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Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe

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ABSTRACT

Large-scale fluctuations in global climate and resulting changes in ecology had a profound effect on human evolution and dispersal. Though hominin remains are scarce, studies focussing on the more abundant records of fossil land mammal communities can contribute greatly to our knowledge of the palaeoenvironmental circumstances that influenced and directed the global spread of hominins. To produce a comprehensive and accurate account of the evolution of western Palaearctic habitat diversity between 2.6 and 0.4 Ma BP, information generated from large mammal communities from 221 key sites has been included in this study.

The palaeoecological conditions of the western Palaearctic during the Early and early Middle Pleistocene were principally controlled by the following key factors: (1) a widespread trend of temperature decrease, (2) the periodicity of the global temperature record, (3) the intensity of single climatic stages, (4) the temporal pattern of climatic variation, (5) geographical position, and (6) the distribution of continental water resources. A general picture of the evolution of western Palaearctic habitat diversity saw the replacement of extensive forested terrain by an alternating sequence of varied savannah-like and forested habitats during the 2.6–1.8 Ma span, as well as an alternation between different types of predominantly open habitats between 1.8 and 1.2 Ma. Both of these processes were governed by 41 ka temperature periodicity. During the 1.2–0.9 Ma time span, irregular climatic fluctuations were more common and habitat variability increased. The subsequent 0.9–0.4 Ma interval, a period controlled by 100 ka periodicity, was by comparison more stable, with longer climatic cycles alternating between open and forested landscapes. During the entire Early and early Middle Pleistocene, assemblages of large mammal communities reveal a distinct trend of decreasing continentality between Eastern and South-Eastern Europe on the one hand, and South-Western and North-Western Europe on the other. This trend was due to the effect of the Atlantic Ocean, while in Southern Europe the relatively low continentality was balanced by influences from the Mediterranean Sea.

When plotted against evidence of hominin occurrence, the data on western Palaearctic habitat diversity inferred from large mammal communities indicate clear environmental stimuli for the earliest human dispersal in Europe. These are: (1) a wide range of habitats, implying a high diversity of resources; (2) mild climates with low seasonality, implying a lack of strong environmental fluctuations. Around 1.8 Ma at the latest, hominins of African origin entered the western Palaearctic for the first time, taking advantage of the diversity of habitats and resources, particularly along large river systems. Their subsequent westward spread between 1.7 and 1.3 Ma was restricted to Mediterranean-influenced areas, which offered a high variability of habitats and relatively low seasonality. The increase in environmental

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diversity, which occurred from 1.2 Ma onwards, opened up South-Eastern and Eastern Europe for hominin occupation. According to the available records, North-Western and Central Europe were initially colonized during late Early to early Middle Pleistocene interglacials, when these regions experienced periods of low seasonality and considerable habitat diversity.

1. Introduction

The history of human evolution and dispersal is a complicated one, but the roles played by fluctuations in the global climate and the resulting ecological changes were undoubtedly fundamental (Vrba et al., 1995; Potts, 1998; DeMenocal, 2004). Indeed, many researchers see this influence as the engine driving hominin evolution and technological progress (McNabb, 2005). Palaeoecological investigations based on fossil assemblages are a useful tool with which to reconstruct key environmental changes. Beside the analysis of micro- and macrobotanical records (e.g. Lang, 1994), of invertebrate (e.g. Ložek, 2000), and to a certain extent also lower vertebrate remains (e.g. Holman, 1998), studies of fossil land mammal communities can contribute to our knowledge of how palaeoenvironmental circumstances affected the global spread of hominins. In many cases, mammals shared their habitats with hominins and/or formed key resources for human subsistence. An up-to-date transregional study on the evolution of palaeoenvironmental conditions of the western Palaearctic, based on the assumption that Early to early Middle Pleistocene mammal faunas are indicative of particular environments, is therefore long overdue.

In this study, data compiled from the analysis of large mammal communities, recovered from 221 key sites, have been used to reconstruct principal evolutionary trends of regional habitat diversity for the period 2.6 to 0.4 Ma BP. This time span has been divided into four main intervals (2.6–1.8, 1.8–1.2, 1.2–0.9, 0.9–0.4 Ma), each typified by its own characteristic faunal composition and evolution. The chronostratigraphic positions of the included fossil mammal sites, which provide sufficient information on the evolution of the palaeoenvironment, are compiled in Fig. 1. Corresponding geographic positions are shown in Figs. 2–5. From the analysis of the large mammal communities, principal evolutionary trends of regional habitat diversity were established. Information on early human dispersal and the peopling of Europe was then projected onto the resulting sketch of spatio-temporal patterns of prevailing habitat type for the western Palaearctic. The principal objective of this analysis was to yield conclusions as to whether environmental circumstances were a key factor in stimulating the earliest human colonization of Europe. Our project has been paralleled by a study on North African mammal sites (Sahnouni et al., 2010).

2. Regional evolution in the western Palaearctic

2.1. *The 2.6–1.8 Ma interval*

During the Late Pliocene the global temperature gradually dropped. Between 2.8 and 2.6 Ma the seasonality of the North Pacific, as well as the glacial activity of the Greenland, Scandinavian and North American ice sheets, increased (Flesche Kleiven et al., 2002; Haug et al., 2005); tundra-like landscapes with permafrost soil formed in northern Asia and Beringia (Sher et al., 1979; Westgate and Froese, 2003); and a surge in aridity occurred, as recorded in aeolian deposits north of the Himalayan-Tibetan uplift (Guo et al., 2002). Around 2.6 Ma ago, at the beginning of the Middle Villafranchian, Quaternary glacial/interglacial alternations were initiated in the northern hemisphere (Zubakov and Borzenkova, 1990). These alternations were governed by orbital obliquity cycles and had a 41-ka long periodicity (Lisiecki and Raymo, 2005). All of these climatic changes had significant ecological consequences. Seasonality became more marked, while successive cycles throughout the 2.6–1.8 Ma interval produced progressively cooler and somewhat drier conditions in western Eurasia (Figs. 1, 2).

2.1.1. *Levant and Transcaucasia*

The Lower to Middle Villafranchian transition is characterised by a remarkable decrease of Ethiopian faunal elements in south-west-Asian and European faunas. Whereas the Transcaucasian fauna of Kvabebi (eastern Georgia; Vekua, 1972), dating slightly older than 2.6 Ma, still shows a pronounced African influence with species like *Oryx* (*Aegoryx*) sp., *Eosyncerus ivericus*, *Propotamochoerus provincialis,* and *Kvabebihyrax kachethicus* (updated faunal list in Hemmer et al., 2004), these ungulates are notably absent in younger Eurasian sites of Middle Villafranchian age. However, in the Middle Villafranchian faunal record of the Levant, the presence of *Giraffa* at the site of Bethlehem indicates a continuing African influence in the eastern Mediterranean (Martínez-Navarro, 2004).

The Georgian sites of Diliska and Kotsakhuri illustrate typical Transcaucasian faunal assemblages belonging to the later part of the Middle Villafranchian, i.e. the interval between ca. 2.1 Ma and the onset of the Olduvai magnetosubchron (C2n) (M. Bukhsianidze, pers. communication to R.-D. K.). The faunal assemblage recovered at the site of Diliska, in southern Georgia, lying at approximately 1700 m above sea level, reflects typical high altitude environments in the vicinity of a lacustrine system. Among others, taxa included in the assemblage are: ?*Leptobos* sp., early roe deer *Capreolus* sp., *Cervus* cf. *perrieri*, *Equus stenonis* cf. *vireti*, *Anancus arvernensis*, and *Canis* sp. (Vekua, 1991; Vekua and Lordkipanidze, 1998). The site of Kotsakhuri in the east of the country is more typical of the drier Transcaucasian lowland, the site being situated on a flat offshore zone of the transgressed Caspian Sea (Vekua, 1991; Gabunia et al., 2000; M. Bukhsianidze, pers. communication to R.-D. K.). The faunal record of Kotsakhuri contains a number of medium-sized bovids, ?*Leptobos* sp., at least three cervids of varying sizes, *Paracamelus* sp., *Stephanorhinus* cf. *etruscus*, *Equus stenonis stenonis,* and *Mammuthus meridionalis.* Comprised of numerous freshwater bodies surrounded, to a greater or lesser extent, by open gallery forest, this site provided adequate resources for species requiring moist habitats.

2.1.2. *South-Eastern Europe and Asia Minor*

The first mammal events reflecting global cooling and aridification are well documented in several Early Villafranchian Romanian sites, such as Covrigi, Cernatesti, and Tulucesti (MNQ16a), where *Paracamelus*, *Equus*, and archaic *Mammuthus* are already present in the faunal record (Rădulescu and Samson, 2001; Rădulescu et al., 2003). A few mammoth molars with archaic features have been found in north-western Bulgaria (Galovo and Gorna Meshtitsa), but these could date somewhat later, to around the beginning of the discussed time interval (Markov and Spassov, 2001).

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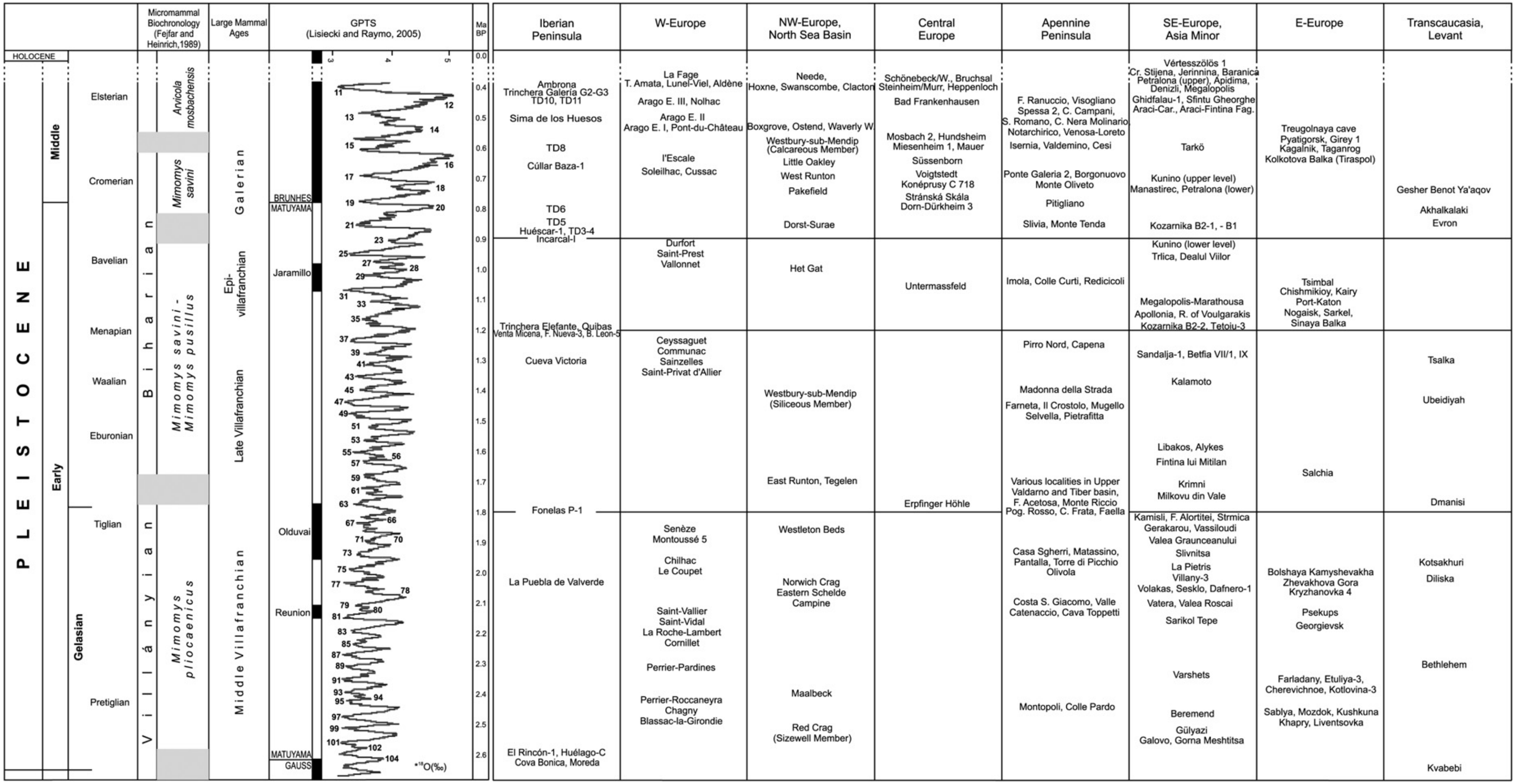

Fig. 1. Chronostratigraphic position of principal fossil mammal sites (2.6–0.4 Ma) of the western Palaearctic, based mainly on the large mammal record. All sites are mentioned in the text. For geographic positions see Figs. 2–5.

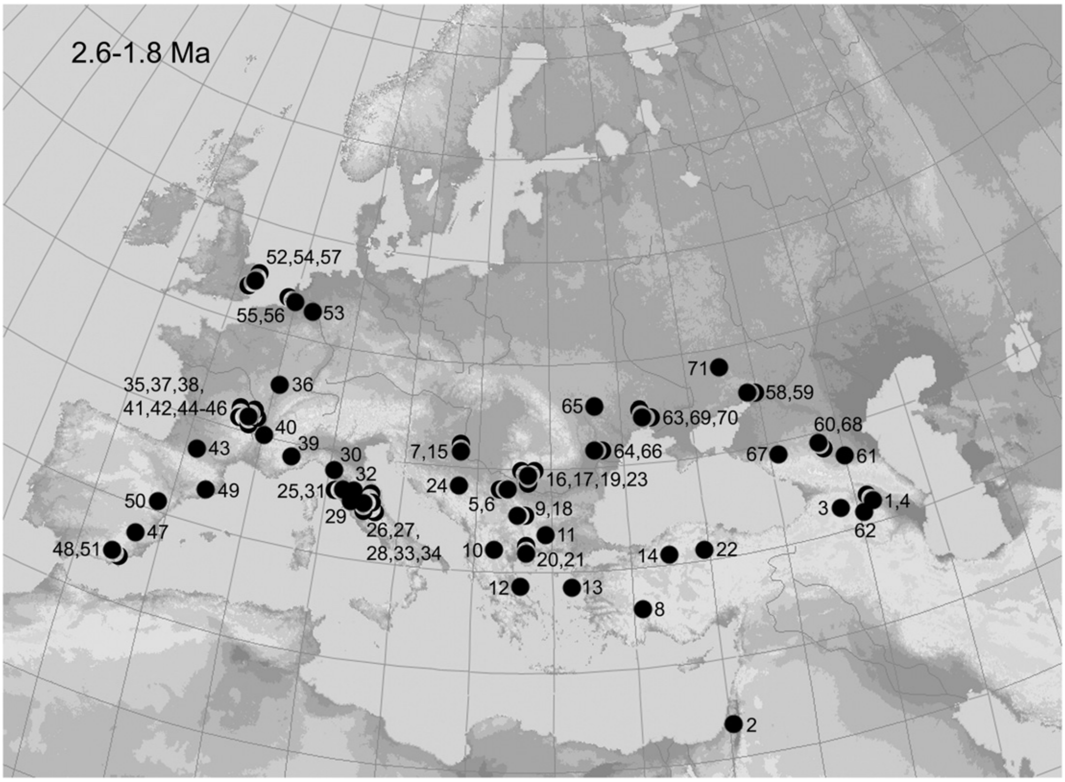

Fig. 2. Principal western Palaearctic fossil mammal sites of the 2.6–1.8 Ma interval, in the order of appearance in the text (see Section 2.1): 1, Kvabebi; 2, Bethlehem; 3, Diliska; 4, Kotsakhuri; 5, Galovo; 6, Gorna Meshtitsa; 7, Beremend; 8, Gülyazi; 9, Varshets; 10, Dafnero-1; 11, Volakas; 12, Sesklo; 13, Vatera; 14, Sarikol Tepe; 15, Villany-3; 16, Valea Roscai; 17, La Pietris; 18, Slivnitsa; 19, Valea Graunceanului; 20, Gerakarou; 21, Vassiloudi; 22, Kamisli; 23, Fantana Alortitei; 24, Strmica; 25, Montopoli; 26, Costa San Giacomo; 27, Valle Catenaccio; 28, Cava Toppetti; 29, Colle Pardo; 30, Olivola; 31, Casa Sgherri; 32, Matassino; 33, Torre di Picchio; 34, Pantalla; 35, Blassac-la-Girondie; 36, Chagny; 37, Perrier-Roccaneyra; 38, Perrier-Pardines; 39, Cornillet; 40, Saint-Vallier; 41, Le Coupet; 42, Senèze; 43, Montoussé 5; 44, Chilhac; 45, La Roche-Lambert; 46, Saint-Vidal; 47, El Rincón-1; 48, Huélago-C; 49, Cova Bonica; 50, La Puebla de Valverde; 51, Moreda; 52, Red Crag (Sizewell Member); 53, Maalbeck; 54, Norwich Crag; 55, Eastern Schelde; 56, Campine; 57, Westleton Beds; 58, Khapry; 59, Liventsovka; 60, Sablya; 61, Mozdok; 62, Kushkuna; 63, Cherevichnoe; 64, Kotlovina-3; 65, Farladany; 66, Etuliya-3; 67, Psekups; 68, Georgievsk; 69, Kryzhanovka 4; 70, Zhevakhova Gora; 71, Bolshaya Kamyshevakha.

Large mammal assemblages dating from the early Middle Villafranchian are rather rare in the Balkans. The Beremend fissure-filling sites in Hungary (Jánossy, 1986) may date to this period, but the fossils that have been found are mostly small mammals, thus preventing reliable reconstructions of large mammal communities. South-eastwards, the Turkish site of Gülyazi (Afyon, Sandikli) has been proposed as being within the MN16 zone (Sickenberg and Tobien, 1971), but a more likely placement could be at the base of the Middle Villafranchian (MNQ16b-MNQ17a). In addition to a large quantity of carnivores, the Gülyazi faunal assemblage includes: *Gazella borbonica*, *G. 'sinensis'* (?=*G. bouvrainae* or *G. emilii*), ?*Gazellospira*, *Leptobos* sp., *Eucladoceros* sp., *Mitilanotherium martini, Paracamelus alexejevi*, *Stephanorhinus "megarhinus"* and *Anancus arvernensis*. Camelids, slender hipparionine horses, bovines and running antelopes are all indicative of an open grassy landscape, while the presence of large deer, giraffes, rhinos and gomphothere proboscideans suggests more bushy-woody environments. The combination of these forms suggests that the landscape featured both savannah and woodland. The overall character of the Gülyazi large mammal assemblage seems to have been inherited in slightly later faunas from the southern Balkans and Asia Minor.

Faunal assemblages from the sites of Varshets (Bulgaria), Dafnero-1, Volakas, Sesklo, Vatera (Greece) and Sarikol Tepe (Turkey) provide a detailed snapshot of localised Middle Villafranchian pre-Oldovaian palaeoenvironments. The large mammal assemblage of Varshets shows strong similarities with typical West European faunas of the MNQ17 zone (Spassov, 1997, 2003). Typical large carnivores recovered from the Varshets assemblage include *Acinonyx pardinensis*, *Puma pardoides* (=*Panthera schaubi* = *Viretailurus schaubi*), *Lynx issiodorensis*, *Megantereon cultridens* and *Pliocrocuta perrieri*. The cervids *Metacervocerus rhenanus* (=*Cervus rhenanus* = *Dama rhenana*), *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*) and a possible undetermined third species, represent the dominant mammal group, while bovids and equids together account for no more than 6% of the quantity of cervid material. The earliest appearance of the ovibovine *Megalovis* is recorded at the Varshets assemblage, and probably originated from the Central Asian plateaus. In comparison to the somewhat older faunal species, the strong cervid signal indicates a rather intensive development of forested areas in the region, which probably coincided with the beginning of the Beregovka warming (Zubakov and Borzenkova, 1990) known from the northern Black Sea region. Considered as a whole, the faunal record recovered from the Varshets locality presents a picture of a mosaic-like landscape alternating between forest and savannah (Spassov, 2003).

