Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): Biochronological implications and significance of the Jaramillo subchron

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ABSTRACT

No ideal method can be used alone to provide an accurate and irrefutable chronology for dating European Early Pleistocene localities. The solution lies in the combination of different, but complementary, approaches for complementing their chronological framework. In that regard, the results of the present study show that biochronology may be a useful additional tool to further refine the chronology of these localities, by providing not only relative chronological information between the sites, but also giving some important indications about a younger or older Jaramillo age.

Our study presents the revised faunal list of each Early Pleistocene levels from the localities of Gran Dolina (TD) and Sima del Elefante (TE), in Atapuerca. Both localities have very likely the richest associations of small mammal species in the Quaternary of Europe. Perhaps the most striking observation is the lack of similarities between the assemblages from each site, which can only be explained by a chronological gap between them. Although the Jaramillo subchron has not been directly identified at Atapuerca, the existing chronostratigraphical framework combined with similarities of the faunal assemblages between Gran Dolina and Vallparadís indicate with some confidence that Sima del Elefante levels are older than the Jaramillo subchron. Consequently, the Early Pleistocene levels of both Atapuerca sites TE and TD are the only sequence from Spain that allows the study of a continuous stratigraphic succession of the interval around the Jaramillo subchron in terrestrial sequences. The biostratigraphy of the Early Pleistocene from Europe, based mainly in the few isolated localities of the Olduvai—Jaramillo time interval, is reinforced by the faunal succession of the Atapuerca sites.

1. Introduction

Large scale correlations with large or small mammals for the European continent must rely upon well-dated faunas arranged in stratigraphic sequences. However, well dated Early Pleistocene faunal sequences immediately prior, synchronous, or younger than the Jaramillo magnetic reversal are scarce in Europe (Markova, 2007; Cuenca-Bescós et al., 2010a,b, 2013; Duval et al., 2011, 2012; Minwer-Barakat et al., 2011). This time range, comprised between roughly 1.2—0.9 Ma, is biochronologically characterized by the end of the Villafranchian and the beginning of the Galerian, a distinctive faunal turnover that took place during this time span in the western Palaearctic region (Kahlke et al., 2011), informally called

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Epivillafranchian. The Villafranchian Mammal Age is a biochronological unit based on large mammals covering the time interval from Late Pliocene to most of the Early Pleistocene in Europe, a concept of regular use within the scientific community of continental stratigraphers in Southern Europe. It roughly spans from around 3.5 Ma to about 1.0–1.1 Ma (Rook and Martínez-Navarro, 2010). The Cava Pirro fauna represents the last faunal unit (FU) of the Villafranchian in Italy, and has human-made, lithic industries (Arzarello et al., 2009; Petronio and Marcolini, 2013; Marcolini et al., 2013). In Spain, the end of the Villafranchian is characterized by the Atapuerca FU 1 (Cuenca-Bescós and García, 2007), notably the oldest occurrence of fossil remains of *Homo* (Carbonell et al., 2008; Toro-Moyano et al., 2013), together with the rodent association dominated by the *Allophaiomys* species *Allophaiomys lavocati* Laplana and Cuenca-Bescos 2000, from the sites of Fuente Nueva-3 and Barranco Leon-5, in Orce (Agustí and Madurell, 2003; Agustí et al., 2006, 2010), and from the TELRU levels of Sima del Elefante, in Atapuerca, (Laplana and Cuenca-Bescós, 2000; Cuenca-Bescós et al., 2010). The Jaramillo fauna from Colle Curti (Abbazzi et al., 1998; Coltorti et al., 1998), in Italy represents the first FU of the Galerian Mammal age, in which the Villafranchian mammals became extinct and some of the direct ancestors of the modern faunal elements appear (Rook and Martínez-Navarro, 2010; Petronio and Marcolini, 2013). The microfauna of the Villafranchian–Galerian boundary characterize the Biharian (Meulen, 1973; Terzea, 1994; Sala and Masini, 2007), in which the faunal turnover concurs at the end of the early Biharian: the extinction of *Ungaromys* and *Allophaiomys*. The beginning of the late Biharian is characterized by the appearance of “modern” *Microtus* in Italy and in Spain (Masini and Sala, 2007; Cuenca-Bescós et al., 2013). This turnover coincides with the transition from climate forced by the 41 ka cycles to the 100 ka periodicity of the late glacial–interglacial periods, known as the Early–Middle Pleistocene transition, or “mid-Pleistocene revolution” (Head and Gibbard, 2005). Three Early Pleistocene sequences in northern Spain may characterize this faunal turnover with microfauna; from older to younger: the Sima del Elefante and the Gran Dolina in the Sierra de Atapuerca, Burgos (Cuenca-Bescós et al., 2001, 2010, 2013; Cuenca-Bescós and García, 2007) and Vallparadís in Catalunya (Minwer-Barakat et al., 2011).

