



## LARGE MAMMALS FAUNAL DYNAMICS IN SOUTHWESTERN EUROPE DURING THE LATE EARLY PLEISTOCENE: IMPLICATIONS FOR THE BIOCHRONOLOGICAL ASSESSMENT AND CORRELATION OF MAMMALIAN FAUNAS

Maria Rita Palombo

Dipartimento di Scienze della Terra, Sapienza Università di Roma, Rome, Italy  
Corresponding author: M.R. Palombo <[mariorita.palombo@uniroma1.it](mailto:mariorita.palombo@uniroma1.it)>

**ABSTRACT:** This research aims to investigate the large mammal faunal dynamics in SW Europe during the late Early Pleistocene. At that time, the climate forcing known as Mid-Pleistocene Revolution (MPR) induced deep, more or less gradual alterations and latitudinal displacements in European terrestrial biomes and exerted great influence on dispersal and dispersion of mammalian species. Large mammals did not generally move in multi-species waves of dispersal, rather each species changed its range depending on the suitability of environmental conditions in respect to its own environmental tolerances and ecological flexibility. Factors driving the remodelling of the range of a taxon, and time and mode of its dispersal and diffusion into SW Europe differed from species to species as from one territory to another, leading to diachronicity/asynchronicity in local first appearances/lowest local stratigraphical occurrences. As a result, correlations and biochronological assessments of local faunal assemblages may be difficult especially when firm chronological constraints are unavailable. Whether the peculiar composition of the late Early Pleistocene fauna, characterised by the persistence of some Villafranchian species and discrete new appearances of some taxa that will persist during the Middle Pleistocene, may be indicative of any high rank biochronological unit is discussed. Evidence from SW Europe suggests that the chronological range of the so-called Epivillafranchian biochronological unit (whatever its biochronological rank could be) may span from about 1.5 (i.e. Lowest local Stratigraphical Occurrence, LISO datum, of, among others, *Homo*, *Xenocyon lycaonoides*, *Canis ex gr. C. mosbachensis*, *Megantereon whitei*, advanced stenooid horses, *Praemegaceros*, *Bison*) and about 0.85 Ma (i.e. Highest local Stratigraphical Occurrence, HISO datum, of *X. lycaonoides*, *M. whitei*, *P. pardoides*). The biochronological unit would tentatively correspond from a biostratigraphical point of view to a virtual "range-zone", i.e. the hypothetical body of strata representing the known stratigraphical occurrence in W Europe of *X. lycaonoides*-*M. whitei*. Nonetheless, several factors (e.g. the confusing taxonomic treatment of some taxa, the heterogeneous consistency of the fossil record in space and time - particularly as regard the number and richness of local faunal assemblages -, taphonomical biases, and the apparent dyachronicity asynchronicity of LISO of some species that dispersed toward Western Europe during the post-Olduvai Early Villafranchian) make it difficult any attempt to "formalise" the "Epivillafranchian biochronological unit" as a European Land Mammal Age (ELMA). All in all, several lines of reasoning suggest an informal use of the term Epivillafranchian, pending a complete revision of the Villafranchian ELMA, its subdivisions and of the rank that each subdivision may actually have.

Keywords: Biochronology, Bioevents, Epivillafranchian, Large mammals, late Early Pleistocene, SW Europe

### 1. INTRODUCTION

Disentangling issues dealing with climate changes, mammal faunal dynamics and its implications for long distant correlations in the continental realm, is a challenging task due to a number of hotly debated, unanswered questions behind them (e.g. Walsh, 1998; Barnoski et al., 2003; Gingerich, 2003; van Dam, 2003; Lindsay, 2003; Prothero, 2004, 2012; Barnosky, 2005; Barnosky & Kraatz, 2007; Prideaux et al 2007; Lawler et al., 2009; Stewart, 2009; Davies et al., 2011; Badgley & Finarelli, 2013; Blois et al., 2013; Fortelius et al., 2014; Fernández et al., 2015 and references in those papers). During the evolutionary history of our planet, especially during the Cenozoic, climate changes were a recurring phenomenon (Zachos et al., 2001) and a number of sequences of ecological and evolutionary events developed on a backdrop of climatic change, both warming and cooling phases (e.g. the Oligo-Miocene so-called Grande Coupure by Stehlin, 1910), although cooling episodes generally had a major impact at the Boreal middle latitudes.

Some organisms, however, seem to have remained "the same" over thousands to perhaps millions of years in the face of environmental perturbations, highlighting that the biotic response of individuals, species and communities to climate warming and cooling events is a highly complex phenomenon. Some other organisms, especially small mammals, rapidly evolved, thus their fossil record could be an important base for the biochronological divisions and regional correlations between distant stratigraphic sequences/successions (see among others e.g. Chaline, 1972, 1987; van der Meulen, 1973; Agustí, 1986; Maul & Markova, 2007; Cuenca Bescós et al., 2010; Maul & Parfitt. S. A., 2010; Minwer-Barakat et al., 2011; Lozano-Fernández et al., 2013; Mayhew, 2013; Palmqvist et al., 2014).

The synergistic action of climate and environmental changes, biotic interactions and feedback processes undoubtedly had some effects on the physiology of organisms as well as on changes in the distribution of species and shifts of the limits of their range. During the Quaternary, in keeping with the vegetational cover and latitudinal displacement of biomes, large mammals, for

instance, more frequently reacted to climate changes by varying the limits of their range than by originating new species in loco (see e.g. Magri & Palombo, 2013; Palombo, 2015a and references therein). As a result, discrete dispersal bioevents, introducing alien species into previously existing large mammal communities, changed their structure, giving rise to new internal dynamics that led to a progressive reorganisation of mammalian faunal complexes.

This is the reason why dispersal is not only one among the fundamental processes in biogeography (crucial for understanding the evolutionary dynamics of organism distribution throughout time and across space) but also a factor to carefully consider for making feasible correlations among local faunal assemblages and fossiliferous distant stratigraphic sequences/successions.

Reconstructing and correlating chronological sequences by means of large mammal fossil record is a problematic task because the continental sedimentary record is highly discontinuous, distribution of sites in time and space is not homogenous, rare species are sparsely represented, and ghost lineages are not so uncommon due to ecological factors and/or taphonomical and sampling biases. In addition, continuous sedimentary sequences are rare and a number of local faunal assemblages lack sound chronological constraints. As a result, the known stratigraphic lowest/ highest occurrence of a taxon within a geographical area does not necessarily reflect the timing of its actual first/last appearances in time (e.g. Lindsay, 2003; Palombo, 2009 and references therein) and the diachronous appearance of a taxon may not necessarily depict its actual dispersal trajectory. Understanding time and mode of biological dispersals and their consequences is therefore of crucial interest for any chronological assessment of local faunal assemblages, as well as for correlations and identification/characterisation of biochronological units.

This research aims to investigate whether the peculiar composition of the late Early Pleistocene fauna (characterised by the persistence of some Villafranchian species and discrete new appearances of some taxa that will have persisted during the Middle Pleistocene) may be indicative or not of any high rank biochronological unit (i.e. European Land Mammal Age, ELAM).

## 2. MATERIAL AND METHODS

The database consists of taxonomically revised lists of large mammal species (with a body weight of at least 10 kg) from selected local faunal assemblages (LFAs) mainly from SW Europe. A few Western European LFAs, having a particular relevance for a better understanding of changes in the fauna structure in the post-Olduvai Early Pleistocene, were added to the analysis. The analysed LFAs range in age from about 1.6 to 0.8 Ma (V5a, V5b and G1 faunal complexes in Palombo, 2014). Besides to LFAs with a sound stratigraphic control, also isolated finds having particular taxonomical or chronological relevance were added to the analysis. The lists were compiled by revising and updating those resulting from previous studies on the Pleistocene mammals from W Europe (see e.g. Breda

et al., 2010; Lister et al., 2010; Kahlke et al., 2011; Palombo, 2014, 2015a). Lutrini were not included in the study because of the scantiness and disproportion of their fossil record in time and space across the studied region. To provide a uniform baseline for the study material, the identifications of species was based on a taxonomical uniform view even for species/specimens whose taxonomy, systematics, and identification are controversial.

## 3. DISCRETE DISPERSAL EVENTS AND LOWEST LOCAL STRATIGRAPHICAL OCCURRENCES OF LARGE MAMMALS DURING THE POST-OLDUVAI EARLY PLEISTOCENE IN SW EUROPE

In the post-Olduvai Early Pleistocene, in SW Europe discrete bioevents led to a progressive reorganisation of mammalian faunal complexes that lasted during the beginning of the Middle Pleistocene. The bioevents mainly consist of dispersals of few carnivores that either disappeared by the end of the Early Pleistocene or were still recorded in the Middle Pleistocene, and of large herbivores, most of which persisted throughout the Middle Pleistocene. A few extinctions of some among the most specialized Villafranchian species, and originations of new taxa in indigenous phyletic lineages are also recorded.

Changes in the suitability of environments and the extent of ecological barriers triggered by climate changes affected time and mode of organism dispersal (see e.g. Colbert et al., 2012; Schlosset al, 2012). During the active diffusion known as secular dispersal (which may take place so slowly that the diffusing species can undergo appreciable evolutionary change during the process), a species range can expand, contract or creep (expand in one direction while contracting in another). Sometimes organisms can move across great distances and a population of the original disperser's descendants may successful establishes at the endpoint, whereas no viable populations may be present in the crossed territories. Moreover, barriers can either prevent the range of some taxa to reach some regions or cause long delays in dispersal, slowing or hampering the spread of a taxon in some territories. All considered, occasional jump-dispersals, the slow, progressive shift of the range (including translation) and the filtering action of barriers synergistically acted during secular-dispersal, leading to the diachronous versus asynchronous local appearances/disappearances of dispersing taxa.

As a result, species-specific patterns of secular dispersal and dissimilarities in the inter- and intra-guild competition (sometimes leading to speciation and extinction events at a local scale) may cause taxonomical composition of faunal assemblages to differ at a local scale even within the same geographical region.