The rich faunal deposits at Volakas, Sesklo and Dafnero-1 in Greece represent a slightly later period during the late Middle Villafranchian and mostly contain previously documented carnivore taxa, though *Nyctereutes* is represented by *N. megamastoides*, and *Ursus etruscus* makes its first appearance. The cervid association of three genera, *Metacervocerus*, *Eucladoceros* and *Croizetoceros*, appears to have remained unaltered, while *Gazella bouvrainae*, *Gazellospira torticornis*, *Gallogoral meneghinii*, *Mitilanotherium martinii* and *Equus stenonis* cf. *vireti* are recognised as typical faunal elements of this period (Koufos and Kostopoulos, 1997). The balanced occurrence of bovids and cervids, the record

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of large stenonine horses, and the predominance of intermediate feeders and grazers, once again suggest a savannah-like woodland environment (Kostopoulos and Koufos, 2000). The period seems to be characterised by the rare palaeotragine *Mitilanotherium* (=*Macedonitherium*), previously documented in Greece (MNQ17–18) and Romania (MNQ18–19), and which apparently expanded eastwards to Tajikistan, through Turkey and further west into Spain (all MNQ17; Kostopoulos and Athanassiou, 2005; Garrido and Arribas, 2008). The extensive mammal faunal record in the eastern sector of this region is best documented by the sites of Vatera (Lesvos, Greece) and Sarikol Tepe near Ankara (De Vos et al., 2002; Kostopoulos and Sen, 1999). In these deposits, bovid, perissodactyl, proboscidean and carnivore associations are similar to those of the southern Balkans, while the cervids appear to be less numerous, indicating a restriction of their forest habitats. The dominance of herbivores mostly associated with open environments could be indicative of an environment dominated by savannah-like bushlands (Kostopoulos and Sen, 1999). *Mitilanotherium* is also present at Vatera, while a small camelid occurs at Sarikol Tepe, presumably inherited from the Gülyazi fauna. The large terrestrial cercopithecid *Paradolichopithecus* is also recorded from Vatera. The genus has already been identified in the Ruscinian of Romania and has been linked to relatively humid environments. In MN16, however, and especially during MN17, this cercopithecid shows a much wider distribution, ranging from Spain to Tajikistan, regions which are both normally associated with more arid mammal communities (Van der Geer and Sondaar, 2002; Eronen and Rook, 2004; see Section 2.1.5).

In the north, Villany-3 (Hungary), Valea Roscai and La Pietris (Romania) give a much more restricted picture of the large mammal association of this period. Villany-3 is a rich karstic locality of MNQ17 complexion, though it evidently spans a longer time period (probably until MNQ18a *sensu* Spassov, 2003). Typical carnivores found at Villany-3 are the mustelids *Baranogale helbingi*, *Vormela petenyii*, *Pannonictis pliocaenica* and *Mustela palerminea* (Jánossy, 1986). The presence of *Hemitragus* at this locality could correspond to a younger level. The Romanian assemblages do not significantly differ from those of the southern Balkans (Rădulescu et al., 2003). La Pietris, at which *Pliotragus ardeus* and the large-sized *E. major athanasiui* are recorded for the first time, possibly dates closer to the subsequent pre-Olduvai cooling. The prevalence of horses over deer could indicate drier, more open landscapes, while the strong signal of the large cursorial beaver, *Trogontherium,* suggests that riparian environments were also present (Spassov, 2000).

At the beginning of the Late Villafranchian (MNQ18a *sensu* Spassov, 2003), the large mammal record of Slivnitsa (Bulgaria) documents the earliest presence of *Ovis*, and probably of *Hemitragus* and *Panthera,* in Eastern Europe, and is the first datum of the so-called "*Canis* event" west of the Black Sea (Spassov, 1997, 2002, 2003). Cervid associations remain unchanged, while stenonine horses show a size decrease and bovids, especially Caprinae, become much more abundant and diverse. The Slivnitsa assemblage marks the emergence of a significant faunal renewal that ought to coincide with the superclimatheme SCT10 of Zubakov and Borzenkova (1990), i.e. during the short-term pre-Olduvaian climatic deterioration known in Georgia as the Meria cooling. Several lines of evidence show that the Meria cooling was accompanied by a freshening of the Black Sea, which could have been the result of a short-term closure of the Bosporus channel, leading to an increase of caprine migrants to the west and causing the extinction of several antelope species.

The slightly younger locality of Valea Graunceanului in Romania (Tetoiu-1 horizon) incorporates several mid-Villafranchian elements such as *Gazellospira*, *Pliotragus*, *Metacervocerus rhenanus*, *Eucladoceros*, *Mitilanotherium*, with native species such as *Equus major athanasiui*. The carnivore assemblage recalls those from earlier horizons. Even though *Nyctereutes* is still present, it possesses more advanced characters than animals recorded at St. Vallier (N.S., pers. observation). *Paradolichopithecus* is also present and has a form close to that of Senèze (France), while the presence of the pangolin *Manis* cf. *hungarica* suggests a relationship with Villany-3 in Hungary (Rădulescu et al., 2003). The strong deer signal, in combination with the presence of pangolins and beavers, indicates that conditions in the region were humid and warm, like those of the Olduvaian.

The Greek localities of Gerakarou and Vassiloudi have ages which are estimated to lie between the sites of Olivola in Italy and Senèze in France (Koufos and Kostopoulos, 1997). Both have yielded a rich macromammalian faunal record of typical Late Villafranchian (MNQ18) character. *P. onca gombaszoegensis* (=*P. gombaszoegensis*) and *Canis etruscus* are associated with newcomers such as *Sus strozzii*, *Pachycrocuta brevirostris* and *Canis arnensis,* while *Gazella*, *Procamptoceras* and *Pliocrocuta perrieri* make their last appearances. Cervids and horses are still an important component of the faunal mix, with the same combination as previously described, but with a marked trend towards size-reduction. With respect to Middle Villafranchian localities of the southern Balkans, the Gerakarou faunal assemblage does not indicate any significant environmental changes. During this period intermediate feeders remain the dominant herbivore group, while browsers balance with grazers, and open to open/mixed dwellers make up more than half of the assemblage (Kostopoulos and Koufos, 2000). Several sites of roughly similar age (MNQ18b sensu Spassov, 2003), such as Kamisli in Turkey (Amasya; Sickenberg and Tobien, 1971), Fantana Alortitei in the Tetoiu-2 faunal horizon of Romania (Rădulescu and Samson, 2001), and Strmica in Dalmatia (Malez, 1986), have yielded analogous faunal associations to those from Slivnitsa and Gerakarou, suggesting rather homogeneous palaeoenvironmental conditions across the entire region.

2.1.3. *Apennine Peninsula*

Due to the Late Pliocene temperature drop in the Apennine Peninsula, subtropical warm, moist conditions progressively gave way to cool, moist conditions. Several browsing ungulates, namely *Procapreolus cusanus*, *Pseudodama lyra, Sus minor* (=*S. arvernensis*), *Tapirus arvernensis*, *Stephanorhinus jeanvireti*, *Anancus arvernensis* and *Macaca sylvanus* thrived in the forests, while *Mammut* (*Zygolophodon*) *borsoni*, and the mobile, gregarious, large-sized grazing bovid *Leptobos stenometopon* flourished in open grassland areas. Hunters requiring dense cover in order to stalk or ambush their prey would have found scattered areas of woodland and shrub vegetation suitable for their needs. And in fact a wide variety of solitary, ambushing carnivores, such as *Acinonyx pardinensis*, *Puma* ex gr. *P. pardoides*, *Lynx issiodorensis*, *Megantereon cultridens*, *Homotherium crenatidens, Pliocrocuta perrieri*, *Chasmaporthetes lunensis*, several mustelids, *Agriotherium insigne*, *Ursus etruscus*, *U. minimus*, *Nyctereutes megamastoides*, *Vulpes alopecoides* and viverrids, inhabited the Early Villafranchian woodlands and grasslands.

During the colder phases the vegetation of the Italian peninsula was divided into two major climatic zones (Bertini, 2003). In northern Italy, moister conditions favoured the diffusion of high altitude, *Picea*-dominated coniferous forests. Further south, from 2.46 Ma on, herbaceous and steppe vegetation, with a steady diffusion of *Artemisia*, spread in response to a long, relatively warm interval. This kind of vegetation also characterised the succeeding Early Pleistocene glacial phases. During the interglacial periods, deciduous, warm-temperate vegetation replaced subtropical forests (Bertini, 2003).

As a result of the drop in temperature during this interval, Middle Villafranchian herbivores found themselves exposed to increasingly harsh conditions. These environmental changes doomed some of

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the original faunal elements to extinction. Species such as *Leptobos stenometopon*, *Procapreolus cusanus*, *Sus minor*, *Stephanorhinus jeanvireti, Tapirus arvernensis*, *Mammut borsoni*, *Agriotherium insigne*, *Ursus minimus*, and viverrids all disappeared. Yet, at the same time, these environmental changes opened the way through Italy for various newcomers, and over the course of the Middle Villafranchian faunal diversity became increasingly rich thanks to the appearance of many new species. The spread of grasslands encouraged the appearance of new large- (*Equus stenonis*, *E. livenzovensis*) to very large-sized (*Mammuthus meridionalis*) grazers. This was the time of the so-called "Elephant-*Equus* event", which occurred roughly at the Gauss/Matuyama magnetic chron boundary (Azzaroli, 1995), and which has been demonstrated at Montopoli (Lower Valdarno, Tuscany). This important fossiliferous locality, together with the late Middle Villafranchian sites of Costa San Giacomo, Valle Catenaccio, Cava Toppetti (all Umbria) and Colle Pardo (Latium), and those of the early Late Villafranchian of Olivola (Massa Carrara), Casa Sgherri (Pisa), Matassino (Upper Valdarno, Florence), Torre di Picchio (Umbria), and Pantalla (Umbria), document other new appearances. These include the omnivorous suid *Sus strozzii*, as well as an array of browsing and grazing ungulates, such as *Gazella borbonica*, *Gazellospira torticornis*, *Gallogoral meneghinii*, *Hemitragus* sp., *Leptobos* ex gr. *L. merlai* - *L. furtivus*, *Eucladoceros falconeri*, *E. tegulensis* (=*E. ctenoides* = *E. senezensis*), *Croizetoceros ramosus*, and *Stephanorhinus etruscus*. The significant quantities of the large-sized *Leptobos* and *Equus* indicate that these animals probably lived in herds, at least during particular times of the year. These herds of grazers most probably fled harsh environmental conditions (Mazza, 2006), as wildebeest and zebra do today; *Leptobos* spp. and *Equus stenonis* can be considered their ecological equivalents. Herds of large-sized ungulates are more easily subdued by carnivores that use cooperative hunting behaviours, such as canids, lions and spotted hyaenas, than by lone hunters. During this time, also, *Canis etruscus* dispersed into Europe and reached Italy, where the earliest record of the species occurs at Costa San Giacomo. The spread of this pack-hunter marks the beginning of the so-called "wolf event" (Azzaroli, 1983, 1995; Azzaroli et al., 1988; Rook and Torre, 1996; Palmqvist et al., 1999; Sardella and Palombo, 2007).

2.1.4. Western Europe

In Western Europe also, the Middle Villafranchian period began with climatic cooling, reducing the warm and humid forest habitat of *Stephanorhinus jeanvireti* and *Mammut borsoni*, both typical species of the Early Villafranchian seen at, for example, Vialette (Haute-Loire) (MN16a; Lacombat et al., 2008). However, as documented at the site of Chagny (Saône et Loire), *Tapirus arvernensis* still persisted at the beginning of the Middle Villafranchian (Guérin, 1980), indicating the continued existence of at least some local forested areas. Overall, however, the climatic change led to more favourable environments for the spread and expansion of large herbivores adapted to grassland. *Leptobos* ex gr. *L. merlai* – *L. furtivus, L. etruscus* and *E. stenonis* s.l. replaced *Leptobos stenometopon* and more ancient members of the genus *Equus*. The above-mentioned forms of *Leptobos* have been documented at Blassac-la-Girondie (Haute-Loire), Chagny (Saône et Loire), Perrier-Roccaneyra and Perrier-Pardines (Puy-de-Dôme), Cornillet (Alpes-de-Hautes-Provence), Saint-Vallier (Drôme), Le Coupet (Haute-Loire) and Senèze (Haute-Loire) (Heintz et al., 1974; Crégut-Bonnoure and Valli, 2004), together with the appearance of new bovids, i.e. *Gazellospira torticornis* at Perrier-Roccaneyra, Perrier-Pardines, Cornillet, Le Coupet and Senèze; *Procamptoceras brivatense* in Montoussé 5 (Hautes-Pyrénées) and Senèze; *Megalovis latifrons* at Senèze; and *Gallogoral meneghinii* at Saint-Vallier, Chilhac (Haute-Loire) and Senèze (Clot et al., 1976). In addition to the above-mentioned species, *Gazella borbonica* was also widespread at most of these localities. Such a diversity of bovids underlines the importance of grazers in the faunal communities of the West European Middle Villafranchian. Browsers roaming in the remaining forests included the cervids *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*), "*Cervus*" *philisi* and *Croizetoceros ramosus.* At Blassac-la-Girondie (Haute-Loire), Senèze, and possibly Chagny a large member of the Alceinae has also been documented. The ubiquitous *Stephanorhinus etruscus* had been present in Western Europe since the end of the Early Villafranchian, as documented by finds at Perrier-Étouaires (Guérin, 1980), and was the only rhino of the Middle Villafranchian. The occurrence and increasing abundance of *Equus stenonis* s.l. at Blassac-la-Girondie, Perrier-Pardines, Cornillet, La Roche-Lambert, Saint-Vidal (Haute-Loire), Saint-Vallier, Le Coupet, Chilhac and Senèze (Heintz et al., 1974; Heintz and Dubar, 1981; Bœuf et al., 1992; Eisenmann, 2004; Delson et al., 2006) are indicative of the extension of grasslands during this period. The very large-sized *Mammuthus meridionalis* first spread around 2.5–2.2 Ma, in tandem with *Anancus arvernensis,* which has been recorded at Saint-Vallier (Guérin, 2004), Le Coupet (Heintz et al., 1974) and Chilhac (Bœuf and Barbet, 2005). By modifying its diet, reflected in the rising number of lamellae within the individual molars, *Mammuthus meridionalis* was able to survive the deforestation of the landscape during the Middle Villafranchian. Within this time interval, the last recorded occurrence of this species occurs in Chilhac at around 2.0 Ma.

During this period, the carnivore group in Western Europe was dominated by solitary felids, which had been present since the Early Villafranchian: *Lynx issiodorensis* at Perrier-Roccaneyra, Perrier-Pardines and Saint-Vallier (Argant, 2004); *Acinonyx pardinensis* at Saint-Vallier and Senèze, along with the widespread *Homotherium crenatidens*. In addition to the newcomers, such as *Megantereon cultridens* at Blassac-la-Girondie, Perrier-Pardines, Saint-Vallier, Chilhac and Senèze, and *Puma pardoides* (=*Panthera schaubi* = *Viretailurus schaubi*) at Saint-Vallier. Early Pliocene species, such as *Pliocrocuta perrieri* and *Chasmaporthetes*, remained in the area, and indeed survived the whole of the Middle Villafranchian. The ursids, however, suffered: *Agriotherium* went extinct, and *Ursus minimus* was replaced by *Ursus etruscus.* Canids, and in particular the genus *Canis* from Blassac-la-Girondie, Saint-Vallier, Chilhac and Senèze, fared much better. This group enjoyed an extraordinary development during this period, and had obviously taken advantage of the open habitat. Other taxa that benefitted from the varied Middle Villafranchian environment included *Vulpes alopecoides*, *Nyctereutes,* and various mustelids.

2.1.5. Iberian Peninsula

Up to around 2.6 Ma the presence of *Metacervocerus rhenanus* (=*Cervus rhenanus* = *Dama rhenana*), *Tapirus arvernensis*, *Anancus arvernensis* and others browsers, indicates that extended forests had developed over the Iberian Peninsula under warm and humid conditions. Ambush-hunting carnivores of the period include *Chasmaporthetes*, *Agriotherium* and *Nyctereutes megamastoides.* A gradual drop in temperature, however, provided the setting for Middle Villafranchian climatic conditions in South-Western Europe, which became progressively cooler and drier. These environmental changes led to a progressive shift in the faunal composition. Alongside existing species such as *Anancus arvernensis*, newcomers such as *Stephanorhinus* cf. *etruscus, Equus livenzovensis* and *Mammuthus meridionalis* became more adapted to forested savannahs as more open areas began to appear across the landscape. The sites of El Rincón-1 (Albacete) and Huélago-C (Granada), which are dated to around 2.6 Ma, reflect the high diversity of browsing and grazing artiodactyls present during this period. Species such as *Gazella borbonica, Gazellospira torticornis*, *Leptobos* cf. *elatus*, *Eucladoceros* cf.

tegulensis (=*E.* cf. *ctenoides* = *E.* cf. *senezensis*), *Croizetoceros ramosus*, Giraffidae indet., *Stephanorhinus etruscus* and *Equus livenzovensis* (Azanza et al., 1989; Alberdi et al., 1997, 2001) all thrived, suggesting a rich and diverse environment consisting of both forested and open regions.

Macaca and *Paradolicopithecus* were both present between 2.6 and 2.0 Ma (MN16–17) in the northwest of the Iberian pensinsula, as recorded by the finds from Cova Bonica (Garraf massif, Barcelona) and La Puebla de Valverde (Teruel basin). Cercopithecids of the genus *Macaca* were commonly found in Early Villafranchian woodlands and are associated with humid areas, although from MN17 on they inhabited a wider range of humidity levels (Eronen and Rook, 2004). The large cercopithecid *Paradolicopithecus arvernensis* co-existed with *Macaca* during MN16 in humid environments in northern Spain, but during MN17 was distributed across more arid environments, like Moreda in southern Spain (Eronen and Rook, 2004). Sondaar et al. (2006) have hypothesised that *P. arvernensis* lived at forest edges bordering a savannah-like landscape.

Around 2.3 Ma the Iberian Peninsula was dominated by Mediterranean “warm” *Artemisia* steppes (Suc et al., 1995), the expansion of which clearly illustrates the opening-up of the landscape. However, correlated sites with extensive records of large mammals are still lacking. Evidence from La Puebla de Valverde, dated at 2.04 Ma (Sinusía et al., 2004), confirms the existence of forested areas, which provided habitats for species such as *Metacervocerus rhenanus*, *Macaca* sp. and *Paradolicopithecus arvernensis*, alongside those associated with more open landscapes, such as *Equus stenonis* and ambush carnivores such as *Lynx issiodorensis, Megantereon cultridens*, *Pliocrocuta perrieri*, *Chasmaporthetes lunensis*, *Ursus etruscus*, *Nyctereutes megamastoides* and *Vulpes alopecoides* (Heintz, 1978).

2.1.6. North-Western Europe and the southern North Sea Basin

The interval 2.6–1.8 Ma is represented in Britain chiefly by the Red and Norwich Crag Formations. The Red Crag Nodule Bed, c. 2.7 Ma, including the temperate, forested Waltonian Stage (correlated to the Reuverian C of the Netherlands) includes ‘exotic’ faunal elements making their last appearance in the British record, such as *Tapirus*, *Hipparion*, *Mammut borsoni* and *Parailurus* (Stuart, 1982) plus Early Villafranchian deer (Lister, 1999). The fauna of the Red Crag proper is mainly of Pre-Ludhamian age (ca. 2.5 Ma, correlated to the Praetiglian), a cool interval with regional boreal trees, *Erica* heath and grasses. The mammals include grazing or mixed-feeding species such as the large stenonine horse *Equus bressanus* (=*E. major* = *E. robustus*) and early mammoth *Mammuthus rumanus* (Lister and van Essen, 2003), as well as woodland elements such as gomphothere *Anancus arvernensis* and beaver *Castor* sp. The succeeding warm Ludhamian and cool Thurnian stages are not represented in the mammal record, but the tapir (*Tapirus arvernensis*) from Maalbeck, The Netherlands may be of Tiglian A = Ludhamian age (Van Kolfschoten, 2001).

The Norwich Crag, of the Antian/Bramertonian temperate stage (ca. 2.0 Ma, in the interval Tiglian C1-4b) has yielded *Equus bressanus*, *Mammuthus meridionalis*, *Anancus arvernensis* and the deer *Eucladoceros* in a mixed temperate forest (Head, 1998), plus cheetah *Acinonyx pardinensis* implying open areas (Turner and Antón, 1997; Turner, 2009). The mineralised ‘Black Bones’ assemblage dredged from submarine deposits in the Eastern Schelde, The Netherlands includes *Eucladoceros falconeri*, *A. arvernensis* and *M. meridionalis*, and is roughly of this age, as are remains of *E. falconeri* from the Campine Formation of Belgium (Germonpré, 1983; Van Kolfschoten, 1991, 2001). The Baventian to Pre-Pastonian a stage (ca. 1.85 Ma, correlated to Tiglian C4c) saw very cold climate with grassland, heath and park tundra biomes represented in pollen spectra (Head, 1998; Gibbard et al., 1998). Large mammal fossils directly provenanced to this episode are rare, but from the ‘Weybourne Crag’ (now part of the Wroxham Crag Formation) and Westleton Beds of Norfolk, the latter representing a climatic amelioration towards the end of this stage (Richards et al., 1999), have come the early moose *Cervalces* (=*Alces*) *gallicus* and *M. meridionalis* (Lister, 1998).

2.1.7. Central Europe

The Central European fossil record of large mammals from the 2.6 to 1.8 Ma interval is very limited. As a consequence, the existing record does not provide sufficient information of any significance with which to determine the evolution of the palaeoecological conditions of this time.