From a biostratigraphic point of view, the Early Pleistocene epoch may be ordered by stacking the species of *Allophaiomys*, usually by their first occurrence (LO) and last occurrence (HO), into biozones (the lower and upper boundaries are defined by the first and last appearance data in the stratigraphy, the LOs and HOs, that is, the lowest and highest stratigraphical occurrence in a section or local area, after Woodburne, 2006; Woodburne et al., 2009; Cuenca-Bescós et al., 2010). This biozonation is not a numerical dating method per se, as the biozones are only chronologically defined as being relatively older and younger than each other. Faunas may nevertheless be defined as being prior or posterior to a given global event. In that regard, the Jaramillo Subchron whose chronology is around 1 Ma (1.07–0.99 Ma) could be used as a chronological landmarck for Early Pleistocene faunas in Spain. The accurate dating of the evolutionary LO or HO of a species using ages calibrated by radiometric methods, interpolation between radiometrically calibrated magnetic reversals, marine isotopic stages (MIS), or astronomically tuned events, are known as first appearance data (FADs) and last appearance data (LADs). FADs and LADs are then biochronological markers. Thoughtfulness is needed, because the LO or HO of a species in a particular region may, however, be controlled by environmental factors and not correspond to its FAD or LAD because ecological and environmental changes may cause migration of a species into or out of a region, or cause marked changes in the relative abundance of the species within the region (Woodburne, 2006; Woodburne et al., 2009).

On the other hand, the microfaunal record available in Spain around Jaramillo time is perhaps one of the richest of Europe within a limited area. Several Early Pleistocene localities with a somewhat robust chronologic framework have been excavated, such as Atapuerca, Orce and Vallparadis (Cuenca-Bescós et al., 1995, 1999, 2001, 2005, 2010; Agustí and Madurell, 2003, 2010; Bischoff et al., 2007; Berger et al., 2008; Madurell-Malapeira et al., 2010; Duval et al., 2011, 2012; Minwer-Barakat et al., 2011; Falgueres et al., 2013; Toro-Moyano et al., 2013). From a biostratigraphic perspective, our purpose is to explain why the faunas from Sima del Elefante levels TE7–TE14 have the biostratigraphic characteristics of other sites dated prior to Jaramillo subchron, such as Vallparadis-Cal Guardiola D3 (Mimwer-Barakat et al., 2011) or Fuente Nueva 3, and Barranco León 5 (Duval et al., 2011, 2012; Toro-Moyano et al., 2013).

The main objective of the present work is to track the significance of the faunal turnover that characterises the end of the Early Pleistocene, and could have occurred before to the Jaramillo subchron in terrestrial sediments. To achieve this goal, we studied the composition and distribution of the small mammal assemblages of two Early Pleistocene sites from the Sierra de Atapuerca that have been continuously excavated over the last 20 years: Sima del Elefante and Gran Dolina. Results are compared to those from other sections in Spain such as Orce and Vallparadis, the latter being the only one in Spain where the Jaramillo Subchron has been unambiguously identified (e.g. Madurell-Malapeira et al., 2010). Different types of multivariate analysis on the correspondence between the stratigraphic layers and their faunal content were performed for the Atapuerca sites in order to evaluate the significance of the Jaramillo event in the fossil record of small mammals from Spain.

2. Sima del Elefante and Gran Dolina sites

Both sites consists of long stratigraphic terrestrial sequences (18–19 m) that fill the caves of the karst system from Las Torcas, formed during the Neogene/Early Pleistocene in the late Cretaceous marine limestone strata that outcrop in the Sierra de Atapuerca (Ortega et al., 2013). The caves document an almost continuous archaeological and paleontological succession that spans nearly one million years of the history of the Quaternary (Carbonell et al., 1995, 2008; Cuenca-Bescós et al., 1995, 1999, 2001, 2010; Cuenca-Bescós and García, 2007; Rodríguez et al., 2011, 2014).