In SW Europe, discrete dispersal bioevents of taxa originally coming from both Asia and Africa led to a complex interplay among inter-sub-region dispersals and temporary shifts in the amplitude of the range of some species. The process, merging previously independent taxa in new palaeocommunities, triggered changes in the taxonomic and structural composition of mammalian

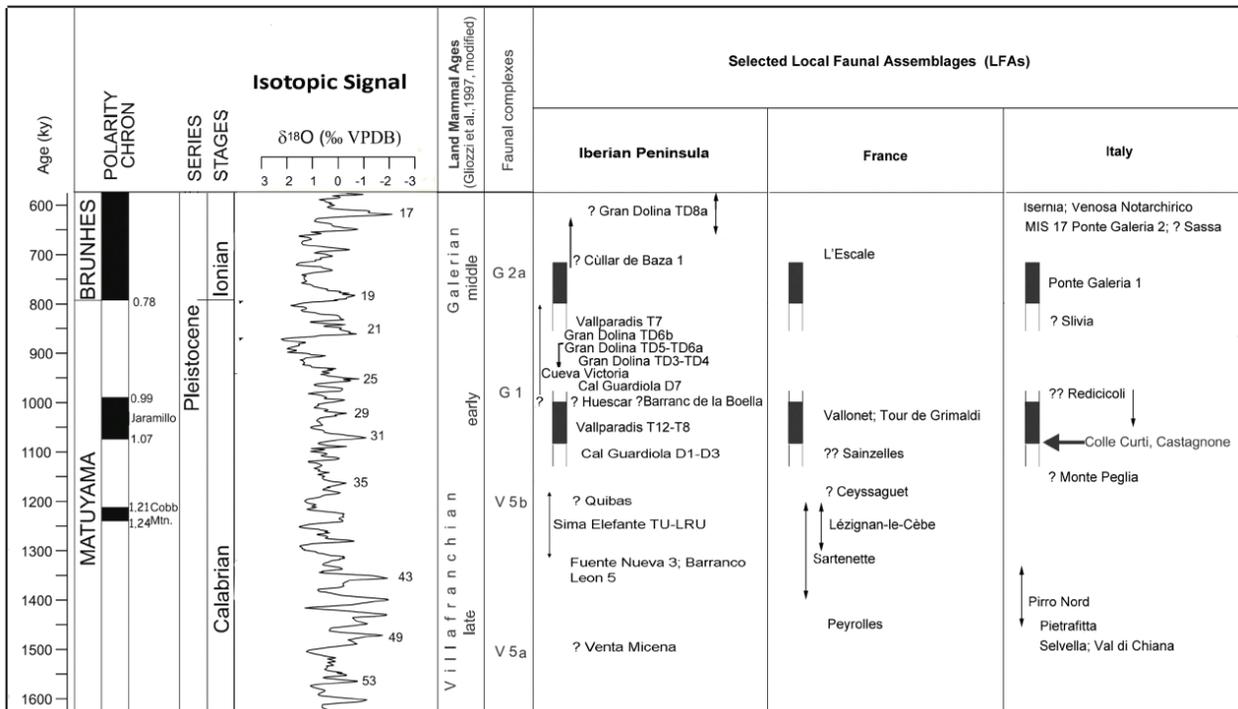


Fig. 1 - Biochronological setting and chronological scheme for the post-Olduvai Early Pleistocene mammalian record from SW Europe.

faunal complexes. Mammals having a broad niche and high ecological tolerance persisted in face of alien species invasion and environmental changes, whilst the most specialized one disappeared (Palombo, 2014, 2015a, b and references therein).

Available data indicate that during the late Early Pleistocene, the local lowest stratigraphical occurrence (LISO) of a number of large mammal species was asynchronous across most of Europe. Only a few diachronous LISO permit to follow the displacement/enlargement of the limit of the species' range throughout time (Palombo, 2015b and references therein). Several factors (e.g. the different impact of global climate changes in different geographical settings, differences in species resilience and variability in competition and predation patterns within local faunal complexes, heterogeneity of the fossil record in space and time and taphonomical biases) may have caused asynchronous appearances, though their interplaying is challenging to disentangle. As a result, the correct chronological order of LFAs and the correlation among fossiliferous stratigraphic sequences may be difficult to ascertain. Hence, the successions of SW European FCs here proposed (Fig 1) and the resulting chronological assessment of SW European LFAs can be regarded as the "best-fit" allowed by available data.

### 3.1. Major bioevents within the large carnivore guild

The European carnivore guild was progressively renewed throughout the late Early Pleistocene, though the lowest and highest stratigraphical occurrences of some species were slightly asynchronous across the

region (Fig 2).

The middle sized canid *Canis mosbachensis* (whose taxonomy and phylogenetic relationships divide scholars, see e.g. Thenius, 1954; Kurtén, 1968; Bonifay, 1971; Kurtén & Poulanos, 1977; Pons-Moyà, 1987; Palmqvist et al., 1999; Sotnikova, 2001; Olive, 2006; Brugal & Boudadi-Maligne, 2011), was recorded for the first time in the Mediterranean region about 1.5 Ma in the 'Ubeidiya LFA (Jordan Rift Valley, Israel), and may have dispersed towards SW Europe roughly in the same period. The species, indeed, is recorded at about 1.5-1.4 Ma (V5a FC) in the Iberian (Venta Micena LFA) and Italian (Pirro Nord LFA) peninsulas, together with the larger, hypercarnivorous *Lycaon*-like dog *Xenocyon lycaonoides*, which originated by anagenetic evolution from *Xenocyon falconeri*. In France the two canids are first reported later, shortly before (*C. mosbachensis*, V5b FC) and during (*X. lycaonoides*, G1 FG) the Jaramillo palaeomagnetic event respectively (cf. Martínez-Navarro & Rook, 2003; Moullé et al., 2006; Olive, 2006; Brugal & Boudadi-Maligne, 2011; Palombo, 2015a for contrasting opinions).

The African sabre-toothed cat *Megantereon whitei* possibly dispersed towards Europe shortly after the Olduvai-Matuyama paleomagnetic inversion. In Spain and Italy the species is recorded roughly at the same time at Venta Micena (Spain), Pirro Nord and Argentario promontory (Italy). *M. whitei* is reported in Greece (Apollonia 1 LFA, =*M. cultridens* in Koufos, 2014) and maybe in France (Ceyssaguet "couche 2" =*M. cultridens* in Tsoukala, 2004; Argant & Bonifay, 2011) for the first time shortly before the Jaramillo palaeomagnetic event,

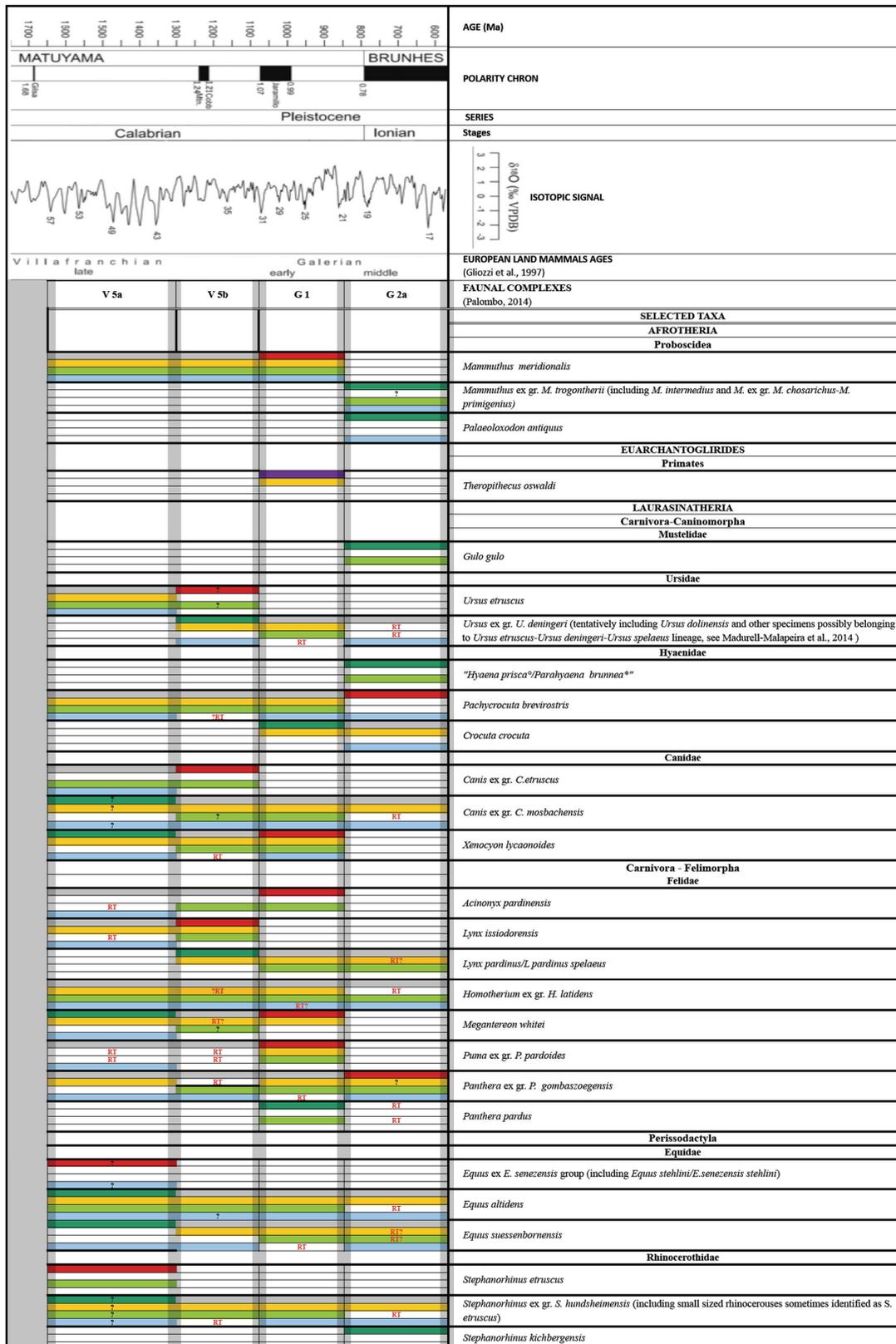
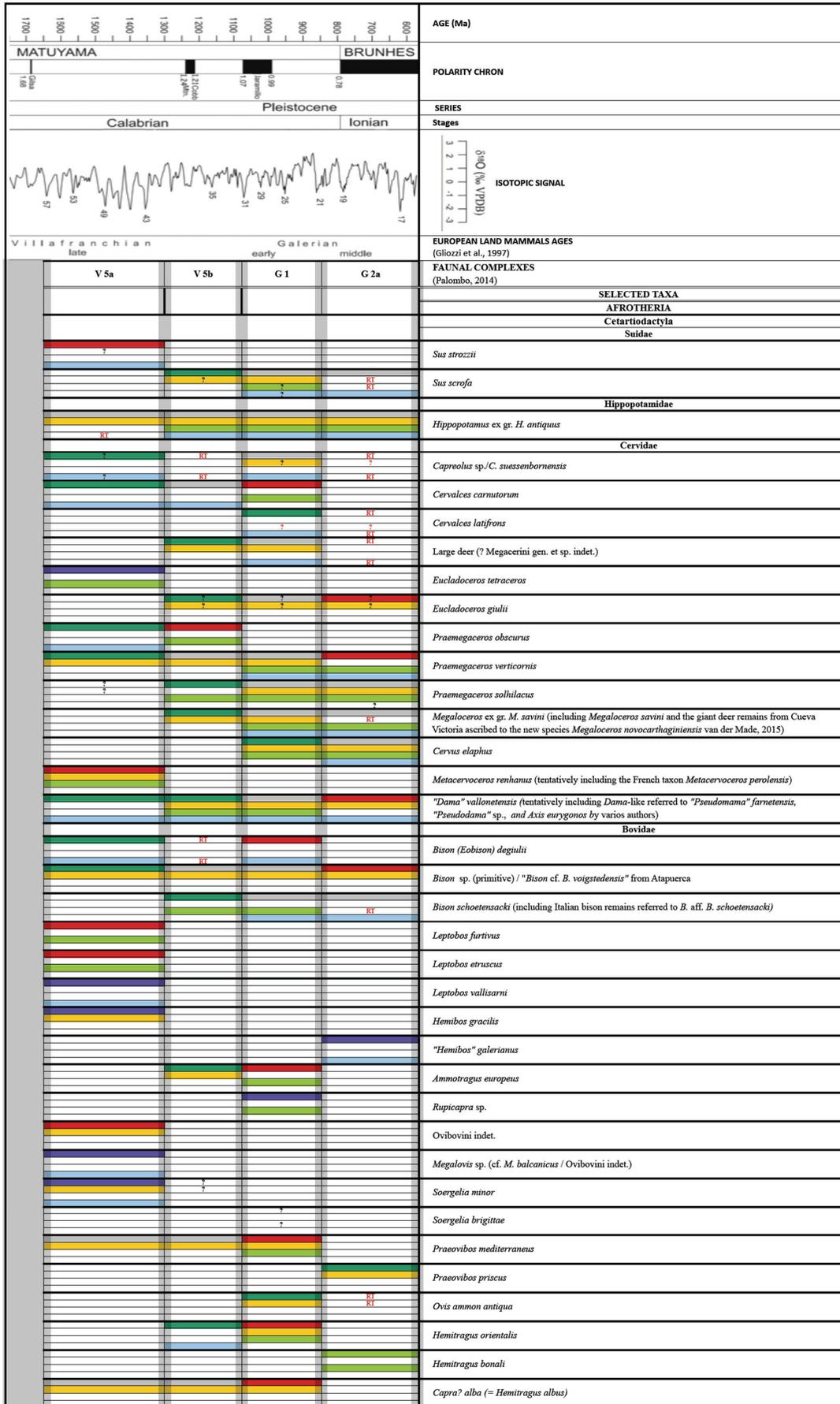


