bifaces are reported solely from the western margins where they are made on a variety of raw materials such as flint, basalt, and metamorphic rocks. No bifaces have yet been found in the eastern Arabia that borders the Persian Gulf. Of special interest are the reports concerning sites or find spots along the Red Sea, another potential route of hominins. The excavation at Saffaqaq (Whalen et al., 1983, 1984) provided a rich Acheulian assemblage made primarily of andesite with bifaces, cleavers, and numerous flakes. The depth of the deposits that contain artifacts (ca. 0.90m) probably reflects repeated occupations. Farther south in Yemen, excavations of open-air sites embedded in Pleistocene formations, many of which are rich in gravels or angular rock fragments, unearthed several series of core and flake assemblages and bifaces without animal bones (Amirkhanov, 1991). In addition, surface collections clearly indicate the presence of Late Acheulian industry. If no lithics remains are found in the anterior of Arabia during the Lower Paleolithic suggesting hominin migration into this region, then the site of An Nafud (Thomas et al., 1998) dated to the Early Pleistocene exhibits many of the African taxa present in the Southern Levant (*Crocuta crocuta; Pelorovis cf. oldowayensis; Oryx sp.*) as well additional African alcephelines and bovids whereas Palaearctic species such as cervids
are notably absent. This would suggest that Africa fauna could disperse where early
*Homo* could or would not. Further confirming the disjunct between the two dispersal
patterns.

We should therefore return to the question concerning the nature of long distance
migrations of hominins, whether it was based on “leapfrog” bursts of movements or
gradual spreading out of small groups. Several scholars proposed that climatic changes
determined the timing, mode and motivation for the out of Africa of early *Homo*
erectus/ergaster* (Potts, 1998; Dennell, 2004). It has been suggested that the expansion of
grassland habitats into higher latitudes (30°N), during the Late Pliocene and Early
Pleistocene climatic amelioration provided the favorite habitats that facilitated human
survival (Vrba, 1988, 1995; Wynn, 2004). As the paleo-climatic information reflects
alternating drier and wetter intervals it could have determined the closing and opening of
natural corridors and thereby allowing *Homo* and other taxa to move from one region to
the next (Vaks et al., 2002; Raia et al., 2006).

Indeed, the Aullan dispersal event (ca. 1.8 Ma) was associated with favor
ecological conditions permitting hominins and a few African taxa to reach Eurasia.
However, the paleoecology of the Early Pleistocene sites across southwestern Asia
(Dmanisi, ‘Ubeidiya, GBY) based on both flora and fauna indicates that the hominins
survived in a mixed landscape of open parkland with forested surrounding hills (van Zeist
and Bottema, 2009; Belmaker, 2009; Tappen, 2009; Belmaker, in press). Moreover, the
prevailing environmental conditions are not sufficient to explain the differences between
the lithic industries, whether ‘core and flake’ in the Caucasus region or the Early
Acheulian in the Jordan Valley. Probably these two particular industries reflect the
activities of different groups of hominins who by their traditional learning employed
different stone artifacts.

Successful adaptations to new ecological niches away from the savanna
environment had its price. Probably more than one of the hominin lineages has
disappeared i.e., simply died out, when they had too few members to keep a viable
mating and reproductive system. Such local and temporal extinctions are possibly one of
the reasons, together with low archaeological visibility, why the number of Lower
Paleolithic sites, even in well-researched areas, is still so small. Therefore the current
distribution of lithic industries across Eurasia is undoubtedly incomplete due to paucity of
field research in several regions, indicating that there is no real cultural continuity and
that what we view as a constant stream of migrants, was actually interrupted many times
(e.g., Dennell, in press).

Chronologically, the earliest hominins reaching southwestern Asia after leaving
Africa were the makers of ‘core and flake’ industries, and is probably why this kind of
simple way of obtaining sharp edges spread across Asia and Eastern Europe. It is not
impossible that even migrants in later time (such as the makers of the Karari industry)
carried the ‘core and flake’ production into the same areas. This would explain why the
Acheulian contexts dated to 1.5 Ma to 0.25 Ma demonstrate interstratifications with those
who manufactured cores and flakes (sometimes with additional types such as spheroids).
The continuous occupation of southwestern Asia by the makers of the Acheulian
industry needs to be stressed. The contrast with the neighboring regions is striking. No
Acheulian sites are known from Iran, but plenty were recorded in Southern Asia (e.g.
Petraglia, 1998). A few sites with bifaces are known in China beyond the “Movius line”
(e.g., Hou et al., 2000). Between the Zagros and the western margins of the Indus valley there are suitable raw materials for making bifaces, but those who needed and knew how to make these tool-types were not present in these region. Natural boundaries such as the mountain ranges of the Caucasus limited early hominin moves as shown by the decreasing numbers of Acheulian handaxes (Liubin, 2002).