2.1.8. Eastern Europe

In Eastern Europe, the Middle Villafranchian large mammal fauna underwent a particularly significant renewal. While species that thrived in humid and forested habitats, such as tapir and lophodont mastodon, did not adapt to the open steppe and forest-steppe landscapes, taxa more suited to the new landscapes appeared, i.e. *Gazellospira*, *Cervalces* (=*Alces*), *Eucladoceros*, *Paracamelus*, *Equus*, archaic forms of *Mammuthus*, *Homotherium crenatidens*, *Meles* and *Canis*.

Eastern European animal associations of the early part of the Middle Villafranchian have been related to zone MN17 and are characterised by the Khapry Faunal Complex (Gromov, 1948). Typical faunal elements of this complex include the cervid genera *Arvernoceros* and *Eucladoceros*, *Paracamelus alutensis*, *Elasmotherium chaprovicum*, *Equus livenzovensis*, *Anancus*, and an early member of the Eurasian mammoth line *Mammuthus meridionalis gromovi* (Titov, 2008). A central Asian influence is evident from the appearance of the small camel and the elasmothere (Bajgusheva et al., 2001). The deer *Arvernoceros* continued to thrive during this period and *Anancus* and the giraffid *Palaeotragus* roamed in more humid areas. The structure of the Khapry faunal assemblage indicates a widespread occurrence of forest-steppe landscapes in a correspondingly dry climate. Species associated with xerophilous habitats are lacking, and those of forested areas are scant. The summers were hot and the winters were warmer and drier than those of today. The absence of species adapted to dry habitats, together with the abundance of species typical of semi-open to open habitats, suggests that the prevailing landscape of the period was savannah.

The south of the European part of Russia, Ukraine, and some regions of Moldova, Romania and the southern Black Sea Region may be distinguished as the Black Sea Region faunal province. Faunas of this province have been recorded at Khapry, Liventsovka, Sablya, Mozdok, Kushkuna, Cherevichnoe, Kotlovina-3, Farladany and Etuliya-3 (Alexeeva, 1977; Titov, 2008).

During the later Middle Villafranchian a gradual change occurred in the faunas of the Eastern European region, caused by increasing aridity. The Khapry Faunal Complex was replaced by the Psekups (=Odessa) Complex, comprising species such as *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii*, *Eucladoceros* cf. *tegulensis* (=*E.* cf. *ctenoides* = *E.* cf. *senezensis*), *E. orientalis*, *Stephanorhinus* cf. *etruscus*, *Equus* cf. *major*, and the typical southern elephant *Mammuthus meridionalis meridionalis*. Under these conditions *Paracamelus alutensis* and the bunolophodont mastodons, *Anancus,* became less numerous. In addition to the type locality at the Psekups River near Krasnodar, the faunal records from Georgievsk (northern Caucasus), Kryzhanovka 4 and Zhevakhova Gora (north-western Black Sea area), and Bolshaya Kamyshevakha (south of Kharkov), also belong to the Psekups Complex.

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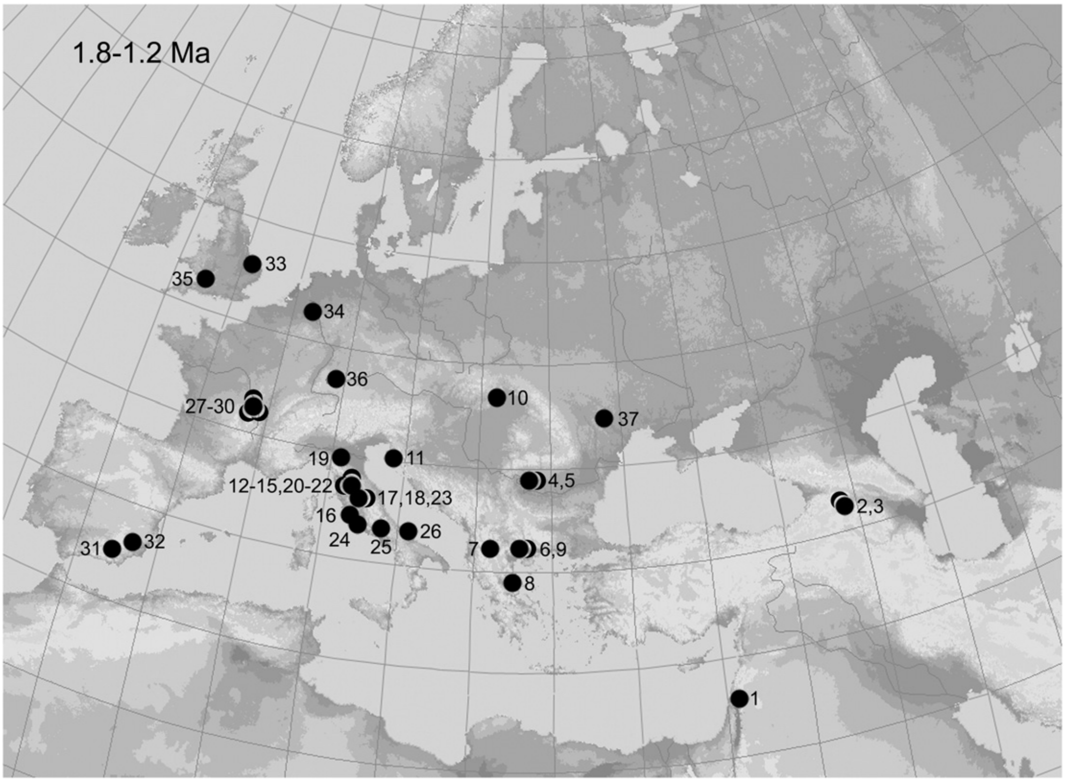

Fig. 3. Principal western Palaearctic fossil mammal sites of the 1.8–1.2 Ma interval, in the order of appearance in the text (see Section 2.2): 1, Ubeidiyah; 2, Dmanisi; 3, Tsalka; 4, Milkovu din Vale; 5, Fintina lui Mitilan; 6, Krimini; 7, Libakos; 8, Alykes; 9, Kalamoto; 10, Betfia VII/1, IX; 11, Sandalja-1; 12, Upper Valdarno; 13, Poggio Rosso; 14, Casa Frata; 15, Faella; 16, Monte Riccio; 17, Fontana Acetosa; 18, Tiber basin; 19, Il Crostolo; 20, Mugello; 21, Selvella; 22, Farneta; 23, Pietrafitta; 24, Capena; 25, Madonna della Strada; 26, Pirro Nord; 27, Ceyssaguet; 28, Sainzelles; 29, Saint Privat d'Allier; 30, Communac; 31, Fonelas P-1; 32, Cueva Victoria; 33, East Runton; 34, Tegelen; 35, Westbury-sub-Mendip (Siliceous Member); 36, Erpfinger Höhle; 37, Salchia.

2.2. The 1.8–1.2 Ma interval

The Middle to Late Villafranchian transition experienced a further drop in temperature as climatic cycling remained dominated by the 41 ka periodicity (Lisiecki and Raymo, 2005). The cycles of cool and temperate climatic events became more clearly defined and regular. The onset of the Late Villafranchian saw the arrival of *Homo* in Eurasia (e.g., Lordkipanidze et al., 2007) (Figs. 1, 3).

2.2.1. Levant and Transcaucasia

During the Late Villafranchian, the Levantine area continued to be influenced by the African fauna, as illustrated by the high number of Ethiopian species in the fossil record of Ubeidiya (Israel), which dates to approximately 1.5–1.2 Ma: *Oryx* sp., *Pelorovis oldowayensis*, Giraffidae indet., *Kolpochoerus olduvaiensis*, *Hippopotamus gorgops*, *Equus* cf. *tabeti*, *Crocuta* etc. (Tchernov and Guérin, 1986; Guérin et al., 1996; Martínez-Navarro et al., 2009). The site of Ubeidiya was formed in a fluvio-limnic environment, but its fauna reflects a more open landscape, such as savannah or tree savannah.

The huge fauna of Dmanisi, Georgia, dated to 1.77 Ma, differs completely from the older fauna of Kvabebi with its strong African affinities (see Section 2.1.1). The Dmanisi assemblage is clearly of Eurasian character, as demonstrated by the high number of cervid species and individuals (updated faunal list in Lordkipanidze et al., 2007). Several of the faunal elements recorded at Dmanisi are also common in the Middle Villafranchian contexts of Western Asia and Europe: *Gallogoral meneghinii sickenbergii*, *Eucladoceros* cf. *tegulensis*, (=*E.* cf. *ctenoides* = *E.* cf. *senezensis*), *Palaeotragus* sp., *Mammuthus meridionalis* (typical form) and *Pliocrocuta perrieri*. More modern forms include *Bison* (*Eobison*) *georgicus*, *Pontoceros* sp., *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii,* and *Cervus abesalomi*. The palaeo-landscape of the Dmanisi area was characterised by remarkable differences in humidity and vegetation across its terrain. Whereas the immediate area of the fossil site was situated in a forested valley, indicated by taxa such as *Bison* (*Eobison*), *Eucladoceros*, *Dama nestii* and *Cervus abesalomi*, the wider region was largely made up of tree savannah and open grasslands inhabited by Antilopini indet. and *Equus* cf. *altidens*, and by semiarid rocky areas with *Gallogoral meneghinii*, *Capra dalii*, and *Testudo graeca.* The presence of *Hystrix refossa* also indicates the existence of temperate climatic conditions.

The mammal assemblage of Tsalka in the south of Georgia belongs to the later Late Villafranchian. The site was situated c. 1600 m above sea level in a meandering river gorge that passed through a predominantly open landscape. The faunal assemblage includes *Bison* (*Eobison*) sp., *Dama* cf. *nestii*, *Eucladoceros* sp., a megacerine deer, *Equus stenonis*, *Mammuthus meridionalis*, *Homotherium crenatidens* and *Canis etruscus* (Vekua et al., 1985; Vekua and Lordkipanidze, 1998; M. Bukhsianidze, pers. communication to R.-D.K.), all species which reflect warm climatic conditions.

2.2.2. South-Eastern Europe and Asia Minor

There are few localities that are isochronous to Dmanisi in South-Eastern Europe. Among them, with signs of oncoming aridification, are probably the Romanian localities Milkovu din Vale and Fintina lui Mitilan. Milkovu din Vale is of post-Olduvaian age,

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and its faunal assemblage shows the co-existence of the small camel *Paracamelus alutensis* and *Mammuthus meridionalis*. At the site of Fintina lui Mitilan megacerines make their first appearance in the region. The cervids are accompanied by *Megalovis*, *Leptobos*, *Mitilanotherium*, *Equus stenonis mitilanensis*, *E. bressanus* (=*E. major* = *E. robustus*) and *Trogontherium boisvilleti* (Rădulescu and Samson, 2001).

To the south, the Greek localities Krimni, Libakos and Alykes provide a snapshot of the contemporaneous faunas and environments in this region. The faunal assemblage of Krimni (Mygdonia Basin) is possibly the oldest, and is closer to the beginning of the time interval. It contains *Gazellospira* cf. *torticornis*, *Leptobos* aff. *vallisarni*, *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*), *Stephanorhinus etruscus,* and a small form of *Equus stenonis* (Koufos and Kostopoulos, 1997). Also recorded at Krimni is a bovid that has so far been identified as *Leptobos*, and which could, in fact, represent the first documentation of early bison in the Balkans. The slightly younger faunas of Libakos (Grevena Basin) and Alykes (Thessaly) are similar to the Italian Tasso faunas. *Gazellospira torticornis*, *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Canis arnensis,* and *Canis etruscus* have been recovered from Alykes, while *Pontoceros ambiquus mediterraneus*, *Leptobos* sp., *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii eurygonos*, *Eucladoceros* cf. *tegulensis*, *Mitilanotherium martinii*, *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Stephanorhinus etruscus*, *Equus stenonis* (small)*, Mammuthus meridionalis*, *Pachycrocuta brevirostris,* and *Enhydrictis ardea* have been documented at Libakos. The entire faunal assemblage marks the last occurrence of *Gazellospira*, leptobovines and giraffids in the Balkans, and the entrance of striking new migrants, which originated either from Africa (*Hippopotamus*), or Asia (*Pontoceros*). This renewal in the faunal record indicates the expansion of open grassy landscapes over this region.

Most of the newcomers appear to have been well established in a relatively short time-frame. The Greek fauna of Kalamoto (Mygdonia Basin) contains *Bison* sp., *Praemegaceros pliotarandoides*, *Hippopotamus antiquus*, *Stephanorhinus etruscus*, *Equus stenonis* (large), *Mammuthus meridionalis,* and *Pachycrocuta brevirostris* (E. Tsoukala, Thessaloniki, pers. communication to D. K.). The predominance of bison and large horse, together with hippo and a megacerine cervid, suggests open and mild environmental conditions.

At the end of the Late Villafranchian, the faunas of Betfia VII/1 and Betfia IX from the Waalian stage of Romania (~1.3–1.2 Ma) are mostly categorised by micromammals, but they also record the last occurrence of *Megantereon* and of thermophilous *Macaca sylvana florentina* in South-Eastern Europe (Terzea, 1995). The broadly isochronous Croatian karstic locality of Sandalja-1 has yielded *Leptobos*, *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii*, *Sus strozzii*, a stenonine equid, *Ursus* sp., *Canis* sp. (=*C. etruscus* after Malez, 1975) and *Macaca*. *Ursus* remains are of unspecific determination and demonstrate mixed features which have also been recorded at Vallonet (France) and Pirro Nord (Italy) (Spassov, 2003), and possibly at Kozarnika (NW Bulgaria) (N. S., pers. observations). The combination of species found at Sandalja-1 indicates the presence of mixed tree savannah-like landscapes and a moderate, relatively mild climate.

2.2.3. Apennine Peninsula

A drop in temperature marked the transition to the Late Villafranchian in the Apennine Peninsula too (Bertini, 2003). The open vegetation of the arid and cool-to-cold phases was dominated by *Artemisia* and *Ephedra*, while warm-temperate deciduous forests gradually developed during the more humid interglacials. Faunal diversity kept increasing, peaking in the first half of the Late Villafranchian, as illustrated by the assemblages from several localities in the Upper Valdarno such as Poggio Rosso, Casa Frata and Faella (Florence), as well as by those from Monte Riccio (Latium), Fontana Acetosa (Umbria), and many others in the Tiber basin. New grazers, i.e. *Procamptoceras brivatense*, *Praeovibos* sp., *Leptobos etruscus, L. vallisarni*, *L.* ex gr. *vallisarni* (more advanced), *Bison* (*Eobison*) *degiulii, Equus stehlini*, *E. altidens*, *E.* ex gr. *E. bressanus* – *E. suessenbornensis*, and several new mixed feeders and browsers, i.e. *Cervalces* (=*Alces*) *gallicus*, *Pseudodama* sp., *Pseudodama farnetensis*, *Eucladoceros dicranios*/*E. ctenoides*, *Praemegaceros* (=*Megaceroides*) *obscurus*, *Praemegaceros* aff. *solilhacus, Stephanorhinus* aff. *hundsheimensis*, appeared during this interval. These groups were dominated by large-sized species that either co-existed with or replaced some of the Middle Villafranchian survivors, and which sometimes also succeeded each other.

Many carnivores living during the transition to the Late Villafranchian benefitted from the turnover in prey. Others, however, did not fare as well. The jaguar-like *Panthera* ex gr. *P. onca gombaszoegensis*, *Felis lunensis*, the formidable bone-cracker *Pachycrocuta brevirostris* (*Pachycrocuta* event; Palombo et al., 2008), *Pannonictis nestii*, *Martes* sp., several new mustelids, an arctoid *Ursus*, the large, hypercarnivorous wild dog *Lycaon* [=*Canis* (*Xenocyon*)] *falconeri*, and the jackal-like *Canis arnensis*, joined the Italian carnivore community. *P. brevirostris*, *L. falconeri* and *C. arnensis* were cooperative hunters, or exhibited group hunting in stressed environmental conditions (Mazza, 2006). They therefore joined the already-present group hunter, *Canis etruscus*. Predators unlikely to subdue animals exceeding their own size (i.e. *Pliocrocuta perrieri*, most of the original mustelids, and *Vulpes alopecoides*) disappeared, together with solitary, stalking carnivores (i.e. *Chasmaporthetes lunensis*). The ambushing hunters, as well as *Puma* ex gr. *P. pardoides*, also became more sporadic. *Megantereon cultridens* was replaced by the African *Megantereon whitei* (some authors doubt the existence of this species in Europe: Hemmer, 2001), which arrived accompanied by the solitary *Vulpes praeglacialis* and two new pack hunters, *Lycaon lycaonoides* and *Canis* ex gr. *C. mosbachensis*.

In short, during this interval the Apennine Peninsula gradually turned into a savannah, alternating between cool, open periods, and temperate, relatively more wooded landscapes. The region was inhabited by animals ecologically equivalent to savannah-dwellers of present day Africa (elephants, black rhinoceroses, wildebeest, elands, impalas, zebras, jackals, wild dogs, hyenas, leopards, cheetahs, etc.).

After this turbulent phase of faunal turnover, herbivore diversity gradually but steadily declined. This phase is well documented at the sites of Il Crostolo (Reggio Emilia), Mugello (central Italy), Selvella and Farneta (Chiana Valley), Pietrafitta (Perugia), Capena (Rome), Madonna della Strada (L'Aquila) and Pirro Nord (Gargano). One by one, smaller-sized browsing and grazing ruminants disappeared, as the larger-sized ungulates, especially grazers, prospered. Based on the proportional numbers of remains found, some of these large-sized grazers, such as equids and leptobovines, apparently built up vast populations. The collapsing diversity of the herbivores led to a rise in interspecific competition among the carnivores. *Acinonyx pardinensis*, *Megantereon whitei*, *Lycaon lycaonoides* and *Canis etruscus* became extinct and were not replaced (Palombo et al., 2008).

2.2.4. Western Europe

Whereas faunas of the first half of the Late Villafranchian are not well represented in France or other Western European areas, the fossil record of the second part of the Late Villafranchian illustrates a clear faunal change in comparison to the Middle Villafranchian. This faunal turnover is particularly significant in the herbivore assemblages. *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*) was still present in Ceyssaguet (Haute-Loire), but new mixed feeders and browsers, including *Cervalces* (=*Alces*) *carnutorum* at Sainzelles, *Praemegaceros* (=*Megaceroides*) *obscurus* at Ceyssaguet, *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*) at Saint Privat d'Allier and Sainzelles (Haute-Loire), and *Stephanorhinus hundsheimensis* at Saint Privat d'Allier, Sainzelles, Communac and Ceyssaguet (Kaiser and Croitor, 2004; compilation of references of these localities in Lacombat, 2005), have been recovered. Newly-appearing grazers indicating a development of open grasslands include *Bison* sp. at Saint Privat d'Allier, Sainzelles and Ceyssaguet, and *Equus altidens* at Saint Privat d'Allier, Sainzelles, Communac and Ceyssaguet. Following the extinction of *Anancus arvernensis* during the Olduvai magnetosubchron (C2n), *Mammuthus meridionalis* was the only remaining very large-sized species. However, at the end of the Late Villafranchian, finds from Ceyssaguet show that *Mammuthus meridionalis* was joined by *Palaeoloxodon antiquus* (Aouadi, 2001).

The carnivore group, by its nature, is less abundant in the fossil record; nevertheless, this group also reflects the widespread faunal turnover during this period. New canids, *Lycaon* [=*Canis* (*Xenocyon*)] *lycaonoides* and *Canis mosbachensis* at Sainzelles, were already adapted to the newly-developing open landscapes, while the saber-toothed cat, *Homotherium crenatidens,* was ubiquitous and spread into both open and wooded habitats. Late Villafranchian fossil assemblages are also characterised by *Pachycrocuta brevirostris*, which left traces of both its bone accumulating and cracking activities at many sites.

2.2.5. Iberian Peninsula

During the Middle to Late Villafranchian transition, the marked drop in temperatures favoured the entrance of new species into Iberia, leading to an increase in faunal diversity. The site of Fonelas P-1 (Guadix-Baza, Granada; 1.8 Ma) is illustrative of the typical faunal mix of this period, with both native and newly-arrived species. Typical native species include *Gazellospira torticornis*, *Metacervocerus rhenanus* (=*Cervus rhenanus* = *Dama rhenana*), *Eucladoceros* sp., *Croizetoceros ramosus*, *Stephanorhinus etruscus*, *Mammuthus meridionalis*, *Acinonyx pardinensis, Lynx pardinus spelaeus*, *Megantereon cultridens*, *Homotherium crenatidens,* and *Vulpes alopecoides*. New arrivals, predominantly of Asian, and in some cases African origin, are represented by *Praeovibos* sp., *Capra baetica*, *Leptobos etruscus*, *Mitilanotherium* sp., *Potamochoerus magnus*, *Equus* cf. *bressanus* (=*E.* cf. *major* = *E.* cf. *robustus*), *Pachycrocuta brevirostris*, *Hyaena brunnea*, *Meles iberica, Lycaon* [=*Canis* (*Xenocyon*)] *falconeri*, and *Canis accitanus* (Arribas et al., 2009). The bushpig, *Potamochoerus*, was first recorded in the African continent during the Pliocene, and is associated with bushy gallery forests, but its route into southern Iberia has not, as yet, been clarified. Another notable development of the western Palaearctic faunal turnover was the continuing spread of canids after 1.8 Ma. Both the successive dispersal of different canid lineages and the emergence of *Pachycrocuta* during this period could be indicative of a change to more open habitats (Palombo et al., 2008).