Fig. 2 - Biochronological setting of selected post-Olduvai Early Pleistocene large mammals from SW Europe (Spain =orange; France =green, Italy =bue)  
 The data on which this table is based were established by using First/Last Historical Appearance (FHA/LHA) bioevents inferred from the lowest/highest occurrences of fossil remains in fossiliferous levels of key Iberian, French and Italian localities (LSDk/HSDk =Lowest/ Highest known Stratigraphical Datum). As discussed in Palombo (2009), the lowest and highest stratigraphical records of a taxon, respectively correspond to the "terminus ante quem" and "terminus post quem" of the actual time of the origination and extinction bioevents (FHA/ LHA). Hence, new discoveries may substantially change the chronological range of taxa on which the scheme proposed here is based.  
 RT =Ranging-through taxa  
 ? =doubtful presence because of uncertain taxonomical identification and/or unsure chronological setting of finding sites



and at about 1.1 Ma in central Europe (e.g. Untermassfeld, Germany, =*M. cultridens adroveri*, Hemmer, 2001).

The time of dispersal of the leopard in Eurasia is uncertain. The species is not reported thus far in the Early Pleistocene of Asia, while its presence in Europe has been questioned due to the arguable identification of two lower carnassial teeth from Le Vallonnet, tentatively identified as *P. pardus* (De Lumley et al., 1988; Moullé et al., 2005). During the early Middle Pleistocene *P. pardus* was certainly present in Italy (e.g. Valdemino LFA, Masini & Sala, 2007), while it is doubtfully reported in the Iberian peninsula (*Panthera* sp., Sima de los Huesos LFA, see Gracia et al., 1997 for a discussion), where it was present for sure in the late Middle Pleistocene (Cueva del Congosto LFA, Palombo et al., 2009).

Remains of cheetah-like cats identified as *A. pardinensis* were reported from a number of SW European late Early Pleistocene LFAs, though they would not represent the same taxon within the *A. pardinensis* 'macrospecies'. Their presence may be related to a dispersal event (see Hemmer et al., 2008, 2011 for a discussion). The subspecies *A. pardinensis pleistocenicus*, descendant of the Asian subspecies *A. p. linxiaensis*, dispersed towards Europe during the late Early Pleistocene climatic worsening and aridification increasing. The LISO in WEurope (about 1.05 Ma at Untermassfeld, Germany, and Le Vallonnet, France) is slightly younger than that in North China (about 1.25 Ma, Qiu, 2006) (Hemmer, 2001; Hemmer et al., 2011; Kahlke, 2006; Spassov, 2011).

The spotted hyaena appeared in Europe later, by the end of the Early Pleistocene. Its LISO is at Atapuerca (Trinchera de Ferrocarril, Northern Spain) in the TD4W level of Gran Dolina (García & Arsuaga, 2001), dated to about 0.9 Ma (Berger et al., 2008). In Italy, the spotted hyaena is first recorded about 0.72–0.68 Ma BP in the Ponte Galeria 2 LFA (Roman Basin) (Palombo & Milli, 2011; Sardella & Petrucci, 2012), and a bit later in France at about 0.6–0.5 Ma BP (Grotte XIV, Cénac-et-Saint-Julien, Langlois, 2002).

Some members of the large carnivore guild, first recorded in the post-Olduvai Early Pleistocene, likely originated from lineages already present in SW Europe. For instance, the hypothesis that the remains from Le Vallonnet (1.0 Ma, France), Gran Dolina TDW4 (ca. 0.9 Ma, Northern Spain) and Vallparadís (CGRD5, EVT10, EVT7 and EVT6, ca. 1.0–0.83 Ma, Vallés-Penedés Basin, Spain) may belong to the cave bear lineage (*Ursus* ex group *U. deningeri*) cannot be discounted (Dabney et al., 2013; Madurell-Malapeira et al., 2014 and references therein).

Tempo and mode of the appearance of extant European lynxes are debated as well as the taxonomic rank of the Middle Pleistocene South European ones. *Lynx issiodorensis*, a widespread species recorded in a number of Early Pleistocene sites, is regarded by most authors as the common ancestor of the European (*Lynx pardinus* and Asian (*Lynx lynx*) lineages. *Lynx spelaeus/Lynx pardinus spelaeus* (see Boscaini, 2014 and references therein for a discussion) is first recorded in Italy at Valdemino (? MIS15, Nocchi & Sala, 1997; Ghezzi et al., 2014) and in France at L'Escale (ca. 0.6–0.5 Ma; Bonifay, 1971) and Arago Cave (ca. 0.55 Ma; MIS14;

Moigne et al., 2006). The LISO of the species, however, may date back to the late Early Pleistocene, though the identification of the scanty remains found in the French LFAS of La Sartanette and Le Vallonnet (respectively dated to about 1.3 and 1.0 Ma) is challenging.

The disappearance, i.e. the highest local stratigraphical occurrence (HISO), of some large Villafranchian carnivores was sometimes nearly contemporaneous, sometimes slightly asynchronous across the studied region. *Pachycrocuta brevirostris* is last recorded in Spain in the EVT7 layer of Vallparadís Section dated to about 0.86 Ma (Duval et al., 2015), and in Italy in the Slivia LFA, believed to be close in age to the Early to Middle Pleistocene transition (Palombo, 2009 and references therein). The species seems to have disappeared in France in the post-Jaramillo Early Pleistocene, while it is still recorded in central Europe during the early Middle Pleistocene (e.g. Süssenborn LFA, Turner & Anton, 1996). Vallparadís Estació (layer EVT7) records the HISO of the puma-like cat *P. pardoides* in Europe (Madurell-Malapeira et al., 2010b). In Italy the species is last recorded in the Pirro Nord LFA (Petrucci et al., 2013) and in France even earlier [but see Hemmer (2001) as regards to the lower carnassial teeth from Le Vallonnet discussed above].

*Panthera gombaszogensis* was the Villafranchian felid that lasted for the longest time in Europe. Its disappearance was apparently diachronous. The species is last recorded in Italy at the Early to Middle Pleistocene transition (Slivia LFA), in Spain in the earliest Middle Pleistocene (Gran Dolina TD8a LFA, Van der Made, 2013), in France in the early Middle Pleistocene (Grotte XIV LFA Cénac-et-Saint-Julien, ?MIS 15, MIS 13) (see Langlois, 2002), and finally in southern Poland in the late Middle Pleistocene (Biśnik Cave, MIS 9 or MIS 10) (Marciszak, 2014). The species was also recorded at Atapuerca in the Sima de los Huesos LFA (minimum age 427±12 ka, Arnold et al., 2014) by Morales et al. (1987), but the poor diagnostic morphology of some metatarsals, intermediate in dimension between the jaguar like cat and the leopard, prevents any firm specific identification (Gracia et al., 1997).

### 3.2. Major bioevents within the primary consumer and omnivore guilds

Changes in the guild of primary consumers recorded in the post-Olduvai Early Pleistocene consist of: i) discrete appearances of herbivores mainly dispersing into SW Europe from Asia via East Europe and Africa, ii) some originations of new species within phyletic lineages already present in SW Europe, and iii) discrete disappearances of the less ecologically flexible taxa in the face of alien species invasion and the climate instability, forerunner of the Mid-Pleistocene Revolution/Transition (MPR/T) (in its broadest definition between 1.2 and 0.5 Ma, Head & Gibbard, 2005; McClymont et al., 2013) (Fig 2).

Among bioevents believed to be related to the climate worsening and increasing in aridity, the replacement of *Leptobos* representatives (e.g. *Leptobos (Smertiobos) etruscus*) by *Bison* species, more gregarious, and adapted to open, somehow arid environment, is regarded as an important event, reflecting the climatic

and environmental change.

The LISOs of primitive, small *Bison* in SW Europe are traced between 1.6-1.2 Ma. in Spain (Venta Micena, Fuente Nueva-3, Barranco León-5 and Atapuerca Sima del Elefante TE9), and in Italy (Pirro Nord) (Martinez Navarro et al., 2011; Van der Made, 2013; Masini et al., 2013; Palombo, 2015b). In France a more advanced species, *Bison schoetensacki*, is present at the time of Jaramillo subchron (Le Vallonnet) (Moullé et al., 2006 and references therein). In the same period a primitive species, *Bison menneri*, with quite long, slender metapodials is recorded in central Europe at Untermassfeld (Germany) (Sher, 1997), together with a long-legged large deer *Eucladoceros giulii*. The latter has been regarded as the final, large stage of the *Eucladoceros* lineage in W Europe, and one among the epitomes of the "Epivillafranchian" biochronological unit (see inter alios Kahlke H-D., 1997, 2001; Croitor & Kostopoulos, 2004; Kahlke R-D., 2009).