In brief, we have no persuasive explanation why the Acheulian is not represented in the vast area between the Zagros and Baluchistan. A similar observation concerns Eastern Europe where only ‘core and flake’ industries were found and stand in marked difference with the proliferation of handaxes in Western Europe.

While we agree that technological innovations and their social role are also considered as an important adaptation for dispersal (Carbonell et al., 1995; Larick and Ciochon, 1996), we wonder how exactly the technological innovations assisted in the survival or organization of those early hominin groups, and in particular given the lack of correlation between lithic technology, typology and environment. Detaching a few flakes from a nodule can be done in different ways, as it often depends of the fracture mechanics of the raw material, its size, shape and volume (Hovers and Braun, 2009 and papers therein).

Therefore, if we accept the notion that adaptation to a specific environment during Lower Paleolithic times, did not influence the way stone tools were shaped, we have to adopt the position that it was due to the intrinsic behavioral capacities, unique to hominins, that facilitated the moves from Africa into new territories. It should be remembered that the initial dispersal of hominins has been attributed to both morphological and behavioral characteristics such as the capacity for long distance
walking (Steudel, 1994), endurance running (Bramble and Lieberman, 2004), heat adaptation (Walker and Leakey, 1993), greater brain capacity (Aiello, 1993; Aiello and Wheeler, 1995) and social structure (Kroll, 1994). Even the release from tropical diseases that allowed for an increase in population size in higher latitudes (Bar Yosef and Belfer-Cohen, 2001), does not explain what happened to the various groups in Asia.

The variability selection hypothesis states that the adaptability of hominins to a wide range of habitats and specifically to a variable climate in Africa may have provided a pre-adaptation to survival in novel environments (Potts, 1998, 2002). While we agree that the presence of hominins in a wide range of environments in Eurasia supports this hypothesis, however, this explanation is valid for the “longue durée” when a period of one million years or more is considered. In addition, hypothesizing what may constitute the pre-adaptability traits is rather intriguing. These may include an increase of resource exploitation by using of stone tools, wooden tools that did not survive, and fire. For the latter there is hardly any solid evidence prior to 0.8 Ma in GBY (Goren-Inbar et al., 2004; Alperson-Afil and Goren-Inbar, 2007; Alperson-Afil, 2008). Additional pre-adaptations would have been the importance of high-energy foods such as meat, tubers or other vegetal sources during the initial dispersal. The increase in body and brain size required a better quality diet and often the contribution of protein seems to have been the main source (Aiello and Wheeler, 1995; Cordain et al., 2000; Aiello et al., 2001; Cordain et al., 2001; Aiello and Wells, 2002). Hence, hominins evolved to become more active hunters and gatherers when compared to their ancestors, and these capacities required larger territories (Walker and Shipman, 1996). Specifically, a high proportion of meat in the diet was seen as a critical for the success of hominins and this proposition was supported,
according to various authors, by the taphonomic analyses of faunal remains (Brantingham, 1998; Hemmer, 2000; Domínguez-Rodrigo et al., 2002; Domínguez-Rodrigo, 2002; Domínguez-Rodrigo and Pickering, 2003). The colonization of the temperate Europe after 0.7 Ma is thought as facilitated by a decrease in the number of carnivore competitors and the ability of hominins to acquire larger quantities of meat (Palombo and Mussi, 2006), although the role of large game hunting could signal more a social expression than the need for meat (J.D.Speth, personal communication).

In sum, this paper provides an overview of the environmental conditions that prevailed during the Lower and Middle Pleistocene in southwestern Asia indicating that regional topographic configuration played a primary role in shaping the effects of climatic amplitude on the biotic responses of flora and fauna. The emphasis on climatic shifts and regional ecological variability is commonly seen as the sound background for the archaeological contexts and therefore facilitating the understanding hominin population dynamics. Hominins were able to disperse into regions that were beyond the their sub-tropical and tropical African homeland (Bosinski, 2006; Dennell 2009) and in routes, times and into environments unrelated to other large African taxa both carnivore and herbivore suggesting a unique biological, behavioral and cultural suite of characters which allowed them to do so. However, without a better understanding the reasons for success and failure of survival of various hominin migrant groups, and whether it depended on their ability to keep their mating and reproductive systems, we will need to resort to oversimplifications of the “human success”.