During the 1.8–1.5 Ma interval, *Soergelia*, *Bison* (*Eobison*), *Hemitragus*, *Equus stehlini* and *E. altidens* were among new grazers entering the Iberian Peninsula. Mixed feeders moving into this area during this period include a megacerine deer (*Megaceroides*), *Stephanorhinus etruscus* / *S. hundsheimensis* and *Theropithecus*. The presence of the large cercopithecid *T.* cf. *oswaldi* in the record could indicate a migration event from Africa into Southern Europe during the Late Villafranchian. The extant *T. gelada* is graminivorous and a genuine grazer. Isotopic analysis of *T. oswaldi* from Swartkrans (South Africa) revealed that it was more of a C4 grazer than a browser, although more fruits were apparently consumed than observed in modern *T. gelada* (Codron et al., 2005). Among the new immigrants recorded at Cueva Victoria (Murcia), dated to 1.3 Ma, are *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Equus altidens*, *Pachycrocuta brevirostris, Lycaon falconeri* and *C. etruscus* (Agustí and Moyà-Solà, 1991, 1992; Guerrero-Alba and Palmqvist, 1998). The Iberian Late Villafranchian fossil record reflects an interval with landscapes dominated by herbaceous open savannahs and a temperate climate.

2.2.6. North-Western Europe and the southern North Sea Basin

It is likely that the bulk of the Early Pleistocene large mammal fauna found in the clay conglomerates and associated marine deposits of the lower part of the Cromer Forest-bed Formation (CF-bF) in eastern England is of Pastonian interglacial age (Lister, 1998). At most localities the collections are mixed with early Middle Pleistocene material, but at East Runton a relatively 'pure' assemblage occurs (Stuart, 1988; Lister, 1996), and is of similar age to the classic Tegelen fauna of The Netherlands of TC5–6 age (Van Kolfschoten, 2001; Van den Hoek Ostende and de Vos, 2006), c. 1.7 Ma. Between them, the faunas of these two localities include *Leptobos* cf. *elatus*, *Cervalces* (=*Alces*) *gallicus*, *Metacervocerus rhenanus* (=*Cervus rhenanus* = *Dama rhenana*), several species of *Eucladoceros*, *Sus strozzii*, the browsing rhinoceros *Stephanorhinus etruscus*, *Equus stenonis*, *E. bressanus* (=*E. major* = *E. robustus*) and *Mammuthus meridionalis*: a mix of grazers, browsers and mixed feeders, indicating a rich and diverse interglacial habitat, reflected also in the large Carnivora *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Pliocrocuta perrieri* and *Ursus etruscus* at Tegelen. The loss of *Eucladoceros falconeri* and *Anancus arvernensis*, relative to the preceding interval, is notable.

The interval 1.7–1.2 Ma is poorly-known in North-Western Europe, but the restricted fauna of the Siliceous Member at Westbury-sub-Mendip (Somerset, UK) probably represents a temperate episode in this interval (Bishop, 1982; Andrews et al., 1999; Preece and Parfitt, 2000), with woodland elements such as *Stephanorhinus etruscus*, as well as the large hyaena *Pachycrocuta brevirostris.*

2.2.7. Central Europe

The large mammal record of the 1.8–1.2 Ma period in Central Europe is even more fragmentary than that of North-Western Europe, and, as such, provides scarce information about the prevailing palaeoenvironment. The still imperfectly-studied faunal assemblage of the Erpfinger Höhle (Baden-Württemberg) in southern Germany, of late Middle to early Late Villafranchian age, comprises *Gazellospira torticornis*, *Megalovis latifrons*, *Cervalces* (=*Alces*) *gallicus*, "*Cervus*" cf. *philisi*, *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*), *Croizetoceros ramosus*, *Stephanorhinus etruscus*, *Equus bressanus* (=*E. major* = *E. robustus*) and *Mammuthus meridionalis*, reflecting a mixed landscape composed of both forested and more open areas. Recorded carnivores from this site are *Panthera onca toscana* (=*P. toscana*), *Pliocrocuta perrieri*, *Chasmaporthetes* cf. *lunensis* and *Ursus etruscus* (Lehmann, 1957).

2.2.8. Eastern Europe

In Eastern Europe there are a very few unambiguously dated early Late Villafranchian mammal localities, and the beginning of this period is still characterised by the Psekups (=Odessa) Faunal Complex (see Section 2.1.8). Remains of *Mammuthus meridionalis meridionalis* from Salchia in Moldova are also attributed to this interval.

Though the faunal record in Eastern Europe is patchy and inconclusive, it is most likely that the Late Villafranchian period in this region saw an increase of arid conditions and a subsequent growth of steppe-like areas. However, when compared to the structure of the large mammal assemblages during the Middle Villafranchian, no radical reorganization can be inferred.

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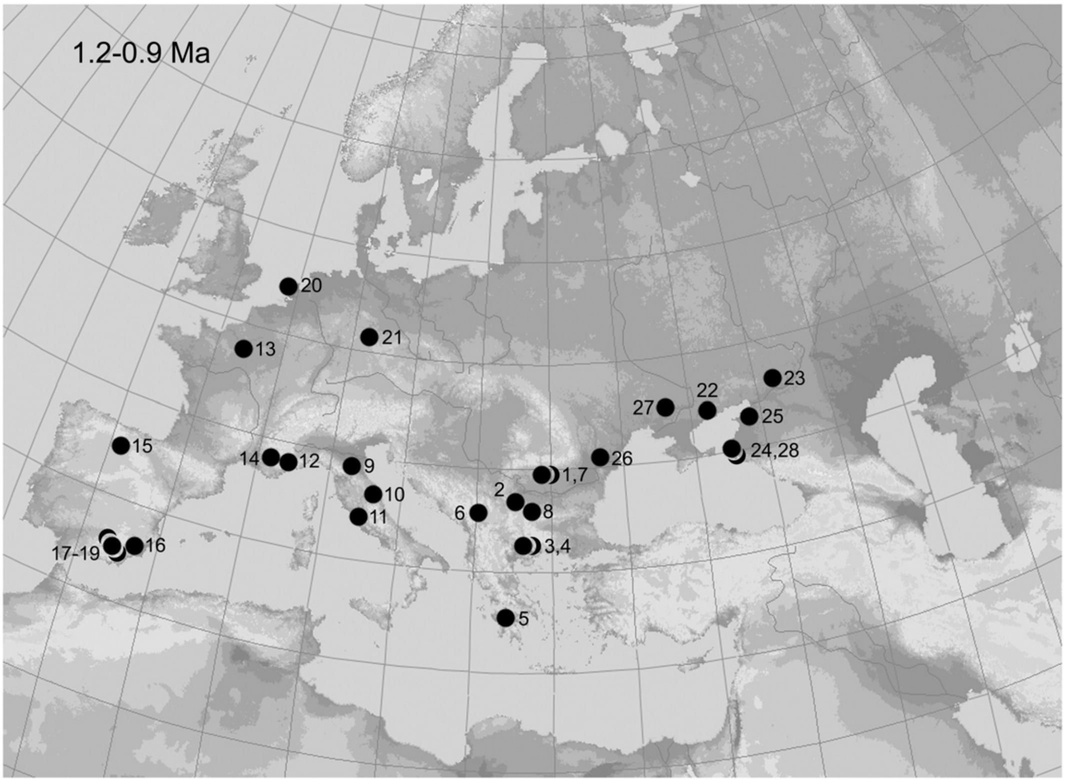

Fig. 4. Principal western Palaearctic fossil mammal sites of the 1.2–0.9 Ma interval, in the order of appearance in the text (see Section 2.3): 1, Tetoiu-3; 2, Kozarnika B2–2; 3, Apollonia; 4, Ravine of Voulgarakis; 5, Megalopolis-Marathousa; 6, Trlica; 7, Dealul Viilor; 8, Kunino (lower level); 9, Imola; 10, Colle Curti; 11, Redicicoli; 12, Vallonnet; 13, Saint-Prest; 14, Durfort; 15, Trinchera Elefante; 16, Quibas; 17, Venta Micena; 18, Fuente Nueva-3; 19, Barranco León-5; 20, Het Gat; 21, Untermassfeld; 22, Nogaisk; 23, Sarkel; 24, Sinaya Balka; 25, Port-Katon; 26, Chishmikioy; 27, Kairy; 28, Tsimbal.

2.3. *The 1.2–0.9 Ma interval*

The 1.2–0.9 Ma time span represents the final phase of the interval dominated by 41 ka periodicity in the global climatic record. This period is characterised by significant fluctuations in δ^{18}O values, in contrast to those recorded from the earlier part of the Matuyama magnetochron (Lisiecki and Raymo, 2005, Fig. 4). The increased climatic instability of this interval created a significant climatic variability in subtropical Africa (DeMenocal, 2004), and the ecological preconditions for faunal turnover in the western Palaearctic. The distinctive character of the resulting fauna supports the idea of a separate chronostratigraphical unit, the Epivillafranchian, wedged between the Villafranchian and Galerian biochrons (Kahlke, 2007) (Figs. 1, 4).

2.3.1. *Levant and Transcaucasia*

At the time of writing, no sufficiently abundant mammal faunas of Epivillafranchian age have yet been recovered in the Levantine and Transcaucasian regions.

2.3.2. *Asia Minor and South-Eastern Europe*

Relatively few large mammal sites of Epivillafranchian age have been identified in the Balkans, and none has yet been found in Turkey. However, despite the lack of confirmed large mammal sites, sporadic finds of a comparable age have been found interspersed throughout the entire region.

At the onset of this period in Romania, the faunal assemblage recovered from the Tetoiu-3 horizon provides the first record of *Soergelia* and *Praeovibos* in South-Eastern Europe. Alongside these, remains of primitive *Bison* and *Cervalces* (=*Alces*) cf. *carnutorum* have been recovered (Rădulescu and Samson, 2001). The oldest levels of Kozarnika Cave (archaeological complexes 11c–14 = biozone B2–2) in north-western Bulgaria, meanwhile, have yielded various species, including the bovids *Procamptoceras* cf. *brivatense*, *Ovis* sp., *Rupicapra* sp., *Hemitragus* cf. *orientalis*, *Megalovis* aff. *balcanicus* and *Soergelia* aff. *intermedia*, as documented by Fernandez and Grégut-Bonnoure (2007). Fernandez and Crégut-Bonnoure place this assemblage in MNQ18, but the obvious uncertainty of some of the determinations makes this association relatively unreliable in terms of biochronology. The same is true for the remainder of the large mammals from the B2–2 level, most of whose identification relies on limited material. The species documented from B2–2 include: *Cervalces* cf. *latifrons*, *Equus* cf. *altidens*, *Mammuthus* cf. *trogontherii*, *Puma pardoides* (=*Panthera schaubi* = *Viretailurus schaubi*), *Homotherium latidens*, *Pliocrocuta perrieri*, *Martes* cf. *vetus*, *Ursus* cf. *etruscus*, *U.* cf. *deningeri* (note by N. S.: affinities with *U. dolinensis*), *Vulpes praeglacialis*, *Cuon* cf. *stehlini*, and *Canis etruscus*. Although Guadelli et al. (2005) place the large mammal assemblage of the Kozarnika lower level (B2–2) at an approximate age of 1.4 Ma, it is more likely that the assemblage is closer to the beginning of the Epivillafranchian (N. S. and D. K., pers. comment).

The large mammal assemblage of Apollonia (northern Greece), dated to the beginning of the 1.2–0.9 Ma interval (Spassov, 2003), represents the most complete fossil assemblage of the South-Eastern European Epivillafranchian. The following species, among others, have been recorded at the site: *Pontoceros ambiguus mediterraneus*, *Soergelia brigittae*, *Praeovibos mediterraneus*, ?*Ovis* sp., *Hemitragus orientalis*, *Bison* sp., *Arvernoceros* sp., *Praemegaceros pliotarandoides*, *Stephanorhinus* sp., *Equus apolloniensis*, *Lynx issiodorensis*, *Megantereon cultridens*, *Pachycrocuta brevirostris*, *Meles dimitrius*, *Ursus etruscus*, *Vulpes alopecoides*, *Lycaon* [=*Canis* (*Xenocyon*)] sp., *Canis apolloniensis*, and *C. etruscus* (Kostopoulos, 1997;

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Koufos, 2001; Kostopoulos et al., 2002; and pers. data D. K.). From the same period, and within the same lithostratigraphic unit, the mammal fauna from the Ravine of Voulgarakis includes *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Equus* sp. and *Canis apolloniensis* (Koufos, 2001). The Apollonia/Ravine of Voulgarakis faunas possess various novel features for the Balkans, the most significant being the total replacement of the bovid assemblage by multiple caprine lineages, together with the predominance of early bison. These palaeoecological parameters imply an open grassy landscape with a clear dominance of intermediate feeders and grazers, as well as an absence of browsers (Kostopoulos and Koufos, 2000). The presence of semi-aquatic forms (e.g. *Hippopotamus*), alongside elements with affinities for dryer environments (e.g. *Pontoceros, Praeovibos*), are possible indicators of moderate climatic conditions.

The slightly younger Megalopolis-Marathousa site in southern Greece has yielded a similar fauna, though most of the recorded species need taxonomic revision. The faunal association, including a large bovine, *Praemegaceros* sp., *Hippopotamus antiquus*, *Stephanorhinus* sp. and *Equus* cf. *aluticus*, provides strong evidence that, during this period, homogeneous environmental conditions spread as far south as the Peloponnese.

Northwards, the large mammal assemblages of Trlica in Montenegro and Dealul Viilor in the Tetoiu area of Romania possess similar faunal characteristics and are probably younger, but are still within the Epivillafranchian. *Megalovis balcanicus*, *Soergelia intermedia*, *Bison* (*Eobison*), *Cervalces* cf. *carnutorum*, *Eucladoceros giulii*, elaphine deer, *Stephanorhinus* cf. *hundsheimensis*, *Equus stenonis, E.* cf. *bressanus* (=*E.* cf. *major* = *E.* cf. *robustus*), *Panthera* cf. *onca gombaszoegensis* (=*P.* cf. *gombaszoegensis*), *Lynx* sp., *Homotherium* cf. *crenatidens*, *Pachycrocuta brevirostris*, *Ursus etruscus*, *Vulpes* sp., *Lycaon falconeri*, and *Canis etruscus*, among others, are reported from Trlica (Crégut-Bonnoure and Dimtrijević, 2006). *Bison* cf. *schoetensacki*, *Soergelia* cf. *elisabethae* and advanced *Mammuthus meridionalis* are mentioned from Dealul Viilor, and in isochronous Romanian layers *Equus* cf. *suessenbornensis* and *E. aluticus* have been recorded (Rădulescu and Samson, 2001; Rădulescu et al., 2003).

The recently discovered, and probably contemporaneous, karstic locality of Kunino in south-western Bulgaria has yielded large mammals which could correspond to two different levels (see also Section 2.4.2). *Ovis* sp., *Cervalces latifrons*, a very large *Equus* sp., *Canis apolloniensis* and *C.* cf. *etruscus* are credited to the lower level (N. S., pers. observations) and could, therefore, belong to the Epivillafranchian. The documented ungulates suggest an open grassy habitat with moderately dry/cold climates.

2.3.3. Apennine Peninsula

The latest Early Pleistocene in Italy was marked by the appearance of a new grazer, *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), and two new mixed feeders, *Praemegaceros* (=*Megaceroides*) *verticornis* and *Stephanorhinus hundsheimensis*. These species herald the faunal renewal that marks the interval between the Villafranchian and the Galerian faunal communities. The localities that document this phase are those of Imola (northern Italy), Colle Curti (Macerata) and Redicicoli (Rome).

At first, the Epivillafranchian faunal turnover produced a mixture of incoming and surviving taxa. As extinctions increased, i.e. *Praemegaceros* (=*Megaceroides*) aff. *solilhacus*, *Sus strozzii*, *Lynx issiodorensis, Enhydrictis ardea*, *Pannonictis nestii*, *Meles thorali*, *Ursus etruscus*, *Lycaon falconeri*, *Canis arnesis*, and *C. etruscus*, new species started to appear, such as *Bison schoetensacki, Mammuthus trogontherii, Meles meles* and *Ursus* with some cave bear features. Animal biodiversity surged, prompted by the renewed diversification of the vegetation and concomitant increase in the variety of ecological niches, which were also favoured by Italy's rough physiography. During the Epivillafranchian period new floras gradually mixed with the dwindling resident vegetation. A varied, evolving flora (Bertini, 2003) provided numerous opportunities for a wide variety of animals with diverse habits and ecological preferences.

2.3.4. Western Europe

The Epivillafranchian period in Western Europe was also characterised by a flux of new migrants, alongside elements that had their roots in the western Palaearctic Villafranchian. New grazers of Asian origin, like *Bison schoetensacki* at Vallonnet cave (Alpes-Maritimes) (Moullé et al., 2006), Saint-Prest (Eure-et-Loire) (Guérin et al., 2003) and Durfort (Gard) (Brugal, 1994), as well as *Praeovibos* sp. and *Hemitragus bonali* from Vallonnet, are characteristic of open environments and/or cold conditions. The increasing biodiversity of the bovids contrasts with the relative stability of the cervids during this period. Most of the recorded large and medium-sized species of this interval had originated during the Late Villafranchian: *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Stephanorhinus hundsheimensis*, *Equus altidens* and *Mammuthus meridionalis.*

Felids of Villafranchian origin were still numerous. *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Acinonyx pardinensis*, *Puma pardoides* (=*Panthera schaubi* = *Viretailurus schaubi*) and *Homotherium crenatidens* were joined by the newly-arrived *Felis silvestris* and *Lynx spelaea*, both indicators of forested landscapes in the area of Vallonnet cave (Moullé et al., 2006). *Ursus dolinensis* replaced *Ursus etruscus,* and in so doing established the Palaearctic cave bear lineage (García, 2003). The canids were joined by *Alopex praeglacialis* (Vallonnet). *Pachycrocuta brevirostris*, recorded at both Vallonnet and Saint-Prest, was widespread and responsible for numerous bone accumulations in the region.

2.3.5. Iberian Peninsula

Significant deposits containing Pleistocene faunas older than the Jaramillo subchron have been found in Spain at Trinchera Elefante (Sierra de Atapuerca; TE9–12, 1.21–1.1 Ma; Cuenca-Bescós and García, 2007; Carbonell et al., 2008), Quibas (Murcia; c. 1.2 Ma; Montoya et al., 2001), Venta Micena, Fuente Nueva-3, and Barranco León-5 (Guadix-Baza basin, Granada; c. 1.3–1.2 Ma; Moyà-Solà et al., 1981; Agustí and Moyà-Solà, 1991; Turq et al., 1996; Martínez-Navarro et al., 1997).

The large mammal assemblage of Trinchera Elefante (TE-LRU) is coincident with that of the Epivillafranchian biochron proposed by Kahlke (2007), although some additional taxa are preserved in the former assemblage. The TE-LRU fauna comprises *Bison* sp., *Eucladoceros giulii*, *Hippopotamus* sp., *Stephanorhinus etruscus, Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Lynx* cf. *issiodorensis*, *Pannonictis* cf. *nestii, Mustela* cf. *palerminea/praenivalis*, cf. *Baranogale antiqua*, *Ursus* cf. *dolinensis*, *Vulpes* cf. *alopecoides*, *Canis* cf. *arnensis/mosbachensis*, *Macaca* sp., and *Homo antecessor,* among others. Year-round warm and humid environmental conditions are reflected by the presence of hippos, *Pannonictis* and macaques in the faunal assemblage.

The fossil record of Quibas indicates a warm and dry, rocky terrain inhabited by cf. *Praeovibos* sp., *Hemitragus* cf. *alba*, *Equus altidens*, *Lynx pardinus* and *Macaca sylvanus* (Montoya et al., 2001). At Venta Micena, huge quantities of bones were accumulated by the activities of the large hyena *Pachycrocuta brevirostris* at the margins of the fossil Orce lake (Arribas and Palmqvist, 1998). The palaeocommunity of Venta Micena, which included *Soergelia minor*, *Praeovibos* sp., *Hemitragus alba*, cf. *Bison* (*Eobison*) sp., *Praedama* sp., *Praemegaceros* (=*Megaceroides*) *solilhacus*, *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Stephanorhinus, Equus altidens*, *Mammuthus meridionalis, Megantereon*, *Homotherium crenatidens*, *Lycaon* [=*Canis* (*Xenocyon*)] *falconeri* and *Theropithecus oswaldi*, lived in open landscapes composed of spiny trees and permanent water bodies, comparable to the patchwork of forest, woodland, and savannah that makes up the modern East African rift valley (Arribas and Palmqvist, 1999). Fuente Nueva-3 and Barranco León-5 contain similar mammal associations including *Hemitragus*, *Pseudodama*, *Praemegaceros* (=*Megaceroides*) cf. *obscurus*, *Hippopotamus antiquus, Stephanorhinus hundsheimensis* and *Ursus*. To date, *Mammuthus meridionalis* and *Megantereon* have been recovered only from Fuente Nueva-3 (Martínez-Navarro et al., 2004). At Barranco León-5 bones were transported and concentrated by a riverine system, and both Barranco León-5 and Fuente Nueva-3 seem to have formed in a landscape made up of both open and lightly forested areas.