The replacement of *Eucladoceros* representatives by giant deer belonging to the Asian tribe Megacerini has been regarded as an important component of the the post-Olduvai Early Pleistocene faunal turnover. *Eucladoceros* and large deer belonging to *Praemegaceros* and *Megaloceros* groups (or even *Avernoceos* as claimed by some authors), however, seem to have co-existed in Europe during the post-Olduvai Early Pleistocene (see inter alios Kahlke H-D., 1997, 2001; Croitor & Kostopoulos, 2004; Croitor, 2009; Van der Made & Dimitrijević, 2015 and references in those papers). Authors, for instance, are divided as the identification of the giant deer recorded at about 1.5 Ma in the Venta Micena LFA (V5a FC) [*Praemegaceros solilhacus* in Menéndez (1987) and Vislobokova, (2013); *Eucladoceros giulii* in Van der Made (1999); *Praemegaceros verticornis* in Espigares (2010)], though the hypothesis that the giant deer from Venta Micena may belong to the genus *Praemegaceros* seems to be the most parsimonious. At about that time, *Praemegaceros obscurus* is recorded in Italy in LFAs dating from about 1.5 to 1.3 Ma (e.g. Val di Chiana, Selvella, Pietrafitta, and Pirro Nord LFAs of V5a FC) (Napoleone et al., 2003; Abbazzi, 2004; Croitor, 2006; Petronio & Marcolini, 2013 and references therein). In France the LISO of *P. obscurus* is slightly younger (about 1.2 Ma, Ceyssaguet LFA) (Croitor & Bonifay, 2001 and reference therein), while the presence of the species in Spain is questionable. A part for the disputed presence at Venta Micena (see above), the appearance of *P. verticornis*, generally considered as more advanced than *P. obscurus*, was slightly asynchronous across the studied region. The species is reported shortly before the Jaramillo palaeomagnetic event (about 1.4-1.3 Ma BP) in Spain (Barranco León 5 and Fuente Nueva 3, V5b FC) (Abbazzi, 2010), and during the Jaramillo submagnetochron in Italy (Colle Curti, Coltorti et al., 1998) and possibly in France (Saint Prest, Guérin et al., 2003; Vislobokova, 2013, but see Bonifay, 1981; Geraads, 1990; Lister, 1993 for contrasting opinions). Giant deer of the *Megaloceros* lineage appeared shortly after the *Praemegaceros* ones. A giant deer showing some similarities with *Megaloceros savini* may be present about 1.2 Ma in Greece (Libakos LFA) and in Northern Spain

(Sima del Elefante LFA, Atapuerca) (cf. Van der Made & Tong, 2008). The species is identified roughly at the same time at (Cal Guardiola Layer CGRD2(Terrassa, Catalonia) (Madurell-Malapeira et al., 2015). Specimens identifiable as or closely relate to *M. savini* (i.e. in Spain *Megaloceros novocarthaginiensis* from Cueva Victoria, Van der Made, 2015) were present from the Jaramillo time to the transition to the Middle Pleistocene in Spain, France and Italy, while the species became more common during the early Middle Pleistocene (see e.g. Vislobokova 2011, 2013 and references therein).

A further evidence of the progressive, environmental related modifications of the first consumer guild across SW Europe is given by the roughly synchronous appearance of the slender, middle-sized *Equus altidens* (whatever related to in loco origination or a dispersal from Asia, see Alberdi and Palombo, 2013 and van der Made, 2013 for a discussion), and the slightly asynchronous LISO of the larger *Equus suessenbornensis*. *E. altidens* is recorded, for instance, at about 1.5-1.4 Ma in Spain (Venta Micena LFA) and Italy (Selvella and Pirro Nord LFAs). The species was possibly present in France (Lézignan-le-Cèbe LFA) slightly later, between 1.3 and 1.1 Ma (Lézignan-le-Cèbe LFA) (Bourguignon et al., 2014, 2015). *E. suessenbornensis* is recorded firstly in Italy (Selvella and Pirro Nord), then in Spain (Barranco León 5 and Fuente Nueva 3) and maybe even later in France (Lézignan-le-Cèbe and possibly Le Vallonnet) (Alberdi, 2010; Alberdi and Palombo, 2013; Bourguignon et al., 2015). During the Jaramillo submagnetochron, a horse, *Equus wuesti*, slender but quite larger than *E. altidens*, is recorded in Germany in the Untermassfeld LFA (Musil, 2001). A horse, similar in size to *E. altidens*, but more robust, with wider distal articular surface and stronger keels (*Equus apolloniensis*) was present roughly at the same time in Greece at Apollonia (1.2 to 0.9 Ma) (Koufos et al., 1997; Spassov, 2003), and possibly in the slightly older site of Tsiotra Vryssi (Konidaris et al., 2015). The exact taxonomical position of *E. wuesti* and *E. apolloniensis*, the later believed to show some ass characters (Eisenmann & Kuznetsova, 2004), is controversial, although the hypothesis that they represent different local ecomorphotypes (maybe species?) of the same lineage seems quite reasonable.

During the MPR, and consistently with the spread of open environments in SW Europe, a number of Caprini representatives (subtribe Caprina and Ovisovina sensu Ropiquet & Hassanin, 2005; Hassanin, & Ropiquet, 2009) were recorded, whatever their appearance was related to an intraregional dispersal or they came from Eastern Europe. Among others, *Praeovibos*, already reported at the latest Gelasian-Early Calabrian transition from the Fonelas LFA (Guadix- Baza basin, Spain) (Arribas et al., 2009) and in the Caucasus at Dmanisi (Crégut-Bonnoure, 2007) (=Ovisovini indet. in Buksianidze, 2005), is recorded shortly after the Olduvai/Matuyama palaeomagnetic inversion first in Italy (Casa Frata LFA, V4 FC) (Masini et al., 2013) and then in Spain (Venta Micena and Barranco de los Conejos, V5a FC) (Crégut-Bonnoure, 2007). *P. mediterraneus* is reported around the time of Jaramillo palaeomagnetic event also in France (e.g. Le Vallonnet) and Greece (Apollonia 1) (Crégut-Bonnoure, 2002, 2007).

The “steppe goat” *Soergelia minor* is recorded for the first time in Spain (Venta Micena) and Italy (Monte Argentario) (Martinez Navarro et al., 2012). Whether the geographical distribution range of the more advanced species *Soergelia brigittae* included or not the most of the Mediterranean region (at least from France to Greece, where the species is recorded in the Apollonia 1 LFA, Kostopoulos, 1997) is a matter of debate, due to the contrasting identification of the Caprini remains found at Le Vallonnet and Tour de Grimaldi (see Crégut-Bonnoure 2005; 2007; Crégut-Bonnoure & Dimitrijevic, 2006; Van der Made, 2013 for a discussion). The remains were ascribed by Moullé et al. (2004) to a new species, *Ammotragus europeus*, which was also identified in Spain, at Fuente Nueva 3 (Guadiz-Baza Basin). The presence in Spain in the pre-Jaramillo Early Pleistocene of a bovid closely related to the extant Barbary sheep *Ammotragus levia* poses a question about the alleged dispersal from Africa to Europe of the Barbary sheep as well as the origin of the extant species, seen as endemic of Africa (cf. Geraads, 2010).

Authors also disagree on the identification of Ovirovina remains from Pirro Nord, identified as “Ovibovini” indet. by De Giuli et al. (1987) and as *Megalovis* cf. *M. balcanicus* by Crégut-Bonnoure & Dimitrijevic (2006). Although some affinities with *Megalovis* cannot be discarded, the orientation of horn cores of an unpublished, badly preserved skull and the rather low hypsodonty index of molars make problematic any firm identification of the Ovirovina remains from Pirro Nord (cf. Masini et al., 2013 for a discussion).

There are also some divergences about the identification of a number of European Early Pleistocene Caprina remains. In particular scholars disagree about the taxonomy and systematic of thar/goat remains found in the post-Olduvai LFAs from SW European. A primitive *Capra*, may be descending from *Capra dalii* recorded at Dmanisi (Caucasus) (Bukhsianidze & Vekua, 2006), is recorded in the late Gelasian fauna of Fonelas 1 (Spain) (= *Capra betica* n. sp., Arribas and Garrido, 2008b). During the post-Olduvai Early Pleistocene, primitive Caprina remains are reported in a number of Spanish LFAs, ranging in age from about 1.5 to 0.9 Ma (V5a to G1 FC) (Venta Micena, Barranco León, Fuente Nueva, Quibas, Huéscar 1), but their systematic, taxonomy and phylogeny are controversial. Some authors consider them as belonging to a goat-like taxon “*Capra alba*”, may be descending from the Fonelas 1 goat, for others Spanish remains would belong to the genus *Hemitragus* (*H. albus*), or eventually they might belong to a clade related to *Pseudovis* or *Ammotragus* (cf. Crégut-Bonnoure, 2007 and Van der Made et al., 2008 for a discussion). These uncertainties make it difficult to ascertain whether the appearance of *Capra? alba/Hemitragus albus* related to anagenetic evolution within an endemic lineage or to any dispersal event. During the post-Olduvai Early Pleistocene *Hemitragus* is confidently recorded at Le Vallonnet (= *Hemitragus bonali* in Moullé et al., 2006; = *H. cf. H. orientalis* in Crégut-Bonnoure, 2007).

Among taxa believed to inhabit open environments, *Theropithecus*, a herbivore primate assumed to inhabit rocky environments as its extant relative *T. gelada*, is sparsely reported from few Eurasian sites. The

African baboon appeared in Asia (*T. oswaldi delsoni*) at about 1 Ma BP (Lower Boulder Conglomerate, Mirzapur, Punjab, India) (Delson 1993 and references therein), and roughly at the same time in SW Europe, where it is only recorded in the Cueva Victoria LFA (Murgia, Spain) (Gibert et al., 1995), a site dated to about 0.85 Ma (from 0.98 to 0.78 Ma) (Gibert et al., 2015). *Theropithecus* sp. has claimed to be present at ‘Ubeidiya (Israel) about 1.5 Ma (Belmaker, 2002). Assuming the identification of remains from ‘Ubeidiya as correct, it seems rational to suppose that the African Pleistocene baboon reached SW Asia about 1.5 Ma BP, and then the dispersal of small populations (maybe across poorly suitable territories) enlarged the species range towards Eurasia. Tempo and mode of such a dispersal are, however, difficult to ascertain (cf. Hughes et al., 2008). On the one hand, the alleged dispersal towards Europe by crossing the Strait of Gibraltar (cf. Ferrández-Cañadell et al., 2014) is hardly probable if not impossible (see O’Regan, 2008 for a discussion). On the other, the hypothesis that the species followed a Levantine dispersal route and would be unknown in the European intermediate areas because sub-optimal climatic and environmental conditions caused low population densities and a concomitantly extremely sparse fossil record, needs to be fully substantiated. It is worth noting, however, that some other species are recorded in one or just a couple of SW European sites [i.e. among others, the small sized buffalo from Venta Micena (Spain), which shows some similarities with the Chinese species *Hemibos gracilis*, (Martinez-Navarro et al., 2012), and the problematic remains of “*Ammotragus/Soergelia*” mentioned above]. Therefore, it is conceivable that the scattered distribution of some species depends on taphonomic factors and on the disparity of the fossil record during time and across space in the studied region.