Acknowledgements
We would like to thank the organizers of this volume for inviting us to participate.

MB is funded by the American School of Prehistoric Research at Harvard University.
References


Agustí, J., Vekua, A., Oms, O., Lordkipandize, D., Bukhsianidze, M., Kiladze, G., Rook, L., 2009b. The Plio-Pleistocene succession of Kvabebi (Georgia) and the background to the early human occupation of Southern Caucasus. Quaternary Science Reviews 28, 3275-3280.


Clark, J.D., 1967. The middle Acheulian site at Latamne, northern Syria. Quaternaria 9, 1-68.

Copeland, L., Hours, F., 1981. La fin de l'Acheuléen et l'avènement du Paléolithique Moyen en


Dennell, R.W., 2004. Hominid dispersals and Asian biogeography during the Lower and Early Middle Pleistocene, c. 2.0 - 0.5 Mya. Asian Perspectives 43, 205-226.

Dennell, R.W., 2004. Hominid dispersals and Asian biogeography during the Lower and Early Middle Pleistocene, c. 2.0 - 0.5 Mya. Asian Perspectives 43, 205-226.


Hemmer, H., Kahlke, R.-D., Vekua, A.K., 2001. The jaguar Panthera onca gombaszgogensis (Kretzoi, 1938) (Carnivora: Felidae) in the late Lower Pleistocene of Akhalkalaki (South
Georgia; Transcaucasia) and its evolutionary and ecological significant. Geobios 34, 475-486.


1455 Dordrecht.


whitei (Broom, 1937) (Felidae, Carnivora, Mammalia) in the Lower Pleistocene site of Venta Micene (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. Journal of Archaeological Science 22, 569-582.


Ronen, A., 1991a. The Yiron gravel lithic assemblage, artefacts older than 2.4 Ma in Israel. Archäologisches Korrespondenzblatt 21, 159-164.


Museum University of Pennsylvania, Philadelphia.


Figure legends

Figure 1: Location of major sites mentioned in the texts. Subfigure A includes the near east. Subfigure B includes the Levant and is denoted in the box within subfigure A.
Table 1a: A summary of the distribution of the main carnivores in the Early to Middle Pleistocene of the Near East. References are mentioned in the texts. X denotes presence.

<table>
<thead>
<tr>
<th></th>
<th>Dmanisi</th>
<th>Tsalka</th>
<th>'Ubeidiya</th>
<th>Gilsa</th>
<th>Cobb Mt</th>
<th>Evron</th>
<th>Latmane</th>
<th>Jarash</th>
<th>Dursunlu</th>
<th>Akhalkalaki</th>
<th>GBY</th>
<th>Bear cave</th>
<th>Holon</th>
<th>Hayonim</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Canis etruscus</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Canis mosbachensis</em></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Canis lupus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lycaon pictus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Canis aureus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vulpes cf. V. praeglacialis</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vulpes vulpes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ursidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ursus etruscus</em></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ursus sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ursus sp. small</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ursus deningeri</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ursus arctos</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mustelidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Martes sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Meles meles</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lutra simplicidens</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lutra sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mellivora sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pannonictis pilgrim</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viverridae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Herpestes sp.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Vormela cf. peregusna</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyaenidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pachycrocuta perrieri</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pachycrocuta brevirostris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Crocuta crocuta</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hyaena hyaena</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Felidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lynx issiodorensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Felis sp. size of F. silvestris</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Felis chaus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acinonyx pardinensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Megatherium cf. whitei</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Homotherium crenatidens</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Panthera pardus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------------</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panthera leo</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panthera gombaszoegensis</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1b: A summary of the distribution of the main ungulates in the Early to Middle Pleistocene of the Near East. References are mentioned in the text. X denoted presence.