2.3.6. North-Western Europe and the southern North Sea Basin

The 1.2–0.9 Ma interval is scarcely represented in stratified large mammal faunas of this region. Heavily mineralised bones trawled from the Yarmouth Roads Formation at 'Het Gat', a narrow trench in the southern North Sea, may date to the Bavel interglacial (Jaramillo normal subchron), and comprise a temperate, at least partly woodland assemblage including *Bison* cf. *menneri*, *Cervalces* (=*Alces*) *latifrons*, *Eucladoceros tegulensis* (=*E. ctenoides* = *E. senezensis*), *Praemegaceros dawkinsi*, *Hippopotamus* cf. *antiquus* (=*H.* cf. *amphibius antiquus* = *H.* cf. *major*) and *Homotherium* (Mol et al., 2003).

2.3.7. Central Europe

The Untermassfeld (Thuringia) fossil assemblage, dated to slightly older than one million years, is one of the most complete western Palaearctic fossil mammal assemblages from the 1.2–0.9 Ma interval (Kahlke R.-D., 1997, 2001a,b with studies of numerous authors). The lithological, palaeomagnetic and biostratigraphic characteristics of the fossiliferous sands indicate the most likely time for the formation of this assemblage as MIS 31, which corresponds to a pronounced warm interval that overlaps the base of the Jaramillo polarity subchron (Kahlke, 2006; Maul et al., 2007). Typical faunal elements include the following: *Bison menneri*, *Capreolus cusanoides*, *Cervalces* (=*Alces*) *carnutorum*, *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii vallonnetensis*, *Eucladoceros giulii, Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Stephanorhinus hundsheimensis*, *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Acinonyx pardinensis pleistocaenicus*, *Puma pardoides* (=*Panthera schaubi* = *Viretailurus schaubi*), *Megantereon cultridens adroveri*, *Homotherium crenatidens, Pachycrocuta brevirostris*, *Ursus* cf. *dolinensis* (=*U. rodei*), *Lycaon* [=*Canis* (*Xenocyon*)] *lycaonoides* and *Canis mosbachensis* (Kahlke H.-D., 1997, 2001; Hemmer, 2001; Sotnikova, 2001, etc.). Many of the Untermassfeld mammals differ from typical Villafranchian taxa of similar size, and some of them, i.e. *B. menneri*, *D. nestii vallonnetensis*, *E. giulii*, *U.* cf. *dolinensis* and *C. mosbachensis*, appear only after the end of the Villafranchian (Kahlke, 2007).

The composition of the Untermassfeld fauna undoubtedly indicates warm climatic conditions, and the fossils recovered mainly represent temperate and thermophilous faunal elements. Animals characteristic of cool- to cold-stage conditions are completely absent. Higher summer temperatures than those which occur in the region today are indicated by the find of a freshwater turtle (Maul, 1997). The winter temperatures in the Untermassfeld area at the time of the formation of the site can be estimated by the very frequent occurrence of *Hippopotamus*. With their amphibian lifestyle, the survival of hippopotami in this region would have been ruled out their watery habitats had been covered by ice. Therefore, their abundant presence at Untermassfeld is a clear indicator of mild winters, with minimum air temperatures only a few degrees below zero. Regionally, a temperate warm-humid climate, free from extreme daily or seasonal fluctuations in temperature, prevailed. Extended geological, taphonomical, and palaeozoological-ecological data together provide a detailed picture of the landscape whilst the site was evolving (Kahlke, 2001c, 2006). The river valley comprised a patchwork of wet, humid, and relatively dry locations that offered suitable living conditions to a wide variety of plant communities. Beside habitats of woodland and the less diverse shrub vegetation, dry grassland was common on the south-facing slopes of the river valley. Outside the Werra valley, park-like landscapes and sparsely wooded to open biotopes extended over large distances.

2.3.8. Eastern Europe

The Taman Faunal Complex (Gromov, 1948) contains typical faunas characteristic of the terminal Late to Epivillafranchian of Eastern Europe. Herbivore species include *Pontoceros ambiguus*, *Bison* (*Eobison*) *tamanensis*, *Eucladoceros orientalis*, *Elasmotherium caucasicum*, *Equus* cf. *suessenbornensis*, and *Mammuthus meridionalis tamanensis*, alongside a carnivore population that includes *Homotherium crenatidens, Pachycrocuta brevirostris, Lutra simplicidens, Lycaon* [=*Canis* (*Xenocyon*)] *lycaonoides*, and *Canis tamanensis* (Vereshchagin, 1957; Forstén, 1999; Sotnikova and Titov, 2009). The diversity of the recorded spectrum of animals suggests that a variety of different habitats was found in this region. The majority of larger herbivores of the Taman Complex – elephants, bison and horses – were grazers, and therefore adapted to more open habitats such as forest-steppe and steppe landscapes.

Most of sites of the early part of the Epivillafranchian period in the south of Eastern Europe were formed by alluvial, deltoid or lagoon deposits (Sinaya Balka, Nogaisk, Sarkel, Port-Katon, Chishmikioy, Kairy, Tsimbal), and were deposited under prevailing warm to nearly subtropical conditions (Vereshchagin, 1957; Vangengejm et al., 1991; Dodonov et al., 2007; Shchelinsky et al., 2008). However, pollen spectra and small-mammal associations recovered from this region indicate a significant drop in temperature and a general trend of increasing aridity during the later part of the 1.2–0.9 interval (Velichko, 1999). At the time of writing, corresponding assemblages of larger mammals have not been recorded from this period. To summarise, the late Epivillafranchian of Eastern Europe was dominated by open steppe landscapes, shaped by increasingly continental conditions. The forested steppe habitats that had occurred in the region between 2.6 and 1.0 Ma gradually disappeared.

2.4. The 0.9–0.4 Ma interval

The 0.9–0.4 Ma interval covers the Early to Middle Pleistocene transition defined by the Matuyama/Brunhes reversal at around 0.78 Ma. It was during this period that climatic cycling switched from 41 ka periodicity to that governed by orbital eccentricity cycles with 100 ka periodicity (Lisiecki and Raymo, 2005, Fig. 4). The amplitude of fluctuations exacerbated glacial phenomena, increasing both seasonality and aridity over northern and middle latitudes of the northern hemisphere (Figs. 1, 5).

2.4.1. Levant and Transcaucasia

In the eastern Mediterranean region the 0.9–0.4 Ma time span is documented by the sites of Evron Quarry and Gesher Benot Ya'aqov in Israel. The Evron fauna, dated to slightly older than 0.8 Ma (Tchernov et al., 1994; Porat and Ronen, 2002), contains, among others, a number of Ethiopian faunal elements, cf. *Alcelaphus* sp., *Hippopotamus* sp. and *Kolpochoerus evronensis*, indicating the ongoing African influence within the Levantine Corridor. Other faunal elements, particularly the elaphine deer, early roe deer cf. *Capreolus* sp. and *Bos* cf. *primigenius*, demonstrate the increasing appearance of Eurasian species, as was also the case in Transcaucasia and Southern Europe between 0.9 and 0.8 Ma. Whereas

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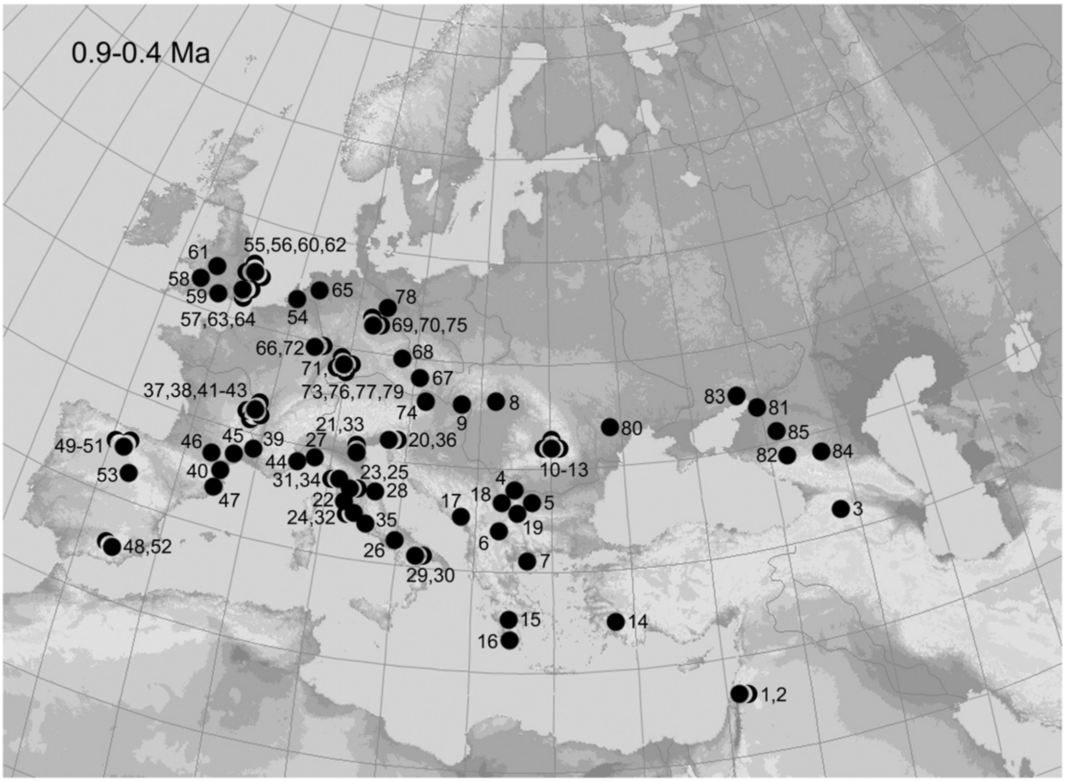

Fig. 5. Principal western Palaearctic fossil mammal sites of the 0.9–0.4 Ma interval, in the order of appearance in the text (see Section 2.4.): 1, Evron; 2, Gesher Benot Ya'aqov; 3, Akhalkalaki; 4, Kozarnika B2–1, –B1; 5, Kunino (upper level); 6, Manastirec; 7, Petralona (lower/upper levels); 8, Tarkö; 9, Vértesszölös; 10, Araci-Carieră; 11, Araci-Fintina Fagului; 12, Ghidfalău-1; 13, Sfintu Gheorghe; 14, Denizli; 15, Megalopolis; 16, Apidima; 17, Crvena Stijena cave; 18, Jerinnia; 19, Baranica; 20, Slivia; 21, Monte Tenda; 22, Pitigliano; 23, Monte Oliveto; 24, Ponte Galeria 2; 25, Borgonuovo; 26, Isernia La Pineta; 27, Valdemino; 28, Cesi; 29, Notarchirico; 30, Venosa-Loreto; 31, San Romano; 32, Cava Nera Molinario; 33, Spessa 2; 34, Cava Campani; 35, Fontana Ranuccio; 36, Visogliano; 37, Soleilhac; 38, Cussac; 39, L'Escale; 40, Arago Ensembles I, II, III; 41, Pont-du-Château; 42, Nolhac; 43, La Fage; 44, Terra Amata; 45, Lunel-Viel; 46, Aldène; 47, Incarcal-I; 48, Huéscar-1; 49, Trinchera Dolina TD 3-4, 5, 6, 8, 10; 50, Sima de los Huesos; 51, Trinchera Galería G2-G3; 52, Cúllar de Baza-1; 53, Ambrona; 54, Dorst-Surae; 55, West Runton; 56, Pakefield; 57, Little Oakley; 58, Westbury-sub-Mendip (Calcareous Member); 59, Boxgrove; 60, Ostend; 61, Waverly Wood; 62, Hoxne; 63, Swanscombe; 64, Clacton; 65, Neede; 66, Dorn-Dürkheim 3; 67, Stránská Skála; 68, Konéprusy C 718; 69, Voigtstedt; 70, Süssenborn; 71, Mauer; 72, Miesenheim 1; 73, Mosbach 2; 74, Hundsheim; 75, Bad Frankenhausen; 76, Steinheim/Murr; 77, Heppenloch; 78, Schönebeck/W.; 79, Bruchsal; 80, Kolkotova Balka (Tiraspol); 81, Kagalnik; 82, Treugolnaya cave; 83, Taganrog; 84, Pyatigorsk; 85, Girey 1.

the presence of hippos at Evron indicates the existence of permanent open water bodies, *Kolpochoerus* supports the presence of a woodland habitat in the near vicinity, and the occurrence of gazelles and hartebeest demonstrates that open steppic landscapes also flourished in the wider environment.

A clear faunal turnover is evident from the assemblage at the site of Gesher Benot Ya'aqov, which dates to 0.8–0.7 Ma (MIS 18). Although this locality retained some of its African character, as indicated by species associated with warmer climates such as *Pelorovis* cf. *bubaloides* and *Hippopotamus amphibius* ssp., a strong presence of immigrant Eurasian species, such as *Cervus* cf. *elaphus*, *Dama* cf. *mesopotamica*, *Megaloceros* sp. and *Stephanorhinus kirchbergensis* (Martínez-Navarro, 2004; Rabinovich et al., 2007) is also documented. The whole assemblage is indicative of a landscape with substantial woodland components.

The fauna of Akhalkalaki in southern Georgia lies immediately below the M/B boundary. Its mammal assemblage is of Palaearctic character and includes, among others, *Bison* sp., *Bos* sp., *Praemegaceros* (=*Megaceroides*) aff. *verticornis*, *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), *Stephanorhinus hundsheimensis*, *Equus suessenbornensis*, *E. hipparionoides*, *Mammuthus* cf. *trogontherii*, *Homotherium crenatidens*, and *Pachycrocuta brevirostris* (Vekua, 1962, 1986; emended faunal list in Hemmer et al., 2001). The overall impression of the landscape around the Akhalkalaki fossil site, at its time of origin, is that of a warm meadow-steppe environment influenced by local montane conditions.

2.4.2. South-Eastern Europe and Asia Minor

Most of the South-East European large mammal assemblages of the 0.9–0.4 Ma interval originate from cave or karst-related deposits, making any secure dating difficult: in fact, in several cases bone assemblages from successive horizons appear to be mixed.

At Kozarnika Cave (NW Bulgaria; see Section 2.3.2), fossiliferous levels B2-1 – B1 have yielded a rich and relatively continuous large mammal fauna in the interval 0.8–0.4 Ma (Guadelli et al., 2005). The assemblage, which includes *Capra* cf. *caucasica*, *Hemitragus* cf. *cedrensis*, *Sus* sp., *Equus* cf. *stenonis*, *E.* cf. *suessenbornensis*, *Mammuthus* cf. *trogontherii*, *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), cf. *Puma pardoides* (note by N. S.), *Meles* sp., *Ursus deningeri*, and *Cuon* cf. *stehlini*, reflects mountainous, open to mixed environments. Remains of *Ursus* approximately the size of *U. deningeri*, in addition to a large lion comparable to *Panthera fossilis* (=*P. leo fossilis*), have been recovered from the karst fissures of Kunino (see Section 2.3.2), of similar age.

The Manastirec cave fauna (former Yugoslav Republic of Macedonia), of clearly Galerian character, includes *Bison* sp., *Sus scrofa*, *Stephanorhinus kirchbergensis*, *Pachycrocuta brevirostris*, and *Ursus deningeri* (Kurtén and Garevski, 1989), whereas the lower fossil levels of Petralona Cave, in northern Greece, have yielded *Praemegaceros*, *Ursus deningeri*, *Lycaon* [=*Canis* (*Xenocyon*)] cf. *lycaonoides* and *Canis mosbachensis* (Tsoukala, 1991). It is likely that the corresponding landscapes included both open and forested habitats.

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In Hungary, the early Middle Pleistocene locality of Tarkö has yielded a rich faunal assemblage with *Ovis* sp., *Bison* cf. *priscus*, *Capreolus suessenbornensis, Cervus* cf. *acoronatus*, *Panthera pardus sickenbergi, Ursus deningeri,* and *Canis mosbachensis* (Jánossy, 1986). The younger locality of Vértesszölös 1 (occupation site), deposited around 0.4 Ma, has a similar faunal spectrum comprising *Bison schoetensacki*, *B. priscus*, *Capreolus suessenbornensis*, *Cervus elaphus* ssp., *Equus mosbachensis* and *Ursus deningeri* (Kretzoi, 1990).

From the Romanian sites of Araci-Carierǎ, Araci-Fintina Fagului, Ghidfalǎu-1 and Sfintu Gheorghe/Cariere Sud in the Brasov depression, unambiguous remains of *Coelodonta* have been recorded. These fossils represent the population of woolly rhinoceros that first migrated into Europe, and therefore the initial formation of the *Mammuthus-Coelodonta* Faunal Complex in the western Palaearctic during MIS 12 (Kahlke and Lacombat, 2008; see Section 2.4.7). Their age, about 0.46–0.4 Ma (Rǎdulescu and Samson, 1985), corresponds well to the associated remains of *Megaloceros savini* and *Equus* cf. *mosbachensis*. The landscape was clearly open, and during this time the so-called mammoth steppe of Asian origin began to expand, for the first time, into the northern part of South-Eastern Europe (Kahlke, 1999).

At the site of Denizli, in south-western Turkey, dated to 0.51–0.33 Ma, travertine deposits have provided a number of large mammal remains, including *Bos*, *Dama* sp. and *Equus* cf. *suessenbornensis* (Etren et al., 2005), which clearly reflect warm (Mediterranean) climatic conditions with at least some open landscape. The Megalopolis open site (Peloponnese), which formed sometime at the end of the early Middle Pleistocene, yielded *Bison priscus*, *Bos primigenius*, *Capreolus* sp., *Dama* sp., *Cervus elaphus*, *Hippopotamus, Sus scrofa*, *Stephanorhinus kirchbergensis, S. hemitoechus, Palaeoloxodon antiquus* and *Crocuta*. This association is rather indicative of the late Galerian age in Southern Europe. The balanced combination of grazers and thermophilous browsers, the increased presence of pachyderms, and the predominance of open dwellers and intermediate feeders, all suggest a range of environments under temperate climatic conditions.

The upper fossil levels of Petralona Cave, dated to ≤0.4 Ma, as well as the Apidima cave in the Peloponnese of roughly the same age, have been interpreted as bone accumulations in the dens of bears, hyaenas and lions. The fauna from the upper level of Petralona includes *Pliotragus macedonicus*, *Capra ibex*, *Bison priscus*, *Bos primigenius*, *Dama dama, Sus scrofa*, *Stephanorhinus hemitoechus*, *Equus petraloniensis* (ex. gr. *E. hydruntinus*), *E. caballus piveteaui*, *Felis silvestris*, *Panthera spelaea* (=*P. leo spelaea*)*, Crocuta crocuta intermedia, Ursus* cf. *arctos*, *U. spelaeus*, and *Vulpes vulpes* (Tsoukala, 1991). Goat, fallow deer, wildcat and fox are also present in the large mammal assemblage recovered from Apidima which, in addition, contains *Cervus elaphus*, *Megaloceros* sp., *Hippopotamus* sp., *Panthera pardus*, *Lynx lynx*, *Martes foina* and *Meles meles* (Tsoukala, 1999). Both of these large mammal associations are indicative of mild, Mediterranean-influenced interglacial climates and mosaic-like environments possessing both open and forested components and, at least in the case of Apidima, the presence of permanent water bodies.

Several cave deposits in Montenegro (Crvena Stijena Cave V–XXXI) and Serbia (Jerinnina and Baranica Caves), from the later part of the Middle Pleistocene, have yielded remains of *Capra ibex*, *Bison priscus*, *Bos primigenius*, *Cervus elaphus*, *Megaloceros giganteus*, *Sus scrofa*, *Equus hydruntinus*, caballine horse, *Panthera spelaea*, *P. pardus*, *Crocuta crocuta spelaea, Ursus spelaeus*, *Vulpes vulpes*, and *Canis lupus* (Malez, 1986; Forstén and Dimitrijevic, 2004). The faunal similarity between the aforementioned Greek fauna, and the Montenegrin and Serbian assemblages, suggests spatial and temporal homogeneity of later Middle Pleistocene interglacial palaeoenvironments throughout the entire Balkans.