Sima del Elefante is located about 500 m south of Gran Dolina (Fig. 1). Both localities are part of the “Trinchera localities of Atapuerca” within the intermediate level of the Sierra de Atapuerca karst complex (Ortega et al., 2013). Given their proximity and well-studied geomorphology, some correlations are possible and a composite stratigraphic column may be drawn, comprising Sima del Elefante lower levels (TELRU) and the Gran Dolina lower levels TD3/4–TD8, where the TELRU represent the lower part, and the Gran Dolina levels TD3/4, TD5, TD6, TD7, and TD8 represent the upper part (Berger et al., 2008; Falgueres et al., 2013; Arnold et al., 2014). This composite stratigraphic section is one of the most complete records of the Early–Middle Pleistocene transition in the terrestrial deposits of Western Europe.

2.1. Sima del Elefante site

The archaeological excavation in Sima del Elefante has revealed a 16 m thick sequence and divided into 16 lithostratigraphic units, named TE7 to TE21 from bottom to top. Sediment inputs during the Pleistocene filled the conduit Galeria Baja-Sima del Elefante, along nearly 10 m, isolating the Sima del Elefante from the rest of the gallery (Ortega et al., 2013). The archaeological and paleontological remains along Galería Baja and upper levels of Sima del Elefante (TE 19), and the lack of other entrances, suggest a direct relation

Fig. 1. Geographic situation of the Sierra de Atapuerca, Vallparadis and Guadix–Baza localities in Spain.

between this gallery and the Sima del Elefante, which could function as an occasional draining input area to the Sima de los Huesos Site, during Middle Pleistocene (Ortega et al., 2013; Arsuaga et al., 2014). Three main sedimentary phases have been identified within the sequence: the lower red unit (TELRU), the middle white unit, and the upper red unit, TEURU (Cuenca-Bescós et al., 2001, 2013; Rosas et al., 2001; Carbonell et al., 2008; Blain et al., 2010, 2011; López-García et al., 2011).

The TELRU unit ranges from the bottom of the Sima del Elefante sequence (level TE7) up to level TE14 and is characterised by an extremely rich paleontological content and a conspicuous red colour, especially in layers TE7–TE9 (see Cuenca-Bescós et al., 2001, 2013; Cuenca-Bescós and García, 2007; Blain et al., 2010). In particular, level TE9 has yielded among the oldest evidence of hominin presence in Atapuerca, documented by Mode 1 lithic artefacts, bones with cut marks in clear association with the vertebrate fossil remains, including a hominin mandible and a proximal manual phalanx (Carbonell et al., 2008; Lorenzo et al., 2015). The phase two, middle white unit, comprises levels TE15–TE17, which are lacking in archaeo-paleontological remains. Finally, the upper red unit (TEURU) is defined from levels TE18 to TE21. Similarly to the TELRU the sediment is dominated by a red colour and is rich in fossil remains as well, but the unit nevertheless differs, with Middle Pleistocene faunas and lithic artefacts, specially abundant in level TE19 (López-García et al., 2011; Arsuaga et al., 2014).

The sedimentary record has been chronologically constrained by a combination of palaeomagnetism, biochronology, and numerical dating. Paleomagnetic data revealed a reversed polarity from the stratigraphic layer TE7 at the bottom to TE16, and a normal geomagnetic polarity above from the base of TE17 (Parés et al., 2006). Based on biochronological evidence, the polarity inversion has been correlated to the Brunhes–Matuyama boundary, suggesting that the lower part of the sequence has a Matuyama age (>0.78 Ma) (see Parés et al., 2006 and Carbonell et al., 2008) for further details. Burial dating based on terrestrial cosmogenic nuclides (TCN) Al–Be measured in quartz grains yielded an age of 1.22 ± 0.16 Ma for level TE9, and 1.13 ± 0.18 Ma for level TE7 located a few meters below. These two ages are internally consistent and cannot be statistically differentiated. They are in good agreement with the Matuyama chronology of the deposits and might suggest a Pre-Jaramillo age for the deposits. Nevertheless, based on the numerical results, a post Jaramillo age is entirely plausible, given the age errors at two sigma.