<table>
<thead>
<tr>
<th></th>
<th>Dmanisi; Tsalka</th>
<th>'Ubeidiya</th>
<th>Bitzat Ruhama</th>
<th>Gibha</th>
<th>Jaramillo</th>
<th>Dursunlu Akhalkalaki</th>
<th>GBY</th>
<th>Denizli Ein Soda Tel Hesi Emirkaya-1</th>
<th>Qesem, Holon Revadim Tabun E, Umm Qatafa, Ooum Zinat</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Elephantidae</strong></td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammuthus meridionalis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammuthus trogontherii</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stegodon sp.</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stegodon mediterraneus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stegodon cf. trigonocephalus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elephas sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeoloxodon antiquus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equidae</td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus stenonis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus suessenbornensis</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus aff. altidens</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus caballus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus mauritianus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus hemionus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Equus hydruntinus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinocerotidae</td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stephanorhinus etruscus</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinoceros merckii</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stephanorhinus cf. hemitoechus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervidae</td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervus (Dama) cf. nestii</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervus abesalomi</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervus elaphus</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucladoceros aff. tegulensis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Praemegaceros obscurus-verticornis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Megaceros sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dama mesopotamica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capreolus sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capreolus capreolus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Giraffidae</td>
<td>1.8 – 1.6</td>
<td>1.6 – 1.2</td>
<td>1.2 – 1.0</td>
<td>1.0 – 0.8</td>
<td>0.8 – 0.5</td>
<td>0.5 – 0.3</td>
<td>0.3 – 0.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeotragus sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Order</td>
<td>Family</td>
<td>Genus</td>
<td>Species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------</td>
<td>---------------</td>
<td>------------------------------</td>
<td>-------------------------------------------------------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Giraffidae</td>
<td></td>
<td>Giraffa camelpardalis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bovidae</td>
<td></td>
<td>Bison georgicus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Leptobos sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bison sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bos primigenius</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gallogoral meneghini</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pelorovis oldowayensis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bos buiaensis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>? Sinoreas sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capra sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capra ibex</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capra aegagrus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Capra dali</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Caprini indet.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ovibovini indet.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pontoceros sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Antilopini indet.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gazella sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gazella cf. gazella</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oryx cf. gazella</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Alcelaphus buselaphus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Camelidae</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Camelus sp.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Suidae</td>
<td></td>
<td>Kolpochoerus olduvaiensis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Kolpochoerus evronensis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sus strozzi</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sus scrofa</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hipposcopotamidae</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hippopotamus georgicus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hippopotamus bekemho</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hippopotamus gorgops</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Hippopotamus antiquus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Primates</td>
<td></td>
<td>Macaca sylvanus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cercopithecidae cf.</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Theropithecus</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2: Faunal and hominin dispersal from Africa to Eurasia in different biozones

<table>
<thead>
<tr>
<th>Date (Ma)</th>
<th>MOIS</th>
<th>Mammalian zone</th>
<th>Caucasian</th>
<th>Anatolia</th>
<th>Levant</th>
<th>African Dispersal(^1)</th>
<th>Hominin dispersals</th>
<th>Cultural entities</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
<td>Early Villafranchian</td>
<td>Kvebebi</td>
<td></td>
<td></td>
<td>Bethlehem</td>
<td>N=2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.8</td>
<td>Middle Villafranchian</td>
<td>Dmanisi, Tsalka</td>
<td></td>
<td></td>
<td></td>
<td>Dispersal event</td>
<td>Core and flake</td>
<td></td>
</tr>
<tr>
<td>1.6 – 1.2</td>
<td>Late Villafranchian</td>
<td>'Ubeidiya</td>
<td></td>
<td></td>
<td></td>
<td>Dispersal event</td>
<td>Early Acheulian</td>
<td></td>
</tr>
<tr>
<td>1.1 – 1.0</td>
<td>Epi-villafranchian</td>
<td>Akhalkalaki Takshe</td>
<td>Dursunlu</td>
<td>Daquara, Latamne, Evron,</td>
<td>N=2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8</td>
<td>19</td>
<td>Gallerian</td>
<td></td>
<td></td>
<td>GBY</td>
<td>N=1</td>
<td>Dispersal event</td>
<td>Acheulian</td>
</tr>
<tr>
<td>0.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.4 – 0.3</td>
<td>8-9</td>
<td>Auralian</td>
<td></td>
<td></td>
<td>Qesem, Revadim Tabun E</td>
<td></td>
<td>Achelo-Yaburidian</td>
<td></td>
</tr>
<tr>
<td>0.3 – 0.13</td>
<td>7-6</td>
<td></td>
<td></td>
<td></td>
<td>Hayonim E, Misliya</td>
<td></td>
<td>Early Mousterian</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) Number of species that left Africa