2.4.3. *Apennine Peninsula*

Many new herbivores, such as different types of megacerine deer, steppe rhino, horses and others, migrated into the Apennine Peninsula during this period, especially from the Asian steppe regions via Eastern Europe. After them came various carnivores, some of which originated from Africa, i.e., lion, leopard and hyaenas. The incomers mixed with the declining Epivillafranchian fauna and successively replaced analogous species. The assemblages from Slivia (Trieste), Monte Tenda (Verona), Pitigliano (Grosseto), Monte Oliveto (Siena), Ponte Galeria 2 (Rome), and Borgonuovo (Siena), which date to 0.9–0.65 Ma, show that the evolving environmental conditions attracted a diverse range of taxa into Italy, including *Bos primigenius*, *Capreolus suessenbornensis*, *Megaloceros savini*, *Praemegaceros* (=*Megaceroides*) *solilhacus*, *Sus scrofa*, *Stephanorhinus hemitoechus*, *Palaeoloxodon antiquus*, *Panthera fossilis*, *P. pardus*, *Hyaena prisca*, *Crocuta crocuta* ssp., *Gulo schlosseri,* and *Ursus thibetanus*. Some of these new migrants, however, soon disappeared during the early Middle Pleistocene, i.e. *B. schoetensacki*, *M. savini*, *P. verticornis*, *P. solilhacus*, *M. trogontherii*, *P. fossilis*, *H. prisca* and *G. schlosseri*, together with the last of the Epivillafranchian holdovers, such as *Pachycrocuta brevirostris*. The latest occurrences of *Pseudodama* and *Homotherium* ex gr. *H. latidens* are documented at Isernia La Pineta (southern Italy), Valdemino (Savona) and Cesi (Macerata) (Sala, 1983, 1992, 1996; Ficcarelli et al., 1997).

Late in the 0.9–0.4 Ma time span a number of new grazers began to appear, i.e. *Hemitragus bonali*, *Hemibos galerianus*, *Bison priscus* and *Equus ferus*. Their appearance indicates an opening-up of landscape in different parts of the Apennine Peninsula. At the same time, new ungulates, such as *Dama clactoniana*, *Cervus elaphus*, and *Stephanorhinus kirchbergensis*, spread into the predominantly forested areas, along with several new carnivores, i.e. *Felis silvestris*, *Gulo gulo*, *Ursus arctos*, *Vulpes vulpes* and *Cuon priscus*.

The African immigrant *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*) disappeared from the Apennine Peninsula during this interval, most probably during a drier and colder period. At the regional scale habitats remained relatively heterogeneous throughout this time (Owen Smith, 1990), as evidenced at the sites of Notarchirico (Potenza), Venosa-Loreto (Potenza), San Romano (Pisa), Cava Nera Molinario (Rome), Spessa 2 (Vincenza), Cava Campani (Pisa), Fontana Ranuccio (Frosinone) and Visogliano (Trieste) (Segre, 1984; Belli et al., 1991; Cattani et al., 1991).

To summarise, during the 0.9–0.4 interval, herbivores, especially those of mid-size, diversified considerably. Guilds were most varied, indicating the existence of articulated ecosystems. Carnivores, in contrast, steadily declined. The climatic gradients caused further expansion of steppe landscapes, which paralleled the inexorable demise of thermophilous flora. Open woodlands, with an ever-increasing spread of conifers, characterised the warmer cycles. During the colder phases the tree cover became patchy and incomplete, with high proportions of steppic, herbaceous vegetation (Bertini, 2003).

2.4.4. *Western Europe*

In Western Europe, the 0.9–0.4 Ma interval was characterised by the extinction of the last representatives of the Epivillafranchian fauna, and the periodic but increasingly extensive spread of steppe-like environments. Some faunal elements of Late Villafranchian to Epivillafranchian origin were still present in the faunal record during the first half of this time period, as recorded at sites like Soleilhac and Cussac (Haute-Loire; compilation of references in Lacombat, 2005). The presence of *Bison schoetensacki* and *Equus altidens*, and the newly immigrant *E. suessenbornensis*, underline a tendency towards landscape opening, while new deer species, *Dama clactoniana* and *Praemegaceros* (=*Megaceroides*) *solilhacus*,

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occupied forested areas and marginal zones. The occurrence of the amphibious *Hippopotamus antiquus*, and of *Stephanorhinus kirchbergensis* and *Palaeoloxodon antiquus* at Soleilhac, indicate a mild climatic period with winter temperatures reaching, on average, a minimum of only a few degrees below zero.

Around 0.65 Ma, the climate grew significantly cooler and drier. This change is recorded by the faunal assemblage from the l'Escale cave (Bouches-du-Rhône; Bonifay, 1974–1975) which includes remains of *Hemitragus bonali, Gulo gulo* and *Vulpes praeglacialis.* Another relatively cold and dry period is indicated by the faunal remains of 'Ensemble I' at the Arago cave (Pyrénées-Orientales), placed in MIS 14 at around 0.57–0.53 Ma (Moigne et al., 2006). *Ovis ammon antiqua*, also reported at Pont-du-Château (Puy-de-Dôme; Pommerol, 1880), and *Hemitragus bonali*, were faunal elements of mountainous areas, while early *Rangifer tarandus*, *Stephanorhinus hemitoechus* and *Equus mosbachensis*, accompanied by *Praeovibos priscus*, roamed across low-relief terrain. Contemporaneous carnivores from similar environments include an early form of arctoid *Ursus*, *Cuon priscus* and *Vulpes praeglacialis*.

Abundant remains of *Dama clactoniana* and *Cervus elaphus* in 'Ensemble II' at Arago, of MIS 13 age, c. 0.53–0.48 Ma (Moigne et al., 2006), suggest a temperate and more humid climatic period. Between 0.48 and 0.43 Ma a further drop in temperature, followed by landscape opening, paved the way for the immigration of *Bison priscus*, as reflected in the 'Ensemble III' of Arago. Remains of *Mammuthus trogontherii*, another steppe dweller of this cooler, drier period, were recently discovered at Nolhac, Haute-Loire (Mol and Lacombat, 2009).

According to recent interpretations, the Middle Pleistocene cold-adapted *Mammuthus-Coelodonta* Faunal Complex (Kahlke, 1999) expanded into Western Europe for the first time during MIS 10 (Kahlke and Lacombat, 2008; see Section 2.4.7). The site of La Fage (Corrèze) has yielded *Coelodonta*, *Rangifer* sp. and *Gulo gulo* (Guérin, 1973; Mourer-Chauviré et al., 2003), species reflecting continental conditions and steppe-like landscapes, possibly with some shrub vegetation.

In contrast to the northern and central parts of Western Europe, the Mediterranean open air sites of Terra Amata (Alpes-Maritimes; Serre, 1987) and Lunel-Viel (Hérault; Brugal, 1984–1985), both dated to around 0.38 Ma, have yielded more thermophilous species. The co-occurrence of *Bos primigenius* and *Stephanorhinus hemitoechus* on the one hand, and *Stephanorhinus kirchbergensis* (site of Aldène, Hérault; Bonifay and Bussière, 1989; Bonifay, 1994), *Cervus elaphus* and *Sus scrofa* on the other, reflects a mosaic-like landscape with temperate conditions, as also indicated by *Palaeoloxodon antiquus*.

2.4.5. Iberian Peninsula

Clues to environmental conditions in the latest part of the Early to the onset of the Middle Pleistocene (0.9–0.6 Ma) in the Iberian Peninsula are provided by the sites of Incarcal-I (Gerona; Galobart and Maroto, 2003; Maroto et al., 2003), Huéscar-1 (Granada; Mazo et al., 1985; Kahlke, 2006), Trinchera Dolina 3-4 (TD3-TD4 = former TDW4), Trinchera Dolina 5 (TD5 = former TDE5 + TDW5) and 6 (TD6) (all Sierra de Atapuerca, Burgos), dated to c. 0.9–0.8 Ma (Falguères et al., 1999, 2001; Berger et al., 2008). Incarcal-I, which includes cf. *Bison*, probable remains of roe deer, a megacerine, *Hippopotamus antiquus*, *Stephanorhinus hundsheimensis*, *Equus stenonis*, *Mammuthus meridionalis*, *Homotherium latidens,* and *Pachycrocuta brevirostris* (Galobart et al., 1996), is indicative of a temperate interval with an open landscape and sufficient humidity for growth of some forested areas. At Huéscar-1 *Palaeoloxodon antiquus*, a forest dweller, is present together with *Hippopotamus antiquus* (=*H. amphibius antiquus* = *H. major*), a species which requires access to permanent water bodies and open grassland. Open habitats are also indicated by *Equus suessenbornensis*. At TD3-TD4, species such as cf. *Bison schoetensacki voigtstedtensis*, *Dama* (=*Cervus* s.l. = *Pseudodama*) *nestii vallonnetensis*, *Cervus* cf. *acoronatus*, *Eucladoceros giulii*, *Equus altidens*, *Homotherium latidens*, and *Crocuta crocuta* ssp. indicate a landscape of open and sparsely-forested areas, while others, such as *Panthera onca gombaszoegensis* (=*P. gombaszoegensis*), *Ursus dolinensis,* and *Sus scrofa* reflect more restricted forest components (Cuenca-Bescós and García, 2007). The fossil jaguar is known to have hunted primarily in the vicinity of water bodies (Hemmer et al., 2001). TD5 and TD6 share most of these taxa, which suggests temperate conditions, especially given the overwhelming dominance of *Dama nestii vallonnetensis*. The mammal record of the upper part of TD5 and level TD6 indicates a complex interglacial period with fluctuations in the degree of relative humidity (Cuenca-Bescós and García, 2007).

The presence of humans during the Middle Pleistocene has been well established at the following sites: Sierra de Atapuerca at Trinchera Dolina levels 8 to 11 (TD8b, TD10 and TD11), dated to c. 0.6–0.2 Ma (Falguères et al., 1999, 2001; Berger et al., 2008); Sima de los Huesos (SH), c. 0.53 Ma (Bischoff et al., 2007); and Trinchera Galería (TG, Units G2–G3), ranging between c. 0.46 and 0.25 Ma (Berger et al., 2008). In addition, human activity has been recorded at the sites of Cúllar de Baza-1 (Guadix basin, Granada; Ruiz Bustos, 1984; Vega Toscano, 1989) and Ambrona (Soria), dated to about 0.4 Ma (Sesé and Soto, 2005).

At the end of the Early Pleistocene, around 0.8 Ma, the south-west-European climate grew significantly drier, which continued through the subsequent interglacial periods (Suc et al., 1995; Bertini, 2000). This transition to drier conditions is well-reflected in the palaeoenvironmental record of the Trinchera Dolina sequence, where the abundance of megaherbivores and the scarcity of forest-adapted mammals are incompatible with the existence of densely forested areas. The large mammal assemblages, in addition to the ones recorded from the sites of Cúllar de Baza-1 and Ambrona, reveal a faunal turnover which included the appearance of new grazers such as *Stephanorhinus hemitoechus, Equus suessenbornensis, E. altidens*, etc., together with mixed feeders such as *Bos primigenius*, *Capreolus priscus*, *Dama clactoniana, Megaloceros,* and *Palaeoloxodon antiquus.* The combined occurrence of both of these groups of animals suggests a dominance of open woodlands in the TD8 to 11 sequence, although the dominant plant species varied according to climatic conditions. Carnivore events characterizing this period include the arrival of *Panthera leo* ssp., the spread of *Crocuta crocuta* ssp., and the appearance of large-sized wolves (*Canis lupus*) and members of the cave bear lineage (*Ursus deningeri–U. spelaeus*).

2.4.6. North-Western Europe and the southern North Sea Basin

The fossil record of the earliest part of the 0.9–0.4 Ma period is limited in North-Western Europe. The few finds from the Leerdam Interglacial at Dorst-Surae in The Netherlands, of late Matuyama age, include *Eucladoceros* sp. and advanced *Mammuthus meridionalis* (Van Kolfschoten, 1990). However, our understanding of the sequence of temperate stages between the Matuyama/Brunhes boundary and the Anglian (=Elsterian) glaciation in Britain (the 'Cromerian Complex', c. 0.78–0.5 Ma) has been greatly refined over the past decade (Preece and Parfitt, 2000, 2008; Stuart and Lister, 2001). Extensive large mammal faunas are known from the type Cromerian West Runton Freshwater Bed (Norfolk), and the Rootlet Bed and associated deposits at Pakefield, Kessingland and Corton ('Pakefield'), Suffolk (Stuart, 1996; Stuart and Lister, 2001; Parfitt et al., 2005; Breda et al., in press; Lewis et al., in press; Lister et al., in press). A recent synthesis of the palaeoecology of the type Cromerian interglacial at West Runton (Stuart and Lister, in press) indicates temperate climate, high precipitation and low seasonality, typical of oceanic, mid-latitude Europe, supporting a diverse ecosystem dominated by forest but with productive open areas as well.

The mammals and other biotic proxies demonstrate full interglacial conditions in both deposits, but key species indicate that they represent different temperate episodes, the Pakefield interglacial distinctly warmer than that of West Runton (Preece and Parfitt, 2000, 2008; Stuart and Lister, in press). The large mammals at both localities include grazing elements, e.g. *Equus altidens* and *Mammuthus trogontherii*, and browsing/mixed-feeding ones, e.g. *Bison schoetensacki*, *Capreolus suessenbornensis*, *Praemegaceros* (=*Megaceroides*) *verticornis*, *Sus scrofa* and *Stephanorhinus hundsheimensis*, as well as a range of large carnivores, *P. onca gombaszoegensis* (=*P. gombaszoegensis*), *P. leo* ssp., *Homotherium latidens,* and *Crocuta crocuta* ssp., together indicating a rich and diverse interglacial environment. Pakefield, in addition, has *Hippopotamus* and the earliest regional record of the woodland elephant *Palaeoloxodon antiquus*. Both localities are placed within the earlier, *Mimomys savini* zone of the 'Cromerian Complex' (c. late MIS 19 – early MIS 15, i.e. c. 0.78–0.6 Ma); their relative ages are uncertain but Pakefield may be older, and they could represent either different isotope stages, or substages of one stage (Preece and Parfitt, 2008).

Moreover, a third temperate episode within the *Mimomys savini* zone, and probably younger than West Runton, has been recognised at Little Oakley (Essex) (Lister et al., 1990; Preece and Parfitt, 2000), with a small assemblage of large mammals similar to that of West Runton, but with warmer conditions suggested by the presence of pond tortoise *Emys orbicularis*.

In the later, *Arvicola mosbachensis* (=*A. cantianus* = *A. terrestris cantiana*) zone of the 'Cromerian Complex' (Fig. 1) there is evidence for as many as three separate temperate stages in the interval MIS 15–13 (ca. 0.6–0.5 Ma), before the Anglian/Elsterian in the British succession. The Calcareous Member at Westbury-sub-Mendip (Somerset) spans two temperate phases separated by a cold interval, with evidence for human activity (Andrews et al., 1999); the interglacial at the hominid site of Boxgrove (Sussex) probably represents an additional phase that may post-date the whole Westbury sequence (Roberts and Parfitt, 1999; Preece and Parfitt, 2000). The temperate levels at both sites contain a diverse assemblage, mainly species of woodland and mixed habitats such as *Bison schoetensacki*, *Capreolus suessenbornensis*, *Dama dama* and *Cervus elaphus,* but also of grassland (e.g. *Equus ferus*). As well as *Stephanorhinus hundsheimensis* at both localities, the 'Pliocene' browsing species *S.* cf. *megarhinus* has been identified at Boxgrove (Breda et al., in press). Elephants have not been identified at either site but the temperate mixed-feeder *Palaeoloxodon antiquus* occurs at the broadly correlative sites of Ostend (Norfolk) and Waverly Wood (Warwickshire) (Preece and Parfitt, 2000; Stuart and Lister, 2001). A rich carnivore guild includes *P. onca gombaszoegensis*, *P. leo* ssp., *Homotherium latidens, Crocuta crocuta* ssp., *Lycaon* [=*Canis* (*Xenocyon*)] *lycaonoides* and *Canis mosbachensis* plus abundant *Ursus deningeri* at Westbury-sub-Mendip, a cave site. Turner (2009) notes that the early Middle Pleistocene represents a peak of diversity of the large carnivore guild in Europe, although the distribution of species across the Westbury sequence hints that not all of them were present in the area at the same time.

The cool interval between the temperate phases at Westbury contains a restricted, more grazing-dominated fauna including *Bison* cf. *schoetensacki* and a caballine horse. The persistence of *Cervus elaphus* and *Stephanorhinus hundsheimensis* is consistent with their known extremely eurytopic feeding ecology (Lister, 1984; Kahlke and Kaiser, 2010). At the top of their respective sequences, Westbury and Boxgrove both show a fluctuating but overall cooling climate, reflected in a clear increase in cold-adapted or open-ground faunal elements including the entry of (very fragmentarily recorded) caprines plus, at Westbury, *Bison priscus* and a single antler-base of reindeer *Rangifer tarandus* (Gentry, 1999), the earliest stratified record in the region.

In general, however, evidence for the large mammal faunas of the cold stages in the interval 0.9–0.4 Ma is very patchy compared to that of the temperate phases. Unstratified remains from the Cromer Forest-bed Formation in Norfolk, probably of early Middle Pleistocene age, include *Gulo gulo* from Mundesley and the large musk-ox *Praeovibos priscus* from Trimingham (Stuart, 1982). Assuming that the ecological tolerance of the wolverine is broadly similar to that of today, and that early Middle Pleistocene *P. priscus* is indicative of colder, continental influenced climate (see Sections 2.4.4 and 2.4.7), they hint at very different environments and mammalian communities in North-Western Europe in the cold intervals between the much better-known temperate episodes.

The faunas of the Hoxnian stage (MIS 11, c. 0.4 Ma), by contrast, are well known, thanks to extensive collections from the type locality of Hoxne (Suffolk), and from the correlated localities of Swanscombe (Kent) and Clacton (Essex), all sites of major archaeological importance. Recent work suggests two or three temperate intervals during MIS 11 (Schreve, 2001, 2004; Ashton et al., 2008). In the lower levels at Swanscombe (Lower Gravel and Lower Loam) and Hoxne (Bed E, pollen zones Ho I–II), the large mammal fauna is consistent with a fully-temperate wooded interglacial, with abundant *Dama clactoniana* (=*D. dama clactoniana*) alongside *Bos primigenius*, *Megaloceros giganteus, Capreolus capreolus*, *Cervus elaphus*, *Sus scrofa*, *Stephanorhinus kirchbergensis*, *S. hemitoechus* and *Palaeoloxodon antiquus*. More open environments are indicated by *Equus ferus* and rare *E. hydruntinus.* Larger Carnivora are limited to *Panthera leo* ssp., *Ursus spelaeus* and *Canis mosbachensis*. There had evidently been major faunal turnover since the latest pre-Anglian interglacial (MIS 13). Both Schreve (2001) and Ashton et al. (2008) correlate this episode with the main, early temperate phase of MIS 11c (ca. 425–395 ka).

In the upper fauna at Swanscombe (Middle Gravels), Schreve (2001) noted a shift towards grassland elements at the expense of those of woodland (i.e. *E. ferus* is dominant rather than *D. dama*), suggesting the later, more open part of the Hoxnian (Ho III–IV), equating to either the latter part of MIS 11c (Ashton et al., 2008) or the shorter temperate phase MIS 11a (Schreve, 2001). Following a cold episode with open landscapes (Bed C of Ashton et al., 2008; probably equivalent to MIS 11b), the large mammalian assemblage from the upper beds at Hoxne (Bed B1–2) represents a third fauna, dominated by *Dama dama*, *Cervus elaphus* and *Equus ferus*, together with species such as *Capreolus capreolus*, *Panthera leo* ssp. and *Macaca sylvanus*. The climate was again fully temperate, with a mix of open and woodland indicators, but Ashton et al. (2008) suggest that the forest was of boreal character in this 'interstadial' that probably equates to MIS 11a (c. 0.37 Ma).

The small fauna from Neede (The Netherlands), with the beaver *Trogontherium cuvieri*, is probably of MIS 11 age. The large mammal assemblage with *Cervus elaphus, Stephanorhinus kirchbergensis* and *Equus* sp. (Van Kolfschoten, 2001) is compatible with the British fauna of this age.

2.4.7. *Central Europe*

A number of rich fossil mammal sites in Germany, the Czech Republic and Austria, dated between 0.8 and 0.5 Ma, show an alternation of increasingly severe climatic phases from the latter part of the Early Pleistocene onwards, until the "pre-glacial" (unglaciated) early Middle Pleistocene in Central Europe. The lacustrine site of Dorn-Dürkheim 3 (Rheinland-Pfalz), associated with a *Mimomys savini*-micromammal fauna, occurs below the M/B boundary (Franzen et al., 2000). Its large mammal assemblage is similar to those of the earliest Middle Pleistocene in Eastern, Central and North-Western Europe. Based on the minimum

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number of recorded individuals, the landscape was dominated by open grassland, as indicated by *Equus altidens*, *E. suessenbornensis*, and the frequently recorded *Mammuthus trogontherii* (Franzen et al., 2000). *Bison schoetensacki*, the generalist *Stephanorhinus hundsheimensis* (Kahlke and Kaiser, 2010), and the elaphine deer *Cervus acoronatus* all suggest the inclusion of patches of forested areas. Cold-adapted mammals, such as those typical of glacial periods (see below, this chapter), are lacking.