Interestingly, levels TE16 and TE17 are dated recently with extended-range luminescence dating techniques (Arnold et al., 2014): level TE16 is dated between 1008 ± 77 and 804 ± 47 ka; level TE17 is dated between 936 ± 77 and 724 ± 43 ka. As the Jaramillo Subchron is constrained between 987 and 1068 ka, it seems plausible to consider level T7–TE14 older than the Jaramillo subchron. Finally, a flowstone separating TE16 (bottom) from TE17 (top), was found to have normal polarity. However, Carbonell et al. (2008) (supplementary information) did not really conclude about the meaning of such a polarity change in TE16/17 given the absence of lateral continuity and its proximity to the main polarity change a few cm above. If the authors do not entirely exclude the possibility of the presence of a normal chron such as Jaramillo Subchron (roughly 0.990–1.070 Ma) or the Cobb Mountain event (1.201–1.211 Ma), they also mention other possibilities such as a present day field overprint, or that the normal-reverse duplet could be a precursor to the Matuyama–Brunhes reversal.

From a biostratigraphic perspectives, the vertebrates of the TELRU levels represent the FU 1 of Atapuerca (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010a,b, 2013), *i.e.* the oldest FU of the Atapuerca record, which is Early Pleistocene. No further biostratigraphic subdivisions have been identified so far in the FU 1 of Atapuerca because TELRU has identical small mammal assemblages from level TE7 to level TE14 (Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013; Cuenca-Bescós et al., 2010a,b, 2013).

New fossil species have been defined from the Early Pleistocene levels of the Sima del Elefante site, *i.e.* the vole *Allophaiomys lavocati* Laplana and Cuenca-Bescós (2000), which has been used as a marker species for the Early Pleistocene in Spain (Agustí et al., 2010; Cuenca-Bescós et al., 2010; Minwer-Barakat et al., 2011; Toro-Moyano et al., 2013). In addition, the first archetypal of the water vole lineage, *Arvicola jacobaeus,* has been defined in the TELRU levels (Cuenca-Bescós et al., 2010).

2.2. *Gran Dolina site*

The Gran Dolina is well known internationally both for its exceptional Early and Middle Pleistocene fossil record and for the thousands of pieces of lithic industry that have been recovered throughout the entire stratigraphic sequence (Carbonell et al., 1995; Cuenca-Bescós et al., 1999, 2001, 2005, 2011; Cuenca-Bescós and García, 2007; Blain et al., 2010, 2012; Rodríguez et al., 2011, 2014). Gran Dolina is the largest section of Trinchera found in the intermediate level of the karst system. It is characterised by a visible sedimentary fill of about 16 m thick, where the sedimentary sequence begins with the TD1–2 level at the bottom, composed by autochthonous facies typical of a closed cave overlain by flowstone. From levels TD3–4 to level TD11, the sequence is dominated by allochthonous sedimentary facies, enclosing evidence of human occupation.

The chronology of the sedimentary record is constrained by a combination of magneto- and biostratigraphy and numerical dating. A reversal in magnetic polarity was detected within unit TD7, which was correlated to the Matuyama–Brunhes (M–B) boundary based on biochronological evidence, suggesting thus that the lower part sedimentary record is older than 0.78 Ma (Parés and Pérez-González, 1995).

Additional numerical dating based on combined U-series/ESR and Luminescence dating methods helped to refine the chronology, from TD6 to the top (Falguères et al., 1999; Berger et al., 2008; Duval et al., 2012). In particular, two series of numerical results are available for the Early Pleistocene layers at Gran Dolina. A Luminescence age of 960 ± 120 ka was obtained from TD7 just below the M–B boundary (Berger et al., 2008). Then, a weighted mean US-ESR age of 766 ± 81 ka was obtained for fossil teeth from TD6 layer enclosing the *Homo antecessor* remains (Duval et al., 2012). A new luminescence age of 831 ± 90 and 856 ± 75 ka has been recently provided for the layer TD6–3, which lies below the samples dated by Berger et al. (2008) and Duval et al. (2012). These data are consistent to indicate a younger than Jaramillo subchron chronology for layer TD6.

The microfauna from TD3/4–TD7 below the M–B boundary is Early Pleistocene; the microfauna from TD7 above the M–B boundary and TD8 is Early–Middle Pleistocene (Cuenca-Bescós et al., 1995, 1999, 2010).

New fossil species have been defined in the levels from the Early Pleistocene (TD3/4–TD6) from Gran Dolina, one new hominin, *H. antecessor* (Bermúdez de Castro et al., 1997), and two small mammals, one vole, *Microtus seseae* (Gil, 1997), and one large red-toothed shrew, *Dolinasores glyphodon*, (Rofes and Cuenca-Bescós, 2009). The stratigraphic section of Gran Dolina is one of the most complete records of the Early–Middle Pleistocene transition in the terrestrial deposits of Western Europe (Cuenca-Bescós et al., 2005, 2011; Blain et al., 2010, 2012, 2013).