The long-term cooling trend and the environmental instability that intensified from about 1.2 Ma possibly facilitated the expansion towards SW Europe of the limits of the range of some generalist, ecologically flexible species. Among others, suids belonging to the so-called “scrofic group” dispersed towards W Europe shortly before the Jaramillo subchron. Suids likely different from the Villafranchian *Sus strozzi* [a species reported for the last time at about 1.5 Ma in Val di Chiana (Italy) (Palombo et al. 2003; Napoleone et al., 2003)], is recorded at about 1.2 Ma in the layer TE9 of Sima del Elefante (Atapuerca, Northern Spain) (= *Sus* sp. in Carbonell et al., 2008; *Sus* gr. *scrofa* in Martinez-Navarro et al., 2015). Primitive, large wild boars were present shortly later (1.1 to 1.0 Ma) in Germany (Untermassfeld) (*Sus scrofa priscus*, Guérin & Faure, 1997), in France (Le Vallonnet) (*Sus* sp. in Moullé et al., 2006) and Spain (Vallparadis Estació layer EVT12 = *Sus scrofa priscus*, Madurell-Malapeira et al., 2010; Gran Dolina TD6B = *Sus scrofa*, Van der Made, 1998) (cf. Palombo, 2015a and references therein).

Elaphine cervids were likely present around the Jaramillo submagnetochron in France at Saint Prest (Grossouvre et Stehlin, 1912; Guérin et al., 2003) (= *Cervus elaphus acoronatus* in Di Stefano & Petronio,

1992), and in Spain at Barranc de la Boella (about 1.0 Ma) (Mosquera et al., 2015). Red deer lacking at the top of the antler even in adult individuals a multi-pointed “crown”, *Cervus elaphus acoronatus*, appeared by the end of the Early Pleistocene in Spain (Atapuerca, Gran Dolina TD6 and TDW4) (Van der Made, 1999) and Italy (Slivia) (a LFA estimated to be older than the Matuyama-Brunhes boundary (Bon et al., 1992; Gliozzi et al., 1997; Palombo et al., 2003; Sala & Masini, 2007). Red deer representatives are also recorded in Germany (Dorn-Dürkheim) (Franzen et al., 2000) and in the Levantine Corridor (*Cervus* cf. *C. elaphus*, Geshel Benot Ya’akov) (Hooijer, 1959). The achievement of a so large geographical range confirms the ecological flexibility of this “generalist” species, a mixed-feeders, inhabiting a variety of environments, even though red deer prefer open woodlands.

The major bioevent in the primary consumer guild recorded at the transition from the Early to Middle Pleistocene is the arrival in SW Europe of two Elephantini (*Palaeoloxodon antiquus* and *Mammuthus trogontherii*). An isolated but well-preserved molar found at Slivia (Istria, NE Italy) may document the first appearance of straight-tusked elephants in SW Europe (Palombo, 1995; Palombo & Ferretti, 2005). *Palaeoloxodon* likely reached Europe from Africa during the latest Early Pleistocene, following a dispersal route along the Levantine corridor and maybe the Balkanic coasts (see Palombo 2015a for a discussion). Timing and mode of the replacement of *M. meridionalis* by *M. trogontherii* in Europe during the Early to Middle Pleistocene transition actually depict a complex scenario susceptible to be differently interpreted (e.g. cladogenic evolution, hybridization) (see Lister et al., 2005 for a discussion).

Although a few species mostly inhabiting forest also appeared in the late Early Pleistocene [e.g. *Capreolus* representatives recorded in Germany (Untermassfeld) (Kahlke, 1997), Italy (Castagnone), (Siori and Sala, 2007), and Spain (Villaluenga del Rosario- El Chaparral) (Pacheco et al., 2011)], the progressive taxonomical and functional change of the herbivore/omnivore guild during the post-Olduvai Early Pleistocene was mainly related to the spread of open landscapes. The synergistic action of cooling, decrease in humidity, the combined effects of forest reduction and grassland extent allowed some large mammals (commonly inhabiting grassland/savannah-like or even mountain environments), to enlarge the limits of their

range into the SW European region, though at difference pace and time.

#### 4. THE BIOCHRONOLOGICAL SIGNIFICANCE OF THE PROGRESSIVE MODIFICATION OF THE MAMMALIAN FAUNA AT THE LATE EARLY TO EARLY MIDDLE PLEISTOCENE TRANSITION IN SW EUROPE

The discrete, sometimes diachronous/asynchronous appearance of a number of large mammals recorded in SW Europe during the post-Olduvai Early Pleistocene results from the complex interplay among a few anagenetic evolutionary processes within indigenous phyletic lineages, discrete dispersal bio-events of taxa originally coming from Asia and Africa, and shifts in the amplitude of the range of some SW European species that triggered intra-regional dispersals (Palombo, 2015a). The filtering effects of ecological and physical barriers, the structure of palaeocommunities, and the resilience of resident mammals may have played a critical role in regulating the pace of the appearances of each taxon in each area. The resident most flexible taxa persisted in face of alien species invasion and environmental changes, while the most specialized disappeared, some others were apparently present either in only one locality or within a small geographical area. As a result, the competition/coevolution dynamics and the taxonomical and structural composition of mammalian palaeocommunities changed at a different pace across the studied region. The difference in time and entity of dispersal events and related phenomena (upset of palaeocommunity internal equilibrium, keystone species extirpation, new inter-guild and intra-guild dynamics) at a local scale became more and more evident across the SW European region at the beginning and during the MPR. It is well known that the transition from the Early to Middle Pleistocene marks a fundamental change in the Earth’s climate system (Maslin & Ridgwell, 2005). From about 1.2 to 0.8 Ma, fluctuations in  $\delta^{18}\text{O}$  values significantly increased (Lisiecki & Raymo, 2005) and orbital obliquity at 41-ka cycles was superseded progressively by a rhythm of about 100 ka (Berger & Jansen, 1994). The amplitude of climatic oscillations significantly increased. Glacial-interglacial cycles acquired a more and more marked asymmetric structure (slow ice build-up, fast melting) thought to be associated

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Fig. 3 - Chronological assessment and faunal list of selected local faunal assemblages (LFAs) ranging in age from about 1.5 to 0.7 Ma.

? = doubtful presence; (?) = highly questionable identification; X? = doubtful identification; X(?) = identification possibly correct, although based on weak morphological/biometrical characters; X<sup>^</sup> = ew bones identified as *Hemitragus* by Van der Made (2013), whereas according to Crégut-Bonnoure (2007) they belong partim to *Hemitragus*, partim to *Soergelia* genus; (?\*) and (X?\*) = large deer identified as *P. verticornis* and *E. giulii* by Guérin et al. (2003) and Lister (fide Breda & Marchetti, 2005) respectively.

Locality, colour of the name: orange = Spain, green = France, Blue = Italy; black = West Europe.

Green square = Lowest local Stratigraphical Occurrence; Gray square = Lowest/Highest local Stratigraphical Occurrence.

<sup>(1)</sup> The group includes *Ursus dolinensis*, *Ursus rodei* and other specimens possibly belonging to *Ursus deningeri-Ursus spelaeus* lineage (see Madurell-Malapeira et al., 2014); <sup>(2)</sup> The group includes specimens identified as *Lynx pardinus spelaeus* and *Lynx spelaeus*; <sup>(3)</sup> including specimens identified as *M. cultridens adoveri* (Hemmer, 2001) and *Megantereon* “advanced form” (Sardella, 1998); <sup>(4)</sup> the identification of specimens from Pirro Nord, already identified as “Ovibovini indet.” (De Giuli et al., 1987) has been questioned by Masini et al. (2013).