The Czech sites of Stránská Skála (Moravia) and infill from the cave C 718 near Zlaty Kun (=Konéprusy C 718, Bohemia), reflect the evolution of mammal fauna in Central Europe just after the M/B reversal, approximately in the time period MIS 19 to 18/17. The talus cone of Stránská Skála contains a sequence of fossiliferous layers suggestive of alternating conditions, from temperate and slightly humid to cooler and steppic (Musil, 1995). Konéprusy has yielded a diverse assemblage of early Middle Pleistocene fossil material, including *Bison schoetensacki*, *Cervalces* (=*Alces*) *latifrons*, *Cervus acoronatus*, *Sus scrofa priscus*, *Equus* cf. *mosbachensis* and *Mammuthus trogontherii*, and even the extinct musk-ox, *Praeovibos priscus* (Fejfar, 1961). This faunal mix reflects different stages in the transition from a warm and humid climatic period to a predominantly cooler and more arid one with open landscapes. The transition most probably occurred sometime in the MIS 18–17 interval.

Dating from the early Brunhes magnetochron, significant faunal remains from Voigtstedt (Thuringia) including *Bison schoetensacki voigtstedtensis*, *Cervalces latifrons*, *Cervus acoronatus*, *Praemegaceros* (=*Megaceroides*) *verticornis*, *Sus scrofa* ssp., *Stephanorhinus hundsheimensis*, *Equus altidens*, and *Mammuthus trogontherii* (result of recent studies by H. van Essen, Leiden; pers. communication to R.-D. K.), clearly demonstrate a warm climatic episode, with a landscape dominated by forest (Kahlke, 1965; Kahlke and Kaiser, 2010). The occurrence of the biostragraphically indicative arvicolid *Mimomys savini* assigns the Voigtstedt fauna to the Late Biharian, most probably to MIS 17 (Maul et al., 2007) at an age of around 0.7 Ma, which is consistent with the large mammal record.

The fluviatile horizons of the site of Süssenborn (Thuringia) represent a longer time interval within the early Brunhes magnetochron (?MIS 16). The mammal fauna (also with *Mimomys savini*) includes characteristic early Middle Pleistocene elements, such as *Soergelia elisabethae*, *Bison schoetensacki*, *Capreolus suessenbornensis*, *Cervalces latifrons*, *Praemegaceros verticornis*, *Megaloceros savini*, *Equus altidens* and *E. suessenbornensis,* together with an extended series of *Mammuthus trogontherii* remains (Kahlke, 1969). Although several climatic oscillations are represented in the sequence, the faunal list, with the constant occurrence of *Mammuthus trogontherii*, and the feeding traits of *Stephanorhinus hundsheimensis* (Kahlke and Kaiser, 2010), imply a long-lasting dominance of open, continentally influenced conditions. The extensive fossil record does not indicate periglacial conditions, nor the formation of a steppe-tundra (Kahlke, 1999). Single occurrences of the early reindeer, *Rangifer tarandus stadelmanni*, and musk-ox, *Ovibos moschatus suessenbornensis,* at Süssenborn have been interpreted as sporadic appearances of winter visitors from sub-Arctic or Arctic regions (Soergel, 1939; Kahlke, 1999).

The younger part of the "pre-glacial" (=pre-Elsterian) early Middle Pleistocene of Central Europe is characterised by biostratigraphically significant *Arvicola mosbachensis*- (=*A. cantianus* = *A. terrestris cantiana*)-micromammal faunas (Von Koenigswald and Heinrich, 1999; Maul et al., 2000). Correlative sites with extended large mammal records of this period are Mauer (Baden-Württemberg), Miesenheim 1 (Rheinland-Pfalz), Mosbach 2 (="Graues Mosbach" with main fauna; Rheinland-Pfalz) and Hundsheim (Lower Austria).

The Mauer faunal record, probably of MIS 15 age, is dominated by forest species such as *Capreolus capreolus priscus*, *Sus scrofa priscus*, *Stephanorhinus kirchbergensis* and a number of mixed feeders such as *Bison schoetensacki*, elaphine deer, *Stephanorhinus hundsheimensis* and *Palaeoloxodon antiquus*. In addition to the herbivores, a diverse guild of carnivores, including *Felis* cf. *silvestris*, *Panthera fossilis*, *P. pardus sickenbergi*, *Pliocrocuta perrieri*, and *Canis mosbachensis* has been recovered (Schreiber et al., 2007). The presence of *Hippopotamus* supports the presence of a warm, humid environment, and the Mauer faunal community, as a whole, implies fully developed interglacial conditions with warm summers and mild, humid winters. These conditions led to a dominance of forests interspersed with more open patches, as hinted by the presence of *Equus mosbachensis*. A similar environment is documented by the site of Miesenheim 1 (Rheinland-Pfalz), which has *Capreolus suessenbornensis*, *Cervus elaphus*, *Sus scrofa*, *Felis* cf. *silvestris*, etc. (Turner, 1990; Van Kolfschoten and Turner, 1996), an assemblage that could be slightly older than the Mauer forest fauna, as suggested by the micromammal record (Maul and Heinrich, 2007).

The faunal assemblages from Mosbach 2 and Hundsheim can both be placed in the MIS 15 or MIS 13 isotope stage (Hemmer et al., 2008). As indicated by the micromammal biostratigraphy (Maul and Heinrich, 2007) both Mosbach 2 and Hundsheim are slightly younger than the Miesenheim 1 and Mauer faunal assemblages. The fossil record of the Mosbach 2 Sands includes the following species: *Praeovibos priscus*, *Bison schoetensacki*, *B. priscus*, *Capreolus suessenbornensis*, *Cervalces latifrons*, *Rangifer tarandus stadelmanni*, *Cervus acoronatus*, *Praemegaceros verticornis*, *Hippopotamus antiquus*, *Sus scrofa priscus*, *Stephanorhinus hundsheimensis*, *S. hemitoechus*, *S. kirchbergensis*, *Equus mosbachensis*, *Palaeoloxodon antiquus*, *Mammuthus trogontherii*, *Panthera fossilis*, *Acinonyx pardinensis intermedius*, *Homotherium latidens*, *Pliocrocuta perrieri*, *Crocuta crocuta praespelaea*, *Ursus thibetanus*, *U. deningeri*, *Lycaon* [=*Canis* (*Xenocyon*)] *lycaonoides*, *Canis mosbachensis* and *Macaca* sp. (an updated list can be found in Hemmer et al., 2008). Such high mammal diversity does not reflect the contemporaneous existence of different habitats in the vicinity of the site, but rather suggests a sequence of changing ecological conditions. This is confirmed by the occurrence of three different species of rhino: the ubiquitous *Stephanorhinus hundsheimensis*, the grazer *S. hemitoechus* (both of which are associated with drier landscapes), and the browser *S. kirchbergensis* (Fortelius et al., 1993; Kahlke and Kaiser, 2010). Moreover, unquestionable indicators of more temperate, Atlantic-influenced climatic conditions are the hippo, woodland elephant and macaque. The existence of forested parts of the Mosbach landscape can also be inferred from finds of *Sus scrofa priscus*. Over long periods, however, the landscape was most likely dominated by steppe, as documented by extensive records of *B. priscus*, *C. latifrons*, *E. mosbachensis* and *M. trogontherii* throughout the sequence. Occasional finds of cold-adapted animals, especially *Rangifer*, indicate an interval with enough continental influence to support reindeer, at least seasonally. All in all, the Mosbach 2 sequence reflects, for most of the represented period, a dry steppe landscape, occasionally interrupted by warmer, humid episodes with extended forests. However, at least one cool-to-cold period, of a more continental-like character, is also evident.

A similar situation is inferred from the Hundsheim fauna, which seems to represent a part of the Mosbach sequence, as shown by the common occurrence of the small cheetah *Acinonyx pardinensis intermedius*, which appeared in Europe only for a very short period (Hemmer et al., 2008). Apart from this high-speed hunter, the presence of *Equus mosbachensis* also suggests the existence of a predominantly open landscape at Hundsheim. Other species, such as *Bison schoetensacki*, *Capreolus capreolus priscus*, *Cervus elaphus* and *Stephanorhinus hundsheimensis* (Frank and Rabeder, 1997) are common.

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Whereas the 0.9–0.5 Ma interval in Central Europe is characterised by regular alternations between warm–humid, moderate, and cool–dry climatic stages, the long-lasting and intense cold period of MIS 12 resulted in the advance of the Baltic ice sheet into this region. At the same time, a cold-adapted mammal fauna, the *Mammuthus*-*Coelodonta* Faunal Complex (Kahlke, 1999), made its first appearance. Records of this earliest western Palaearctic mammoth fauna occur at the site of Bad Frankenhausen (Thuringia), in the gravels of a meltwater delta formed in the vicinity of the advancing Elsterian ice sheet at around 0.46 Ma (Isotopic events 12.4–12.3 sensu Bassinot et al., 1994; Kahlke and Lacombat, 2008). The Bad Frankenhausen fauna comprises *Soergelia elisabethae*, *Praeovibos priscus*, *Bison* sp., *Rangifer tarandus* ssp., *Mammuthus trogontherii* and others, including *Coelodonta tologoijensis*, the earliest woolly rhino reported in Europe (see Section 2.4.2) (Kahlke and Lacombat, 2008). All these faunal elements indicate glacial conditions, clearly demonstrating that during the MIS 12 period, for the first time, a steppe-tundra or mammoth steppe spread from Asia through to Central Europe.

The subsequent MIS 11 is correlated by most authors with the Holsteinian (Nitychoruk et al., 2006), which is one of the most distinctive interglacial complexes of the western Palaearctic Pleistocene (see Section 2.4.6). The faunas from the so-called *antiquus*-gravels (named after *Palaeoloxodon antiquus*) of Steinheim/Murr, and the fossil assemblage recovered from the infill of Heppenloch cave (both Baden-Württemberg), are both commonly associated with this period. The Steinheim *antiquus*-fauna consists nearly exclusively of browsers or mixed feeders, such as *Bos primigenius*, *Megaloceros giganteus antecedens*, *Cervus elaphus*, *Capreolus capreolus priscus*, *Stephanorhinus kirchbergensis*, and *Palaeoloxodon antiquus* (Adam et al., 1995). The Heppenloch assemblage appears to be quite similar, but is lacking giant deer (forest type) and forest rhino, and therefore supports the existence of more open conditions (Adam, 1975). The presence of the water buffalo, *Bubalus murrensis*, a migrant from southern Asia in the Steinheim fauna (Berckhemer, 1927), as well as in the approximately contemporaneous fossil assemblages from Schönebeck/Welsleben (Sachsen-Anhalt; Schertz, 1937) and Bruchsal-Büchenau (Baden-Württemberg; Schreiber and Munk, 2002), underline the warm-humid character of the central European MIS 11 faunal record.

2.4.8. Eastern Europe

Eastern European faunas of the 0.9–0.4 Ma interval are assigned to the Tiraspol Faunal Complex (Gromov, 1948). The most extensive fossil record of the first half of the early Middle Pleistocene in Eastern Europe is that of Kolkotova Balka (Tiraspol) in Pridniesrovie (Transnistria). Typical faunal elements of the Tiraspol Complex include *Bison schoetensacki* (*B.* aff. *priscus* after Sher, 1997), *Cervalces* (=*Alces*) *latifrons*, *Praemegaceros* (=*Megaceroides*) *verticornis*, *Stephanorhinus* cf. *hundsheimensis*, *S. kirchbergensis*, *Equus* cf. *altidens*, *E. suessenbornensis, Mammuthus trogontherii*, *Panthera leo* ssp. and *Ursus deningeri* (Nikiforova et al., 1971; Forstén, 1999). Most of these species inhabit open steppe, or forest-steppe landscapes, reflecting a remarkable degree of continental influence at this site. Finds of two practically complete skeletons of *Mammuthus trogontherii* from the Kagalnik sand pit (Azov) belong to the same fossil assemblage (Tesakov et al., 2007). Representatives of the Tiraspol Complex also occur in the bottom alluvial layers of the Girey sand pit near Kropotkin town, Georgievsk (northern Caucasus; Vereshchagin, 1959).

Fossil assemblages of later parts of the Tiraspol faunal period have been recorded in cave deposits from the northern Caucasus. *Bison schoetensacki*, *Capreolus* cf. *suessenbornensis*, elaphine deer, *Stephanorhinus hundsheimensis*, *Equus altidens*, *Panthera leo* ssp., *Crocuta crocuta* ssp., *Ursus deningeri, Canis mosbachensis*, etc. were discovered in the lower levels of the Treugolnaya cave (Karachay-Circassia; Baryshnikov, 1993, 2007), indicating episodes of drier and warmer climates and the presence of forest-steppe landscapes.

During the final phase of the 0.9–0.4 Ma interval, under fully developed interglacial conditions, *Palaeoloxodon antiquus* spread through a forest zone into southern Russia (Taganrog, Pyatigorsk, Girey 1), Transcaucasia and the lower reaches of the Volga river, and onwards to the Urals (Alexeeva, 1990) and further into Asia.

3. Discussion

3.1. The 2.6–1.8 Ma interval

The 2.6–1.8 Ma interval was a period of perceptible global cooling, forming part of the wider trend of decreasing temperatures following the Mid-Miocene Climatic Optimum (Zachos et al., 2001; see Section 2.1). During this period of 41 ka climatic periodicity (Lisiecki and Raymo, 2005), the early stages of aridification and partial landscape opening were reflected by the large mammal faunas that roamed over practically all western Palaearctic regions during this interval (Fig. 6).

In Eastern and South-Eastern Europe, as well as in Asia Minor, cooling and aridification, as an expression of the increasing influence of continentality, started earlier than in Central, Western and Southern Europe. The deforestation of vast territories, and the establishment of regions with distinctive vegetation, is documented at fossil sites in Romania and elsewhere already from the Early Villafranchian (see Section 2.1.2). After 2.6 Ma, the number of Ethiopian faunal elements in the fossil record decreased in southwest Asia and Europe (see Section 2.1.1). Transcaucasia, Asia Minor and South-Eastern Europe, at the crossroads between Africa, Asia and Europe, became important routes for faunal (including hominin) dispersals, given that the main Alpine morpho-tectonic structures were already largely in place at the beginning of the Pliocene. At the same time, the Balkans represented the westernmost frontier of several Asian mammal dispersals, and was also a gateway to South-Western Europe for fauna coming mainly via Asia Minor and/or the northern Pontic region.

Whereas open grassy landscapes prevailed in both Asia Minor and South-Eastern Europe at the onset of the Middle Villafranchian, the subsequent pre-Olduvaian Middle Villafranchian was characterised by mosaic-like environments made up of savannah habitats and woodland. Both types of landscape stretched from Transcaucasia up to the Balkans and beyond. A brief period of pre-Olduvaian climatic cooling, which may have been connected to a temporary closure of the Bosporus, is particularly reflected in the Bulgarian large mammal record (see Section 2.1.2). The subsequent Olduvaian magnetochron saw periods of warming and increased humidity.

On the Apennine Peninsula, the 41 ka periodicity governing global temperatures gave rise to short alternations between xeric cool-temperate and warm moist phases (see Section 2.1.3), and the original Late Pliocene (Early Villafranchian) forests were replaced by Middle Villafranchian savannah-like settings. This was the time of the so-called “Elephant-*Equus* event”, when smaller-sized browsing and grazing ruminants were first accompanied, and then replaced, by herds of larger-sized grazers. The carnivore response was the so-called “wolf event”, as cooperative predators replaced solitary, stalking and ambushing hunters. As in the eastern and southern regions, Western Europe and the Iberian Peninsula were also affected by the Middle Villafranchian cooling, leading to the spread of grasslands and the accompanying retreat of forests (see Sections 2.1.4 and 2.1.5).

North-Western Europe and the southern North Sea Basin were affected by several particular palaeogeographic factors that

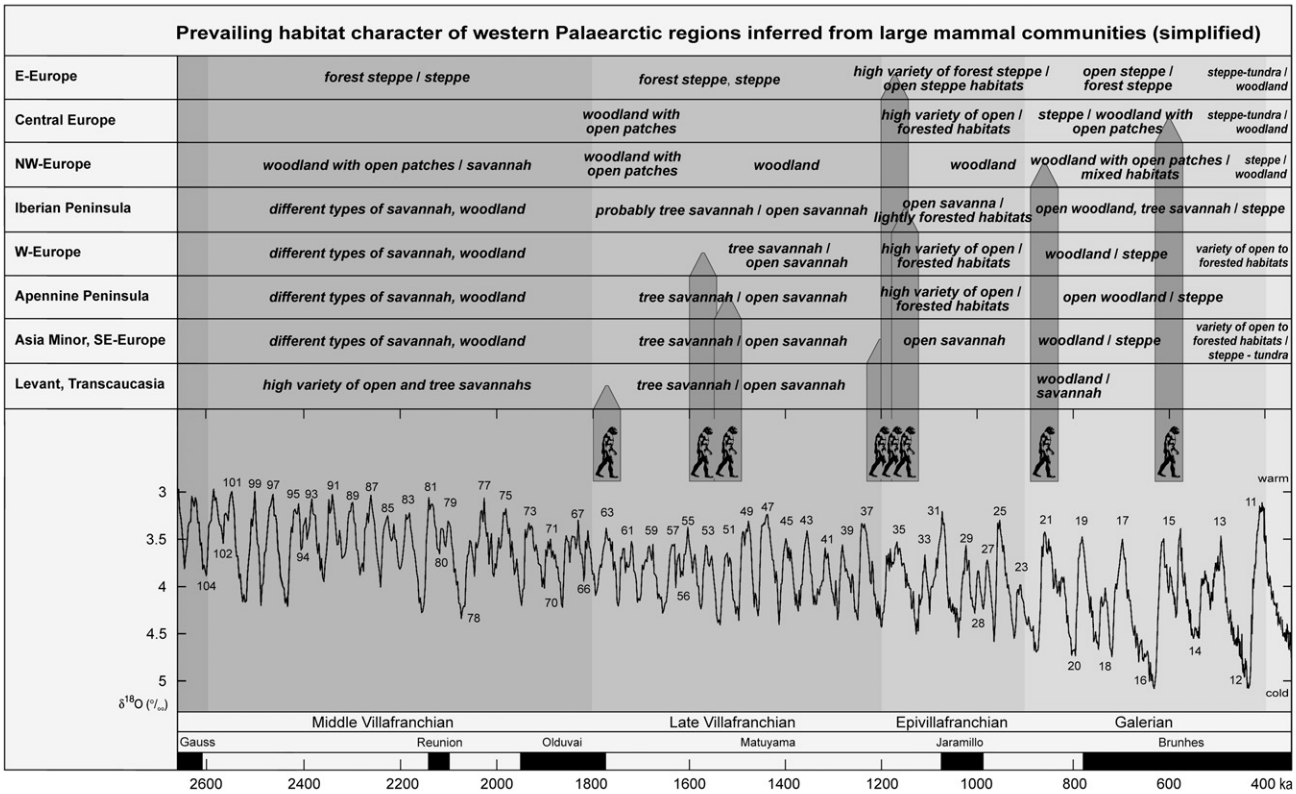

Fig. 6. Sketch of the prevailing habitat character of western Palaearctic regions during the Early and early Middle Pleistocene (2.6–0.4 Ma) inferred from the large mammal fossil records, in relation to global temperatures (after Lisiecki and Raymo, 2005) and the earliest records of human occurrence. Slash: Temporal alternation of habitats; Arrow: initial human occupation of corresponding regions, based on indisputed osteological and/or archaeological evidence (for data see text).

influenced their changing Plio-Pleistocene mammalian faunas. Because of their position on the Atlantic Ocean, these regions show a predominance of species intolerant of continental climates, especially very cold winters. During the 2.6–1.8 Ma interval, climate-driven changes in the large mammal faunas of these regions were less marked than those of more eastern areas (see Section 2.1.6).

The fossil record of Central European large mammals is too fragmentary to provide sufficient information on environmental evolution during the 2.6–1.8 Ma span. In Eastern Europe, a marked turnover in large mammal communities occurred at the transition from the Early to Middle Villafranchian. Thermophile species, which had thrived in the humid Pliocene forest habitats, were replaced by forest-steppe to steppe dwellers, as a clear response to the aridification of the landscape that continued throughout the whole of the Middle Villafranchian.

3.2. *The 1.8–1.2 Ma interval*

The decrease in global temperatures continued during the 1.8–1.2 Ma interval (Zachos et al., 2001). In this span of time, which was still governed by the 41 ka periodicity effect, the individual temperature cycles were of similar intensity (see Lisiecki and Raymo, 2005). These steady climatic alternations led to the increasing specialisation of species and faunas adapted to particular environmental conditions (Fig. 6).