3. Material and methods

The small fossil vertebrate specimens were obtained by washing and sieving the sedimentary materials acquired from the excavations of Sima del Elefante (TE) and Gran Dolina (TD). The washing–sieving processes for the recovery of the microfossil remains are simultaneous to the course of the Atapuerca campaigns, started in 1999, roughly 12–15 tonnes of sediment each field-campaign. The product is a concentrate consisting fundamentally of calcareous fragments from the cave walls, fossil remains of small vertebrates, and fragments of large vertebrates. The concentrates are packed in plastic containers duly labelled with an abbreviation indicating in order, the campaign year, the site and stratigraphic level from which they came, the excavation grid unit, the depth (Z) in cm where appropriate, (e.g. ata02te9bk29z620-630 is the label of a sample excavated during 2002, in level TE9b, square k29 and at a depth of 620–630 cm, from the level 0 of the excavation), enabling us to maintain rigorous stratigraphic and spatial control throughout. Then, the small fossil remains are extracted from these concentrates by using a hand-held or binocular magnifying glass. Afterwards, in the laboratory of the University of Zaragoza, a preliminary classification of the microfossils is undertaken, and the information recorded in the data base of the microfauna of Atapuerca (Cuenca-Bescós, Atapuerca micro DB, unpublished). The specimens studied for this paper are kept in the Palaeontology Museum of Zaragoza University.

After identification and classification of the fossils of small vertebrates, we analyse its distribution along the stratigraphic sequence. A first approach is the presence–absence of species along the stratigraphic section, and any subsequent appearances and disappearances, with which we elaborate presence–absence matrices (PAMs) of taxa throughout the stratigraphic sequence using PAST (Hammer et al., 2001). When analysing the evolution of taxonomic composition in terms of presence–absence and number of taxa (S), in the associations of fossils from each level, we can then take the next step and compare with other fossil associations from sites outside Atapuerca.

We study the layers TD3/4 up to TD8 (TD8a, or lower TD8 in earlier works, see Rodriguez et al., 2011: Table 2) from the Gran Dolina site, that comprise the FU 2, 3, and 5 (Cuenca-Bescós and García, 2007). In Sima del Elefante we study the Early Pleistocene layers TE7 up to TE14 (TELRU). TE15 and TE16, purportedly Early Pleistocene by paleomagnetism and luminescence dating, are sterile (see Cuenca-Bescós et al., 2001, 2005, 2010; Cuenca-Bescós and García, 2007).

3.1. *Abbreviations*

Institutional – MPZ, Museo Paleontológico de Zaragoza, Zaragoza, Spain.

Fieldwork labels and geographic abbreviations – Ata, Atapuerca; TD, Gran Dolina site; TE, Sima del Elefante site; TELRU, Lower Red Unit of TE comprising levels TE7 up to TE14; BLD, Barranco Leon D

(=BL5); FN3, Fuente Nueva 3, Barranco Conejos (BC), Venta Micena (VM); D, Cal Guardiola; EVT, Vallparadis; Z, depth.

Biostratigraphic abbreviations— FU, Faunal Unit; LO, lowest stratigraphical occurrence in a section; HO, highest stratigraphical occurrence in a section; FAD, first appearance data; LAD, last appearance data; PAMs, presence—absence matrices of taxa.

4. Results

The microfaunal elements stem in large measure from fossil owl pellets, scats and collection of small predators, and in lesser proportion, animals that died in the caves. Pellets and scats probably entered the cave with the sediment, and/or as direct roost products of birds and other vertebrates of prey. The studies of the small vertebrates excavated from Atapuerca during the last twenty years, has increased substantially our knowledge of the fossils record of small vertebrates of Early Pleistocene age in Spain (Table 1). The paleontological studies of Eulipotyphla (small insectivore mammals), as well as of rodents, has revealed new species as well as first discoveries in Spain (Cuenca-Bescós et al., 1995, 1999, 2010; Laplana and Cuenca-Bescós, 2000; Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013; Cuenca-Bescós and Rofes, 2007). Recent studies of other small vertebrates in the TELRU layers, such as bats, birds, amphibians, and squamate reptiles, reveals a specific richness unknown in other sites of similar age (Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013; Cuenca-Bescós and García, 2007; Carbonell et al., 2008; Blain et al., 2010; Galan et al., 2014, Nuñez-Lahuerta et al., 2014). The birds are relatively well studied in the level TD 6 of Gran Dolina (Sanchez-Marco, 1999) in contrast with Sima del Elefante TELRU. The present work fills this gap by providing the first microavifaunal list from TELRU. Table 1 shows the complete faunal list of the small vertebrates from Sima del Elefante TELRU and Gran Dolina levels TD3/4—TD8. The distribution of the species of small mammals along the stratigraphic sequences of levels TD3/4 up to TD8, levels TELRU, BLD, FN3, BC, VM, D, and EVT is shown in Table 1. This table is the data base for the PAMs.