Faunal complexes	V5a	?	?	V5b	G1
<b>Selected local Faunal assemblages (LFAs)</b>	<p>c. 1.5 Ma (Napoliene et al., 2003)</p> <p>c. 1.5 Ma (Napoliene et al., 2003)</p> <p>1.469 Ma +/- 12 ka (Lo Bello, 1988; Valli et al., 2006; Nomade et al., 2014)</p> <p>7-15 (referred age, various authors)</p> <p>c. 1.35 Ma (Napoliene et al., 2003), older than Pirro Nord LFA (e.g. Misini and Sala, 2007)</p> <p>7 post-Olivoli/pre-Jaramillo Early Pleistocene (Jorri et al., 2014)</p> <p>1.5-1.4 Ma (referred age, various authors), 1.3 Ma (Napoliene et al., 2003)</p> <p>1.4-1.5 Ma (Thouveny and Bonley, 1994)</p> <p>1.57 Ma (Coccheri et al., 2009); 1.3-1.1 Ma (Bourjalgon et al., 2014, 2013)</p> <p>&lt;0.87 Ma (Rama et al., 1998); 1.4, 1.3 Ma (Thouveny and Bonley, 1994); 1.3 Ma (Meon et al., 2019)</p> <p>c. 1.3 Ma (Dove et al., 2011a, 2012)</p> <p>c. 1.3 Ma (Dove et al., 2011a, 2012); 71.50 ± 0.31 (Arauz et al., 2015)</p> <p>1.4 - 1.1 Ma (Berger et al., 2009)</p> <p>7-12 Ma (Bonley, 1991)</p> <p>1.3-1.0 Ma (Montoya et al., 2003)</p> <p>c. 1.2-1.1 Ma (Jalabert-Magagnoli et al., 2018)</p> <p>Pre-Jaramillo (see Cuencia Bascos et al., 2011)</p> <p>Jaramillo (see Lumley et al., 1989)</p> <p>similar in age to Vallonet (Meulif et al., 2006)</p> <p>Jaramillo (Guerrin et al., 2003)</p> <p>Jaramillo (Gabor et al., 1986)</p> <p>1.1 +/- 0.12 Ma (Monce et al., 2013)</p> <p>Jaramillo (Bor and Sala, 2007)</p>				
<b>SELECTED TAXA</b>					
<b>AFROTHERIA</b>					
<b>Proboscidea</b>					
Elephantini indet.					
<i>Mammuthus meridionalis</i>	X	X			
<i>Mammuthus</i> sp.					
<i>Mammuthus</i> ex gr. <i>M. trogontherii</i>					
<i>Palaeoaloxodon antiquus</i>					
<b>EUARCHONTOGLIRES</b>					
<b>Primates</b>					
<i>Homo</i> sp.				X	
<i>Homo antecessor</i>					
<i>Homo heidelbergensis</i>					
<i>Macaca sylvanus florentinus</i>	X				
<i>Macaca sylvanus sylvanus</i>					
<i>Theropithecus oswaldi</i>					
<b>LAURASIATHERIA</b>					
<b>Carnivora-Caniformia</b>					
<b>Mustelidae</b>					
<i>Gulo gulo</i>					
<b>Ursidae</b>					
<i>Ursus etruscus</i>	X				
<i>Ursus</i> ex gr. <i>U. deningeri</i> (1)					
<b>Hyacnidae</b>					
Hyacnidae indet.					
<i>Hyaina prisca/Parahyaina brunnea</i>					
<i>Pachycrocuta brevirostris</i>					
<i>Crocuta crocuta</i>					
<b>Canidae</b>					
<i>Vulpes</i> sp.					
<i>Vulpes alpecooides</i>					
<i>Vulpes praeglacialis</i>					
<i>Canis</i> sp. (? <i>C. mosbachensis</i> )					
<i>Canis</i> ex gr. <i>C. etruscus</i>	X	X			
<i>Canis</i> ex gr. <i>C. mosbachensis</i>					
<i>Canis pristinus</i>					
<i>Xenocyon lycaonoides</i>					
<b>Carnivora - Feliformia</b>					
<b>Felidae</b>					
Felidae indet. (middle-sized)					
<i>Acononyx pardinensis</i>					
<i>Felis</i> sp.					
<i>Felis silvestris lunensis</i>					
<i>Lynx</i> sp.					
<i>Lynx issiodorensis</i>		X			
<i>Lynx</i> ex gr. <i>L. pardinus</i> (2)					
<i>Hemitherium</i> ex gr. <i>H. latidens</i>	X				
<i>Megantereon whitei</i> (3)					
<i>Puma pardoides</i>					
<i>Panthera gombaszoegensis</i>					
<i>Panthera pardus</i>					
<b>LAURASIATHERIA</b>					
<b>Perissodactyla</b>					
<b>Equidae</b>					
<i>Equus</i> sp.					
<i>Equus senezensis</i> ( <i>Equus s. senezensis</i> and <i>Equus s. stehlini</i> )	X				
<i>Equus altidens</i>		X			
<i>Equus vuestali</i>					
<i>Equus suessenbornensis</i>					
<b>Rhinocerotidae</b>					
<i>Stephanorhinus etruscus</i>		X			
<i>Stephanorhinus</i> ex gr. <i>S. hundsheimensis</i>					
<i>Stephanorhinus kirchbergensis</i>					
<b>Catartiodactyla</b>					
<b>Hippopotamidae</b>					
<i>Hippopotamus</i> ex gr. <i>H. antiquus</i>					
<b>Suidae</b>					
<i>Sus</i> sp.					
<i>Sus strozzii</i>	X				
<i>Sus scrofa</i>					
<b>Cervidae</b>					
<i>Capreolus</i> sp./ <i>Capreolus cusanioides</i>					
<i>Cervalces camutorum</i>					
<i>Cervalces latifrons</i>					
<i>Eucladoceros</i> ex gr. <i>E. ctenoides</i> - <i>E. tetraceros</i>		X			
<i>Eucladoceros giulii</i>					
<i>Megacerini</i> indet.					
<i>Praemegaceros</i> sp.					
<i>Praemegaceros obscurus</i>	X	X			
<i>Praemegaceros solihacicus</i>					
<i>Praemegaceros verticornis</i>					
<i>Praemegaceros dawkinskyi</i>					
<i>Megaloceros novocarthaginiensis</i> (? <i>M. aff. M. savini</i> )					
<i>Megaloceros savini</i>					
Cervidae indet. (middle-sized)					
<i>Cervus elaphus</i>					
<i>Cervus elaphus acoronatus</i>					
? <i>Pseudodama</i>					
<i>Pseudodama fametensis</i> ( <i>Avis eurymonos</i> )	X	X			
<i>Pseudodama</i> sp. ( <i>Avis eurymonos</i> )					
<i>Metacervoceros</i> sp.					
<i>Metacervoceros neubanus</i>					
" <i>Metacervoceros percolensis</i> "		X			
" <i>Dama</i> " <i>vallonensis</i>					
Dama-like deer? <i>Dama roberti</i>					
<b>Bovidae</b>					
Bovinae indet. (large)					
<i>Bison</i> ( <i>Eobison</i> ) <i>degliuli</i>					
<i>Bison mernerii</i>					
<i>Bison</i> sp. (primitive)		X			
<i>Bison</i> "cf. <i>B. voigtstedensis</i> "					
<i>Bison</i> sp. aff. <i>B. schoelensacki</i>					
<i>Bison schoelensacki</i>					
<i>Bison priscus</i>					
<i>Leptobos</i> sp.					
<i>Leptobos etruscus</i>					
<i>Leptobos vallissani</i>	X	X			
<i>Hemibos gracilis</i>					
" <i>Hemibos</i> " <i>galerianus</i>					
Caprini (enlarged tribe) indet.					
Caprini indet. (? aff. <i>Rupicapra</i> )					
<i>Ammotragus europaeus</i>					
" <i>Qulbovin</i> " indet.					
<i>Megalotvis</i> sp. (4)					
<i>Soergelia minor</i>					
<i>Soergelia elisabethae</i>					
<i>Præovibos mediterraneus</i>					
<i>Præovibos priscus</i>					
<i>Ovis ammon antiqua</i>					
<b>Hemitragus orientalis</b>					
<i>Hemitragus bonali</i>					
<i>Capra</i> ? <i>alba</i> (= <i>Hemitragus albus</i> )					
<i>Capra ibex</i>					



with fourth or fifth processional cycles, which have an important control on seasonality. In the course of the MPR, the response of biota was regionally different and vegetation and mammalian taxa varied with different regional timings and modes. As reported by Magri & Palombo (2013) as regard to SW Europe, from about 1.5 Ma there was a general change of both forest composition and mammalian community structure: A substantially similar vegetation dynamics were found across the studied region, (e.g. Suc and Popescu, 2005; Tzedakis et al., 2006; Leroy et al., 2011; Sadori et al., 2013; Combourieu-Nebout, et al., 2015), while the change in faunal composition and structure show significantly different trends at a local scale (Palombo 2014, 2015a, b).

The LISO/HISO of a number of taxa in selected key Early and early Middle Pleistocene European sites (Fig. 3) on the one hand confirms the diachronicity/asynchronicity of some local appearance/disappearance bioevents, on the other puts out that some taxa were present either in only one locality or in a restricted territory. The discrete appearances of species belonging to different taxonomical groups discounts any “migratory wave” model as causal factor for the faunal reorganisation at the time of the MPR, while the scattered record of some species, especially the rare ones, suggests a possible influence of the heterogeneous consistency of the fossil record and taphonomical factors in altering the original composition of each LFA, as well as the actual chronological order of the first/last local appearances.

#### 4.1 The matter of the question

Available evidence indicates that the faunal transition from the Villafranchian to the Galerian European ELMA (tentatively regarded here as encompassing the time slice from about 1.5 to 0.8 Ma during which V5a,b and G1 FCs are recorded in SW Europe, see Palombo, 2014) was not an “abrupt” phenomenon, but a quite long, progressive transformation phase, which sometimes developed in a diachronous way across the European region. A common trait of many SW European late Early Pleistocene LFAs (V5a,b and G1 FC) is their peculiar taxonomical composition, which includes both long-lasting Villafranchian taxa at their latest evolutionary stage and primitive representatives of some lineages, which will characterise the so-called typical Galerian fauna (early Middle Pleistocene, G2 FC in Palombo, 2014).

The resulting large mammal faunal complex was regarded by some scholars either as formed by a mix of Villafranchian and Galerian taxa, or the manifestation of a quite short (Bonifay, 1978; Azzaroli, 1983), thought composite ‘transitional phase’ [e.g. Azzaroli et al. (1988) stated that the “end-Villafranchian dispersal event”, chronologically close to Jaramillo, from 1.0 to 0.9 Ma, “did not take place at once”, or a much longer period of a progressive fauna modification, lasting about 0.6 Ma (Roebroeks & Kolfschoten, 1995), or even more. Agusti & Moyà-Solà (1998), for instance, discarded the concept of an “end-Villafranchian dispersal event” because in their view the dispersal phase had already started during the Olduvai submagnetochron with the arrival in Europe of Asian small and large mammals, such as *M.*

(*Allophaiomys pliocaenicus*, *Lemmus*, and “Ovibovini”). The Agusti & Moyà-Solà’s “phase” in its original meaning, however, refers to the “modernisation” shown by the classic late Villafranchian fauna (as epitomized by the Olivola+Tasso Italian Faunal Units, sensu Gliozzi et al., 1997), ranging in age from about 1.9-2.0 to 1.7-1.6 Ma.

The faunal transition from the Villafranchian to the Galerian ELMA was seen by other researchers as a “bioevent” (or a sum of bioevents) marking the end of the Villafranchian ELMA (=end-Villafranchian event, Azzaroli et al., 1988; Azzaroli, 1995; latest Villafranchian, Koufos, 2001; Final Villafranchian, Spassov 2003), or the beginning of the Galerian ELMA (Gliozzi, 1997), or also an individual high rank biochronological unit (e.g. Protogalerian, Caloi and Palombo, 1995; Epivillafranchian sensu Kahlke, 2000, 2007, 2009; Epivillafranchian sensu Bellucci et al., 2015). The proposed “event/faunal complex/biochron” as defined by scientists differ, however, each other in fauna composition and structure, chronostratigraphical meaning and temporal extent. The “latest Villafranchian”, for instance, would correspond to about the whole Calabrian stage (from ~1.8 to ~0.78 Ma), the “Final Villafranchian” would extend from about 1.6 to 1.1 Ma (Farneta and Pirro FU, sensu Gliozzi et al., 1997) (Spassov, 2003), while Caloi & Palombo (1995) introduced the term Protogalerian as a potential biochronological unit, in the context of a discussion for a reasonable biochronological arrangement for the transition from the Villafranchian to Galerian ELMA. The Italian authors discussed three hypotheses mainly based on the Italian mammal fauna: A) the beginning of the Galerian corresponds to the climate worsening of MIS 22/24, B) the transition from the Villafranchian to Galerian fauna roughly developed at the time of Matuyama-Jaramillo inversion, C) the so-called “transitional fauna” represents an individual biochronological unit, i.e. the Protogalerian, characterised by the “appearance of the “galerian forms”, persisting into the early Middle Pleistocene (as such or with their descendants)” (Caloi & Palombo, 1995, pag. 395). The Italian authors, in view of the first and last historical appearance (FHA-LHA) recorded at that time, proposed for the hypothetical Protogalerian biochronological unit three alternative definitions and temporal extensions. The Protogalerian would correspond to the time slice ranging from about 1.4 (Pietrafitta LFA, characterised by the presence of *Microtus ex gr. M. (Allophaiomys) ruffoi*, small-sized rhinoceroses and primitive megacerines) to 8.0 Ma (Slivia LFA, characterised by the presence of a number of new “Galerian” taxa, typically recorded in the early Middle Pleistocene fauna, and a significant reduction of the Villafranchian ones), or alternatively the Slivia LFA would be included in the “true” Galerian, or even the biochronological unit would have a wider temporal extension and would include the LFAs characterised by the appearance and persistence of voles belonging to the genus *Microtus (Allophaiomys)* (Caloi & Palombo, 1995, pag. 396, fig. 1).

All the terms mentioned above were rarely or not used in literature. Conversely, since the 90s the use of the term Epivillafranchian (regard as a ELMA intermediated in time and composition between the Villafranchian and Galerian ones) has more and more being increasing

in literature. At the time when Bourdier (1961) first introduced the Epivillafranchian (=Epi-Villafranchien), the meaning was, however, different. Bourdier (1961), analysing the geological and palaeontological context of the Quaternary deposits of the Rhône Basin, informally revised the quadripartite subdivision of the Villafranchian as introduced by Viret (1954) for the French faunas (Villafranchien ancien; Villafranchien normal inférieur; Villafranchien normal supérieur and Villafranchien supérieur). The Viret's subdivision was successively simplified, and the resulting Villafranchian three partition (early, middle and late Villafranchian) is widely used by scientists even today, although meaning and temporal extension attributed by authors to each lower-rank biochronological unit differ (e.g. Heintz, 1970 and Azzaroli, 1977). The Bourdier's work hypothesis was, conversely, the facto ignored. Bourdier (1961) added to Viret's partition two new subdivisions, the Proto-Villafranchian for the most archaic faunas (Piacentian in age) and the Epi-Villafranchian for some late Early Pleistocene faunas, such as the Durfort (latest Early Pleistocene, Brugal, 1994; Palombo & Valli, 2004) and Saint-Cosme LFAs.