In contrast to the biogeographic situation during the Middle Villafranchian, in the Late Villafranchian the northern dispersal of the majority of African species via the Levantine Corridor was limited by the Taurus-Zagros range (Martínez-Navarro, 2004). The earliest Late Villafranchian fauna of Dmanisi (Georgia) is of strictly Eurasian character (see Section 2.2.1). At this time, tree savannahs, open grasslands, and extended semiarid areas occurred in western Transcaucasia. Factors favouring the migration and subsistence of species adapted to more humid conditions (including hominins) were valleys with rivers supplying sufficient water resources year-round, as well as belts of diverse riparian vegetation. Mammalian assemblages of end-Villafranchian age indicate warm environmental conditions and the continuing significance of riverine habitats.

During the 1.8–1.2 Ma time interval in South-Eastern Europe, open grassy landscapes in more continentally influenced periods alternated with mixed forest steppes during milder phases. Each habitat was occupied by a different type of fauna, whose elements were mostly of Asian origin (see Section 2.2.2). Similarly, environments in both the Apennine Peninsula and Western Europe reflected the Late Villafranchian climatic trend. These regions gradually turned into savannahs, alternately cool/open and temperate/more wooded. A harshening of environmental conditions became evident during both cooler and warmer phases (see Sections 2.2.3, 2.2.4).

The Middle to Late Villafranchian transition also led to a faunal turnover in South-Western Europe. Migrants from Asia, mostly comprising grazers, reached this region during periods of landscape opening (see Section 2.2.5). The Late Villafranchian also saw the migration of grazers and mixed feeders from Africa. The actual routes followed by these immigrants, however, are still debated (O'Regan et al., 2006). The available Iberian fossil record of the 1.8–1.2 Ma span indicates herbaceous savannahs under temperate conditions.

Late Villafranchian faunal communities of North-Western Europe reflect periodically more humid conditions and correspondingly diverse landscape patterns. Fossil mammal sites of this region are indicative of rich interglacial landscapes inhabited by browsers, mixed feeders and grazers (see Section 2.2.6). Large mammal assemblages associated with cooler periods have been

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recorded neither from this region nor from Central Europe. The only site with extensive fossil records (Erpfinger Höhle), tentatively dated to the Middle/Late Villafranchian transition, includes taxa of both forested and open habitats (see Section 2.2.7).

Because of its long history of dry climates starting before 2.6 Ma BP, Eastern Europe shows no radical faunal turnover during the 1.8–1.2 Ma interval.

3.3. *The 1.2–0.9 Ma interval*

The 1.2–0.9 Ma interval is commonly regarded as the terminal phase of 41 ka periodicity. Nonetheless, after 600 kyr of generally consistent temperature variations, a new regime of global climatic evolution developed. In addition to a less stable frequency, the amplitudes of the global $\delta^{18}O$ record increased (see Raymo and Nisancioglu, 2003, Fig. 1; Lisiecki and Raymo, 2005, Fig. 4). Thus, the 1.2–0.9 Ma interval can be seen as a relatively unstable transitional time span, linking the 41 ka with the following 100 ka periodicity. Some stages were especially warm. In consequence, the western Palaearctic Epivillafranchian large mammal communities differed markedly from their Late Villafranchian counterparts (see Section 2.3) (Fig. 6).

The South-Eastern European fossil record is consistent with the occurrence of widespread areas of grassland during most of the 1.2–0.9 Ma interval, accompanied by temperate to cool conditions, and periodic faunal signals of increasing continentality (see Section 2.3.2). On the Apennine Peninsula and in Western Europe, climatic variability created a renewed variety of habitats, producing ecological niches which new species could exploit (see Sections 2.3.3, 2.3.4). New grazers occupied the open environments, which extended periodically up to the Mediterranean coasts. The Iberian fossil record reflects the dominance of open landscapes, with occasional patches of woodland, under predominantly warm temperature conditions (see Section 2.3.5). The large mammal assemblages of this region are indicative of an Atlanto-Mediterranean climatic influence and consequent lack of intense cool intervals (see also Rodríguez et al., 2010).

During the late Early to Middle Pleistocene the large riverine systems of Europe acted as principal migration routes for species adapted to more humid conditions. *Hippopotamus* recurrently migrated from Africa via the Mediterranean Sea or the Levantine Corridor (Kahlke, 1990). Along these two migration routes, following river valleys, populations spread asynchronously into Transcaucasia and South-Eastern Europe, as well as into Central and Western Europe (Kahlke, 1987).

The fragmentary Epivillafranchian faunal record from North-Western Europe is suggestive of temperate, at least partly forested landscapes, controlled by the climatic influence of the adjacent Atlantic Ocean (see Section 2.3.6). For Central Europe, the Epivillafranchian is documented by just one site, Untermassfeld, which provided a rich large mammal record (see Section 2.3.7). This fossil assemblage reflects the environment of a pronounced warm stage at around 1.05 Ma (MIS 31), where mild and (at least seasonally, during the winter half of the year) humid conditions prevailed. A lower rate of temperature fluctuation is evidence for the extension of oceanic (Atlantic) climatic influence far into Central Europe. The wider landscape around the site was park-like in character. A river valley, interspersed with riparian landscapes and featuring diverse types of forest and open vegetation, provided habitats for ecologically more demanding mammal species.

The limited faunal record of Eastern Europe (see Section 2.3.8) indicates continuing aridification during the 1.2–0.9 Ma period. But even in this region, dominated by forest-steppe to steppe landscapes, large mammal faunas became more diversified.

3.4. *The 0.9–0.4 Ma interval*

The transition from 41 ka to 100 ka dominant cyclicity took around 300 ka. The subsequent 0.9–0.4 Ma interval, as well as the later Middle to Late Pleistocene, was characterised by longer periods of more or less stable warm and cold climatic intervals, modulated by the continuing trend of global cooling (see Raymo and Nisancioglu, 2003, Fig. 1; Lisiecki and Raymo, 2005, Fig. 4). For around 800 kyr, global environments were regulated by a clear 100 ka temperature periodicity. In the western Palaearctic, the faunal turnover that led to the early Middle Pleistocene (Galerian) large mammal communities started at the end of the Early Pleistocene – between 0.9 and 0.8 Ma. The subsequent prolonged climatic cycles caused drastic changes in the structure of mammal faunas, as well as dramatic alternation between different faunal types.

In the eastern Mediterranean and Transcaucasian regions, the Galerian faunal turnover is documented by an increased abundance of mammal species of Eurasian origin. Landscapes around 0.8 Ma varied from prevailing forested habitats to meadow-steppe environments, depending on altitude and latitude (see Section 2.4.1).

Both open and forested habitats also shaped the Galerian landscapes in Asia Minor and South-Eastern Europe (see Section 2.4.2). A milestone in western Palaearctic palaeoecological evolution is the first appearance of the cold-adapted *Mammuthus-Coelodonta* Faunal Complex (Kahlke, 1999), also called “the mammoth fauna”, in the northern part of the Balkans. This mirrors the first spread of steppe-tundra (mammoth steppe), of Central Asian origin, far into Europe, west of the Carpathian bow and beyond (see below), during a period of pronounced cold around 0.45 Ma (MIS 12). Nevertheless, warm stages of early Middle Pleistocene age, particularly during the 0.51–0.33 Ma span, were strongly influenced by Mediterranean climate. During these temperate phases, the Balkans hosted permanently open landscapes as well as forested areas.

The herbivores that immigrated from Asian steppe environments during the 0.9–0.4 interval also reached the Apennine Peninsula (see Section 2.4.3). A general cooling gradient is indicated in this region by the spread of steppes and conifer forests. Tree cover expanded depending on temperature and precipitation. A similar trend is recorded in Western Europe (see Section 2.4.4). From 0.65 Ma onwards, the fossil record of a number of French sites indicates a sequence of climatic cycles, alternating between cool to cold, relatively arid periods, and warmer, more humid intervals. In contrast to South-Eastern and Central Europe (see below), the environmental conditions of the MIS 12 cold period prevented the spread of the Palaearctic mammoth fauna. The fossil record shows no evidence of this fauna reaching Western Europe before MIS 10. By 0.4 Ma, Western Europe was characterised by the mosaic-like landscapes of a fully developed interglacial.

From c. 0.8 Ma onward, the fossil record indicates increasing aridification also in the Iberian Peninsula (see Section 2.4.5). However, periodic temperate intervals provided a sufficient amount of humidity to sustain some forested areas. Between 0.6 and 0.3 Ma open woodland was more dominant in the landscapes, at least in the northern part of Iberia. Due to Atlanto-Mediterranean climatic influences, faunal differences between warmer and colder periods were less pronounced in the peninsula than in North-West and Central Europe. Indeed, there is no evidence of either harsh climatic conditions or extreme environments throughout the 0.9–0.4 Ma period.

The climate of North-Western Europe is influenced by its distinctive geographic situation. Due to its latitudinal position with respect to the Polar Front, it is warmed by the Gulf Stream during

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interglacials, but not during glacials when the Polar Front moves to lower latitudes. These conditions produced a very high faunal turnover between glacial and interglacial episodes, comparable to that in Central Europe. Additionally, the cyclic flooding and exposure of the North Sea and English Channel (the latter not present at all before the early Middle Pleistocene) produced an alternating barrier or land connection to the British Isles. The time span between the M/B boundary and the Anglian/Elsterian (MIS 12) glaciation in North-Western Europe is documented by a number of sites recording phases of temperate, oceanic-influenced climatic conditions characterised by high precipitation rates and low seasonality (see Section 2.4.6). These conditions led to a dominance of woodland with some open patches. The mammal assemblages of cooler phases indicate an increase in more open landscapes. Some isolated finds point to a reduced oceanic influence during glacial periods. However, not all species of the *Mammuthus-Coelodonta* fauna spread into North-Western Europe during MIS 12. The subsequent MIS 11 is documented by a series of fossil-bearing horizons that document an interglacial sequence with a varying amount of woodland and open areas.

During the same time interval the Central European record indicates climate changes similar to those of North-Western Europe. Between 0.8 and 0.5 Ma, the large mammal record from this region documents regularly alternating climatic phases, which swung between moderate and cooler climatic conditions (see Section 2.4.7). Whereas the spatio-temporal extension of steppic landscapes generally increased, pronounced warm periods also caused the development of extended woodland in this region, as recorded, for example, by data probably from MIS 17. During pronounced cold intervals of probale MIS 16 age, species of sub-Arctic to Arctic origins sporadically appeared. These represent the earliest migrations of large mammals from the circumpolar tundra zone into western Eurasia. In stark contrast, a full interglacial developed during the succeeding MIS 15, with warm summers, mild winters and extended forests. This was swiftly followed by a re-opening of the landscape. The intense and long-lasting MIS 12 cold stage caused the greatest advance of the Baltic ice sheet into the western Palaearctic, which was accompanied by the first migrations of the *Mammuthus-Coelodonta* Faunal Complex into Central Europe. The fossil record indicates that the first spread of the steppe-tundra (mammoth steppe) occurred at around 0.45 Ma, via East and South-East Europe (see above) and into the regions north of the Alps. The succeeding MIS 11 is recognised in Central Europe as one of the most distinctive interglacial periods, with extensive forests and a warm, humid climate.

The more fragmentary Eastern European faunal record of the 0.9–0.4 Ma interval (see Section 2.4.8) suggests that the climate was under strong continental influence during most of this time span. This resulted in the spatio-temporal alternation of open steppe and forest-steppe landscapes. Simultaneously with most of the other European regions, MIS 11 developed into a full interglacial period.

4. Conclusions

4.1. Evolution of habitat diversity in the western Palaearctic

During the Early and early Middle Pleistocene (2.6–0.4 Ma), the palaeoecological conditions of the western Palaearctic were principally controlled by the following key factors: (1) a widespread trend of temperature decrease, (2) the periodicity of the global temperature record, with more or less stable temperate stages, (3) the intensity of single climatic stages, (4) the temporal pattern of climatic variation, (5) geographical factors, particularly the configuration of continents and oceans; and (6) the distribution and configuration of continental water resources, especially of large river systems.

Based on the large mammal record, which was influenced by both global and regional environmental changes, four evolutionary stages of western Palaearctic habitat diversity are distinguishable.

The 2.6–1.8 Ma interval (Middle Villafranchian), which saw some pronounced cool periods, fell within the boundaries of the 41 ka dominant periodicity (Fig. 6). After the late Pliocene (Early Villafranchian) aridification of eastern and south-eastern Europe, the western Palaearctic region as a whole experienced the replacement of extensive forest areas by an alternating sequence of varied savannah-like and forested habitats. Whereas in north-western Europe the ecological differences between warmer/more humid and colder/dryer periods were less marked, the east and south-east were influenced by continental climatic conditions from central parts of the Eurasian landmass.

The 1.8–1.2 Ma stage (Late Villafranchian), which was still under a 41 ka dominant periodicity (Fig. 6), was characterised by a more or less uniform alternation of global temperatures. These stable environmental sequences led, for the first time, to clear-cut faunistic specialisations, dividing the large mammal world into assemblages of various forested habitats on the one hand, and those of open landscapes on the other. Newly-appearing species were mainly of Asian origin. In response to the clearly defined climatic cycles, extensive open savannah landscapes, alternating in space and time with tree savannahs, stretched over large areas of the western Palaearctic. Eastern, South-Eastern and South-Western Europe were dominated by open landscapes, whereas around 1.7 and 1.4 Ma, forests became more widespread in the more humid north-west of the continent.

After a long period of stable climatic alternation, the 1.2–0.9 Ma span was caracterised by less uniform climatic cyles, which varied in duration and intensity (Fig. 6). Throughout the entire western Palaearctic, the Epivillafranchian faunal turnover produced new mammal communities, which inhabited an increasing variety of habitats. Large riverine systems acted as migration routes for species requiring moist habitats. Whereas the prevailing open landscapes of Eastern and South-Eastern Europe were periodically affected by increasing continentality, North-Western, and at times also Central Europe, fell under milder, oceanic influences.

Later, during the 0.9–0.4 Ma interval, the ecological conditions of the western Palaearctic were controlled by 100 ka climatic periodicity, accompanied by a progressive drop in temperature (Fig. 6). Longer, relatively stable climatic intervals, oscillating between intense cold and warm periods, led to an extreme alternation between very different landscapes throughout most of Europe. Mammal communities grew increasingly more specialised to the various types of grassy or forested habitats in which they roamed. Despite the increasing aridity of the entire western Palaearctic, the Iberian Peninsula experienced less dramatic habitat alternations compared to Central and Eastern Europe, due to a constant Atlanto-Mediterranean influence. In North-Western Europe the proximity of the Atlantic Ocean caused high precipitation and low seasonality during phases of milder climate. However, when glaciers began to advance, this oceanic influence was reduced, and the resulting alternation of steppic and more forested habitats was comparable to that of Central Europe. Further eastward, open landscapes lasted relatively longer. The more pronounced continentality of Eastern Europe led to an alternation of open and forest-steppe habitats in this region.

Towards the end of the early Middle Pleistocene (MIS 12), modern, cold-adapted mammals made their earliest appearance in Europe. Most of the species present during this period can be traced back to ancestral forms of Early Pleistocene age, which had

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adapted either to tundra-like biomes within the periglacial areas of northern Asia and Beringia, or to central Asian steppe environments. The *Mammuthus-Coelodonta* Faunal Complex spread deep into the western Palaearctic as far as Central Europe, providing evidence for the widespread extension of uniform steppe-tundra habitats. Around 0.43 Ma (MIS 11), the situation changed dramatically as the glacial environment switched to that of a major interglacial. This led to the complete renewal of the western Palaearctic large mammal faunas, which adapted to warmer temperatures and landscapes dominated by forest.

The evolution of habitat diversity throughout the western Palaearctic during the 2.6–1.8 Ma time span was dominated by an alternation of forested habitats and savannahs. This was followed by the alternation of different types of more or less open habitats from 1.8 to 1.2 Ma. Palaeo-landscapes along river systems could show remarkable gradients in relief, humidity and vegetational character (e.g. at Dmanisi, Georgia). Thus, in many cases, the diversity of riverine habitats was significantly higher than in the immediate and broader environs (see Section 2.2). During the 1.2–0.9 Ma span, habitat variability generally increased because of irregular fluctuations in temperature and/or precipitation (see Section 2.3). The subsequent 0.9–0.4 Ma interval consisted of steadier and longer-lasting climatic cycles, with alternating open and forested phases, finally culminating in a full glacial/interglacial cycle.

Throughout the entire Early to early Middle Pleistocene, large mammal communities comprised faunal elements which indicate a marked decrease of continentality between Eastern/South-Eastern Europe on the one hand, and South-Western/North-Western Europe on the other. In North-Western Europe this is particularly apparent during the non-glacial periods (see Section 3.4). In Southern Europe, decreasing continentality was caused by Mediterranean influences which, further westwards, were supported by the effects of the Atlantic Ocean. The strongest oceanic influence is recorded in North-Western Europe. Although the global temperature drop during the 2.6–0.4 Ma time span was paralleled in the western Palaearctic by increasing seasonality, the latter was less pronounced in the regions affected by mild Atlanto-Mediterranean climatic influences.

4.2. *Ecological implications for early human dispersal*

Whereas reliable evidence for the existence of Middle Villafranchian (2.6–1.8 Ma) hominins is so far lacking from the western Palaearctic, the extensive fossil record from Dmanisi demonstrates the advance of *Homo* from Africa via the Levantine Corridor and into Transcaucasia at the onset of the Late Villafranchian, around 1.8 Ma (Vekua et al., 2002; Lordkipanidze et al., 2007). At that time, humans were able to pass through open, and especially arid, areas of the Levant and Transcaucasia by exploiting water and other available resources, in particular from river systems and their surrounding environs. At the time of writing, evidence from lithic artifacts documents the spread of hominins into the Apennine Peninsula (Arzarello et al., 2007) and southern France (Crochet et al., 2009) between 1.7 and 1.3 Ma. Beside the generally dry and open character of these regions, in both cases the accompanying faunal record also demonstrates the regular if patchy existence of humid areas. Between 1.2 and 1.1 Ma, around the onset of the climatically variable Epivillafranchian period, the first hominin occurrences are recorded by fossil and archaeological evidence from South-Western Europe (Carbonell et al., 2008), and by lithic industries from South-Eastern and Eastern Europe (Guadelli et al., 2005; Shchelinsky et al., 2010). The mammal records accompanying these finds indicate variable habitat characteristics but a general availability of water ressources. The earliest current evidence for the occupation of North-West and Central Europe is dated to 1.0–0.8 Ma (Parfitt et al., 2010) and 0.6 Ma (Wagner et al., 2010), respectively. The study of the corresponding large mammal faunas demonstrates well established interglacial conditions, with a wide variety of forested as well as some open habitats. Water resources were available year-round, and seasonality was low. However, during the cold periods of the following MIS 12, hominins hardly survived north of the Alps. Human cultures adapated to glacial environments have only been recorded, in this region, from the late Middle Pleistocene onwards (e.g. Schäfer et al., 2003).

To summarise, when plotted against the pattern of indisputable fossil and/or archaeological evidence, the data obtained on western Palaearctic habitat diversity inferred from large mammal communities indicate the following clear environmental stimuli for the earliest human dispersals in Europe:

(1) A high diversity of habitats, implying a high diversity of resources, supported hominin expansion, as it would have been advantageous to utilize as many natural resources as possible. This strategy would have avoided dependency on special environmental conditions, and offered opportunities for parallel use, combination, or substitution, of resources.
(2) Mild climates with low seasonality, implying a lack of strong environmental fluctuations, also supported hominin dispersal. More stable environmental conditions would have permitted the low-risk application of proved subsistence strategies, rather than the need to develop new ones.

Based on these assumptions, a preliminary sketch of western Palaearctic Early to early Middle Pleistocene hominin dispersal, in relation to the dominant environmental conditions, can be traced (Fig. 6). Around the onset of the Late Villafranchian, at the latest, humans of African origin entered the western Palaearctic for the first time, taking advantage of the diversity of habitats and resources, particularly along large river systems. The subsequent westward spread, between 1.7 and 1.3 Ma, was largely restricted to areas under the influence of Mediterranean climates, with high levels of habitat variability and relatively low seasonality. From 1.2 Ma onwards, the increased environmental diversity of the Epivillafranchian period enabled the continuing colonization of Mediterranean regions. Furthermore, it opened up South-Eastern and Eastern Europe to human occupation. Nonetheless, according to available records, North-Western and Central Europe were only colonized during late Early to early Middle Pleistocene interglacials, when these regions experienced periods of low seasonality and considerable habitat diversity.

Later on, unfavourable environmental conditions forced hominin populations to withdraw from colonized areas, thus complicating the occupation history of the western Palaearctic (Dennell et al., 2010). However, improvements in hunting, gathering, and food-processing techniques, along with other abilities and cognitive capacities, provided new opportunities for subsistence and territorial expansion.

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