According to Bourdier (1961), the Durfort LFA typically represents the "warm" Epi-Villafranchian (= "Post-Villafranchien inférieur" in Bourdier, 1961, tab. 1), corresponding to the "Günz-Mindel" interglacial, and regarded by some authors as roughly correlatable with the "Cromerian", by others with MIS 15. Bourdier (1961) reported from the site *Bison* (*Bos vel Bison*), an advanced *Mammuthus meridionalis* representative "with more tight lamellae, occurrence", and horses "already similar to *Equus caballus*" (see Fig 3 for an updated list). The Saint-Cosme LFA was selected to represent the "cold" Epi-Villafranchian (= "Post Villafranchien supérieur" in Bourdier, 1961, tab. 1), corresponding to the "Mindel glaciation", by some considered roughly correlatable with MIS 12. The faunal list reported by Bourdier (1961) includes "*Equus stenonis*, *Rangifer tarandus?* and semi-archaic molluscs". Whether the "cold feature" of the Saint-Cosme LFA would be confirmed by the attribution of the Saint-Cosme Formation to a glacial phase, although more recent ("recent Riss" in Bonvalot et al., 1984) is uncertain.

A reappraisal of the term Epivillafranchian is due to Kahlke (2000, 2006, 2007, 2009), who state that the taxonomical composition of the European LFAs, ranging in age from the Jaramillo submagnetochron to around the end of the Early Pleistocene, cannot be regarded as a mixture of "older" (Villafranchian) and "younger" (Galerian) elements. These LFAs belong to a "a separate chronostratigraphical unit" (Epivillafranchian ELMA), lasting from about 1, 2 to 0, 9 Ma BP.

According to the German palaeontologist, the Epivillafranchian biochronological unit is epitomized by the Untermassfeld LFA (Germany), the richest and most diversified among the late Early Pleistocene LFAs known in West European at that time (Kahlke, 2007, 2009). Accordingly, the Kahlke's Epivillafranchian biochronological unit is identified by the "*Bison menneri*-*Eucladoceros giulii*-assemblage (i.e. the association of *Bison menneri*, *Eucladoceros giulii*, *Cervus* s.l. *nestii vallonnetensis* (= *Dama vallonnetensis*), *Capreolus cuspidatus*, and *Stephanorhinus hundsheimensis*) and

accompanying faunal elements [e.g. *Alces carnutorum* (= *Cervalces carnutorum*), *Panthera onca gombazsoegensis* (= *P. gombazsoegensis*), *Acinonyx pardinensis pleistocaenicus*, *Megantereon cultridens adroveri* (= *M. witheji*), *Puma pardoides*, *Pachycrocuta brevirostris*, *Ursus* cf. *dolinensis* (= *Ursus* ex gr. *U. deningeri*), *Canis* (*Xenocyon*) *lycaonoides* (= *X. lycaonoides*), and *Canis mosbachensis*] found at the site (Fig. 3).

Whether the Epivillafranchian as defined by the Kahlke (2007, 2009) satisfies or not the characteristic informally recommended by some researches to individuate/define a LMA (see below) it is a still open issue. The question arises, indeed, as regards to the minimum requirements a biochronological unit, i.e. a LMA, has to meet.

#### 4.2. What is a Land Mammal Age? Loose definition, diverse/ambiguous applications and related issues

Biochronology, the prime conceptual method for relating biologic events to the geologic time scale, is an important concept for geochronology, but neither the biochronological principles nor the criteria required to create a biochronological unit have been discussed in any stratigraphic code. Consequently, the biochronological units, in particular LMA, still are loosely defined and diversely/ambiguously used (see Lindsay, 2003, pag 213, 220).

The LMAs' concept was first introduced in the scientific literature about 75 years ago, but no formal definitions of a LMA itself has been published to date. It is however clear that bioevents and characteristics of faunal assemblages are of primary importance in creating a LMA, while the characteristics of the rocks that produced the fossil record, though to be considered, have a secondary significance. Accordingly, a LMA has to be regarded as biochronological entities. It is worth noting, however, that the initial attempt to chronologically order the mammalian fauna (i.e. the North American Cenozoic mammals) that led to the development of LMAs (i.e. North American Land Mammal Ages, NALMAs) based on biostratigraphical principles (e.g. Osborn & Matthew, 1909).

The dawn of the LMAs' concept goes back to the first half of the last century, when a seven-member committee of the American Paleontological Society headed by H.E. Wood introduced in a report published in 1941 the "provincial ages" to chronologically order the North American Cenozoic mammal assemblages (Wood et al., 1941). The report illustrated the conclusions reached by the seven members of the committee, who had appointed in 1939 for presenting a terminology to be used by vertebrate palaeontologists, consistently with the recently published North American stratigraphic guide (Ashley et al., 1933). Wood et al. (1941) characterised each "provincial age" (i.e. a faunal association of mammals that lived during that age) by listing 1) "index fossils" restricted to that age, 2) first and last appearances of fossils appearing /disappearing during that age, and 3) the so-called "characteristic fossils" that, even known from earlier or later ages, were commonly found at the time of the "provincial age". 19 "provincial ages" were defined for the North American Cenozoic mammalian

fauna, only one referring to the Pleistocene. This implies a long persistence in time and a wide geographical extent for each unit. A wide temporal and geographical extent also characterises the “mammal horizons”/“life zones” proposed in the conceptual scheme (Life Zone concept) developed by Osborn & Matthew (1909) to chronologically order the NW America Cenozoic mammalian assemblages. Conversely to “provincial ages”, the “life zones” were based on biostratigraphical more than biochronological principles. Each life zone, indeed, was regarded as a complex of strata containing a particular assemblage of mammalian taxa. Subsequently, the “life zone” concept was differently applied and acquired a biochronological meaning (Matthew, 1924).

As highlighted by Lindsay (2003, pag. 221) “there was precedent in the historical development of NALMAs for the application of both biostratigraphical (e.g., the life zones of Osborn and Matthew, 1909) and biochronological (e.g., the faunal zones of Matthew, 1924) concepts”. This semantic and operational confusion, and the diverse, sometimes ambiguous use of the term “LMA” depend on different concurring factors. On the one hand, the unclear use of terms such as biozone, a entity related to strata, and biochron, a temporal entity originally introduced to indicate the total time represented by a biozone (Williams, 1901), and then sometimes used to indicate the time corresponding to a biochronological unit or the biochronological unit itself. On the other, the fact that the biochronology, in its attempt to define bioevents and chronologically order LFAs actually based on the fossil record available in the continental rocks. To make correlations among LFAs, and relate biochronological units to the geologic time scale, indeed, we have to refer to appearance/disappearance bioevents that are recorded in strata by biological biostratigraphical markers (sensu Lindsay, 2003, pag. 215). Biochronology, however, differs from biostratigraphy because the evolutionary patterns and biological events, which regulate over time the dynamic evolutionary processes leading to taxonomical and structural changes of mammalian fauna, are additional important factors to define any biochronological framework.

All in all, the appearance and disappearance bioevents and the biological aspect (taxonomical composition and ecological structure) that make a mammalian fauna different from earlier and later faunal complexes recorded in the same geographical area, are the main factors we have to consider to properly define a biochronological unit.

Following Tedford (1970), for instance, a biochronological unit should be regarded as non-overlapping and “ecologically adjusted groups of animals with specific geographical limits and chronologic range” (Tedford, 1970, pag. 602). Lindsay (2003, pag. 222) defined more explicitly a LMA as “a relatively short interval of geologic time that can be recognised and distinguished from earlier and later such units (in a given region or province) by a characterizing assemblage of mammals” *de facto*, and correctly, releasing any LMA by the deposits from which its characteristic taxa were derived. LMAs, therefore, have commonly been considered as biological entities (i.e. the natural associations of fossil species), because “the features of

life during LMAs are of primary concern; the features of the rocks that produced the record are of secondary concern” (Lindsay, 2003, pag. 221).

Although a LMA is, therefore, the period during which a peculiar association of mammalian taxa (usually genera according to most of authors), which differ in composition from the groups of taxa found in any other biochronological unit of the same rank, criteria to create it still remain somehow ambiguous. Moreover, given that the mean duration of a large mammal species is about 3 Ma (i.e. 3.21 Ma for larger North American Cenozoic mammals) (Prothero, 2014), it turns out that shorter the focal time slice and smaller the geographical area are, more difficult is to properly define a LMA. A bioevent, for instance, can only be inferred on the basis of the sum of known, local paleobiological data as documented by the fossil record derived from strata (e.g. Walsh, 1998; Palombo, 2009 and references therein). The actual duration of a large mammal species at large geographical scale may be obscured by analysing faunal change over geological short time in a small geographical area due to some regionalism, which in turn may depend on the local dispersal dynamics and competition. Additional drawbacks concern the number of LFAs with unclear or imprecise chronostratigraphic constrains, that may be proportionally higher at small than at large geographical scale, and the fact that an analysis performed on short geological time periods sometimes may force to considered taxa at a low taxonomical rank. This increases the problems related to the different taxonomies applied by authors (sometimes irrespectively of the phenotypic plasticity of taxa, according to which a specie/genotype can produce different phenotypes in different environments) that may mask the actual relationships among LFAs.

#### 4.3. The Epivillafranchian as a biochronological unit

In the attempt to characterise the Epivillafranchian as a ELMA following Kahlke’s definition (Kahlke, 2007, 2009), some difficulties arise. The main problem relates to the confusing/debated taxonomic treatment of a number of taxa (in particular some among those listed by Kahlke (2006, 2009) as “accompanying faunal elements”), the disagreement about their phylogeny and chronological range, and the exclusive presence at Untermaassfeld of a few species that are either only recorded at the site or also dubitatively reported from few other W European sites, and that may be taxonomically or ecologically vicariant of species commonly recorded in other European LFAs. The biochronological assessment of the potential Epivillafranchian LFAs and long distance correlations are therefore problematic, especially if firm chronological constraints are unavailable.

In recent times, the discovery of new rich late Early Pleistocene fossiliferous sites has been changing the already proposed chronological scenarios, and the term “Epivillafranchian” seems to have been acquiring a connotation of “time phase” rather than maintaining the biochronological meaning of “a peculiar association of mammalian taxa differing in composition from the groups of taxa found in any other biochronological unit of the same rank”.

Bellucci et al. (2015, pag. 87) attempted to formal-

ize the Epivillafranchian as a biochronological unit (European Land Mammal Age, ELMA) valid at a European scale by revising and integrating the definition proposed di by Kahlke (2006, 2009) “with data from other European sites to better define the faunal turnover occurred at the end of the Jaramillo Subchron”. The Italian authors defined “the Epivillafranchian ELMA” on the basis of appearance bioevents, regarded as valid at a European scale, which would mark respectively the beginning of the Epivillafranchian and Galerian ELMAs. Accordingly, the Epivillafranchian biochronological unit would chronologically extend between about 1.2 and 0.9 Ma, i.e. the time slice encompassed between the appearance of *P. verticornis* (the Galerian beginning event sensu Gliozzi et al., 1997) and *B. menneri* and the appearance of *C. crocuta* (end of Epivillafranchian and beginning of the revised Galerian) (Bellucci et al., 2015, fig. 2, pag. 87). Moreover, the authors stated that “together with the dispersal of *P. verticornis* and *B. menneri*, the beginning of the Epivillafranchian can be placed in correspondence of the diffusion of *M. savini* and *S. scrofa priscus*” (Bellucci et al., 2015, pag. 87).

There is however some uncertainty related to the chronology of bioevents selected as potential biological chronostratigraphical marks by Bellucci et al. (2015). In particular, *P. verticornis*, identified at Venta Micena by Espigares (2010), was present in the Barranco Leon 5 and Fuente Nueva 3 LFA. Barranco Leon 5 is dated to about 1.4 -1.3 Ma (Duval et al., 2012; Toro-Moyano et al., 2013), while Fuente Nueva 3 may be even older ( $1.50 \pm 0.31$  Ma in Álvarez et al., 2015). Likewise, the spotted hyaena is recorded for the first time at Atapuerca (North Spain), in the TD3-4 level of the Gran Dolina stratigraphic section, one of the most complete with terrestrial deposits recording the Early to Middle Pleistocene transition in Western Europe. The TD3-4 and TD5 levels were dated to about 0.99 and 0.94 Ma (Berger et al., 2008; Moreno-García, 2011).

In addition, the actual phylogenetic relationships of *B. menneri* (well known from the rich sample of Untermassfeld, but poorly doubtfully recorded in other sites) with the Early Pleistocene *Bison* relatives reported in Western Europe, and its actual significance as a “index fossils” are unclear. It still is an open question, for instance, whether the Untermassfeld bison was a taxon geographically restricted to the Western-central Europe, and the putative ancestor of “*Bison voigdstedensis*” [a species recorded in the Gran Dolina LFAs and dubiously reported by Cuenca-Bescós & Gracia (2007) in the Sima del Elefante LFA (TE-LRU level, ATAFU1 faunal unit)] as suggested by Van der Made (2013). Furthermore, *E. giulii* would be already present at about 1.5 in Spain at Venta Micena (Van der Made, 1999) (see discussion above) and the species is tentatively reported for from Sima del Elefante TE9-level (TE-LRU stratigraphic sequence) (Cuenca-Bescós & Gracia, 2007). The actual taxonomical identity of the deer, the identification of some remains ascribed to the species as well as its chronological range are debated, although the presence of slender giant deer during the late Early Pleistocene is undisputable.

Moreover, some Epivillafranchian taxa being part of the “*Bison menneri*- *Eucladoceros giulii*-assemblage” or

accompanying the two “index fossils” [see the definition of the Epivillafranchian ELMA proposed by Kahlke (2007, 2009) and emended by Bellucci et al. (2015)] possibly appeared before the Jaramillo submagneto-chron (e.g. scrofic suids reported from Sima del Elefante TE9, and *Megaloceros savini* recorded in the Cal Guardiola CGRD2 LFA), most were already present at about 1.5 Ma (e.g. *Ursus ex gr. U. deningeri*, *Canis ex gr. C. mosbachensis*, *M. whitei*, *Xenocyon lycaonoides*, *E. altidens*, *E. suessenbornensis*, maybe *Stephanorhinus ex gr. S. hundsheimensis*, *Praemegaceros* spp., the Italian advanced *Dama*-like deer possibly close to *D. vallonetensis*, and primitive *Bison* representatives), and some others, including long-lasting late Villafranchian taxa (i.e. *P. gombaszoegensis*), were still present during the early Middle Pleistocene (Fig. 2a-b, 3).

All things considered, available data suggest that the taxonomical composition and structure of mammalian palaeo-communities had already been changing in SW Europe about 1.5-1.3 Ma, roughly in the same time span of the first human dispersal towards Europe. The first appearance of genus *Homo*, is a bioevent of undeniable relevance to be considered in proposing any biochronological revision of the Villafranchian ELMA. Some other bioevents to take into account are the Highest local Stratigraphical Occurrence (HISO in the latest Early Pleistocene of some carnivores such as those last recorded in some Spanish LFAs. The dirk-toothed cat *Meganteron whitei* and the pack-hunting canid *Xenocyon lycaonoides* were reported for the last time in the Cueva Victoria LFA (Guadiz-Baza Basin), dated to about 0.85 (0.98-0.78) Ma (Gibert et al., 2015). The lycaon-like canis and the puma-like cat *P. pardoides* had their LISO in the post-Jaramillo Early Pleistocene EVT7 layer of Vallparadis Estació section (Catalonia, Spain) (estimated age ranging from 0.99 to about 0.83 Ma, see Fig. 2b) (Alba et al., 2008; Madurell-Malapeira et al., 2010; Duval et al., 2011b, 2015; Lozano-Fernández et al., 2015).

The evidence from SW Europe suggests that the chronological range of the so-called Epivillafranchian biochronological unit (whatever its biochronological rank could be) should span from about 1.5 Ma (LISO datum of, among others, *Homo*, *X. lycaonoides*, *C. ex gr. C. mosbachensis*, *M. whitei*, advanced stenooid horses, *Praemegaceros*, *Bison*) to about 0.85 Ma (*X. lycaonoides*, *M. whitei*, and *P. pardoides* HISO datum). In this way and from a biostratigraphical point of view the Epivillafranchian would tentatively correspond to a virtual “range-zone”, i.e. the complex of bodies of strata recording the known lower/higher stratigraphical occurrence and the presence in W Europe of *X. lycaonoides* and *M. whitei*. The appearance/disappearance of such carnivores would be regarded as biochronological events that acquire the meaning of “biological chronostratigraphical markers”, because “tied to a discrete stratigraphic sequence and related to other stratigraphic sequences and/or chronostratigraphic markers” (cf. Lindsay, 2003, pag. 215 for a discussion).

Nonetheless, several factors (e.g. the debated taxonomic treatment of some taxa, the heterogeneous consistency of the fossil record in space and time - particularly as regard the number and richness of LFAS -,

taphonomical biases, and the apparent diachronicity/asynchronicity of LISO of some species that dispersed toward Western Europe during the post-Olduvai Early Villafranchian) make it difficult any attempt to firmly define the "Epivillafranchian" as a "formal biochronological unit" (i.e. ELMA). Moreover, it should also be noted that any attempt to assign to the Epivillafranchian a ELMA rank implies a revision of the biochronological meaning and status of the sub-biochronological units into which the Villafranchian ELMA is currently subdivided. The early Villafranchian, for example, may have a stronger significance as potential ELMA than the Epivillafranchian actually has.

All in all, several lines of reasoning suggest an informal use of the term Epivillafranchian, pending a complete revision of the Villafranchian ELMA, its subdivisions and the biochronological rank each subdivision may have.

## 5. REMARKS

The structural and taxonomical changes of large mammalian palaeocommunities that led to the establishment of the so-called Epivillafranchian fauna has been regarded as linked to the early phase of the climate forcing known as Mid-Pleistocene Revolution (MIS 36 - MIS15-13). Nonetheless, an initially slight intensification in the amplitude of climatic oscillations is detectable after the quite long MIS 55 interglacial, in particular since about MIS 52, though it progressively increased successively from MIS 36 onward.

The astronomically-forced climate changes and the developing of a new global climatic regime promoted alterations and latitudinal displacements in European terrestrial biomes and was a critical factor in driving faunal turnovers, removing keystone species, exerting great influence on dispersal and dispersion of mammalian across and between continents, in turn triggering new competition-coevolution dynamics that contributed to either the extirpation of some taxa or to the appearances of others by anagenetic evolution in some phyletic lineages.

Large mammals did not generally move in multi-species waves of dispersal, rather each species changed the limits of its range depending on the suitability of environmental conditions in respect to its own environmental tolerances and ecological flexibility. Therefore, taxa answered to climate stimuli at a dissimilar pace and in a different way. Some large mammals, for instance, had already extended the limits of their range to and/or are recorded for the first time in SW Europe at about 1.5 Ma. Some others appeared shortly before or during the early Jaramillo submagnetochron, few just after the Jaramillo-Matuyama palaeomagnetic inversion, some were reported from a number of LFAs, others only from small geographical areas or in a single LFA (Fig. 2, 3). Although few diachronous appearances permit to follow the displacement/enlargement of the limit of a species' range, the majority of LISO (especially but not only that of rare species) documented in the available fossil record are asynchronous at least across the SW European region. It is a challenging task understanding which among several factors (e.g. among oth-

ers the different impact of global climate changes in different geographical settings, differences in species resilience and variability in competition and predation patterns within local faunal complexes, inadequate availability of long stratigraphical sequences, taphonomical and sampling biases) might have caused the asynchronous appearance of several taxa across W Europe in the post-Olduvai Early Pleistocene. As a result, large mammal assemblages may substantially differ in taxonomical composition at regional and local scale, making correlations problematic and the compelling definition of any biochronological unit uncertain.

Based on available data it would be suggested, as working hypothesis, that the "Epivillafranchian biochronological unit" (whatever its biochronological rank could be) should span from about 1.5 Ma (e.g. *Homo*, *X. lycaonoides*, *C. ex gr. C. mosbachensis*, *M. whitei*, advanced stenooid horses, *Praemegaceros*, *Bison*, LISO datum) and about 0.85 Ma (*X. lycaonoides*, *M. whitei*, *P. pardoides* HISO datum). Several lines of reasoning, however, recommend a great caution in formalising this biochronological unit. As said above, a number of factors hamper this attempt. To answer the question on the chronological meaning and the temporal range of the "Epivillafranchian" as well as be able to make correlations between distant sequences, the central challenges are: i) to remove disagreements about the taxonomy and phylogeny of some "Epivillafranchian taxa"; ii) to scrutinise the factors that cause the restricted geographical distribution of a few others; iii) to appraise the significance of heterogeneous consistency of the fossil record in space and time (e.g. number and richness of LFAs); iv) to remove taphonomical biases that may affect the chronological reliability of local first/last appearances especially as regard to rare species; v) to improve the chronostratigraphical constrain of various LFA and understand and eliminate some inconsistencies in absolute geochronological dating provided for others. Moreover, any attempt to properly define the biochronological rank of the "Epivillafranchian biochronological unit" cannot avoid a reappraisal of the Villafranchian ELMA and of the status and significance of its subdivisions.

All in all, available evidence seems to be still inadequate to ascertain whether the late Early Pleistocene LFAs (between 1.5/1.3 to 0.9-0.8 Ma) form or not a well-defined biochronological unit (i.e. an ecologically adjusted groups of animals with specific geographical limits and chronologic range, Tedford, 1970), and what may be its biochronological rank.

Concluding, several lines of reasoning suggest an informal use of the term Epivillafranchian, pending a complete revision of the Villafranchian ELMA, its subdivisions and the relative rank each subdivision (i.e. the Early Villafranchian comparatively to a hypothetical Epivillafranchian) may have.

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