Table 1
Presence—absence data matrix of the microfauna from the Early Pleistocene localities of Atapuerca Sima del Elefante and Gran Dolina.

	Sima del Elefante TE7—TE14 (TELRU) small vertebrates
Osteichtyes	*Salmo* sp., *Leuciscus* sp.
Anura	*Alytes obstetricans*, *Pelobates cultripes*, *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Hyla arborea*, *Rana* sp., cf. *Pelophylax* sp.
Caudata	*Salamandra salamandra*, *Triturus* cf. *Marmoratus*
Squamata	*Lacerta s.l.*, *small-sized indeterminate lacertids*, *Anguis fragilis*, *Natrix* cf. *natrix*, *Natrix* cf. *maura*, *Coronella* cf. *girondica*, *Vipera* sp.
Aves	Anseriformes indet., Falconiformes indet., Galliformes indet., Passeridae indet., *Remiz* sp., *Certhia* sp., Carduelis sp., Motacilla sp., Turdidae indet., *Turdus* sp., Corvidae indet., *Pica pica*, *Corvus monedula*, *Corvus frugileus*
Chiroptera	*Myotis* gr. *myotis/blythii*, *Miniopterus schreibersii*, *Rhinolophus ferrumequinum*, *Rhinolophus* gr. *euryale/mehelyi*, *Pipistrellus* sp., Chiroptera indet.
Eulipotyphla	*Sorex* sp.*1*, *Sorex (Drepanosorex) margaritodon*, *Asoriculus gibberodon*, *Beremendia fissidens*, *Crocidura kornfeldi*, *Galemys* cf. *kormosi*, *Talpa* cf. *europaea*, *Erinaceus* cf. *praeglacialis*
Rodentia	*Sciurus* sp., *Castillomys rivas*, *Apodemus* sp., *Eliomys* sp., *Allophaiomys lavocati*, *A. burgondiae*, *A. nutiensis*, *Arvicola jacobaeus*, *Ungaromys nanus*, *Pliomys* cf. *simplicior*, *Castor* sp.
	Gran Dolina TD3—TD8 small vertebrates
Osteichtyes	*Salmo* sp., *Leuciscus* sp.
Anura	Alytes obstetricans, Pelobates cultripes, Pelodytes punctatus, Bufo bufo, Bufo calamita, Hyla arborea, *Rana* (rousse), *Rana* cf. *ridibunda*
Caudata	*Salamandra* sp.
Squamata	*Blanus cinereus*, *Lacerta* sl., Small sized lacertids, *Anguis fragilis*, *Natrix natrix*, *Coronella austriaca*, *Rhinechis scalaris*, *Malpolon monspessulanus*, *Vipera aspis*
Aves	*Anas* sp., *Anas crecca*, *Falco naumanni*, *Perdix palaeoperdix*, *Coturnix coturnix*, *Porzana* sp., *Limosa limosa*, *Scolopax rusticola*, *Columba livia/oenas*, *Melanocorypha calandra*, *Calandrella* cf. *brachydactyla*, *Galerida cristata*, *Lullula arborea*, *Alauda arvensis*, *Eremophila alpestris*, *Hirundo rustica*, *Anthus pratensis*, *Cinclus cinclus*, *Prunella collaris*, *Prunella modularis*, *Turdus merula*, *Turdus iliacus*, *Turdus philomelos*, *Muscicapa striata*, *Emberiza citrinella*, *Fringilla coelebs*, *Sturnus* sp., *Corvus antecorax*
Chiroptera	*Myotis* sp., *Rhinolophus* sp., *Miniopterus schreibersii*
Eulipotyphla	*Dolinasorex glyphodon*, *Sorex* sp. 1, *Sorex* sp., 2, *Neomys* sp., *Crocidura* sp., *Galemys* sp., *Talpa* sp., *Erinaceus* sp.
Rodentia	*Victoriamys chalinei*, *Mimomys savini*, *Iberomys huescarensis*, *Stenocranius gregaloides*, *Terricola arvalidens*, *Microtus seseae*, *M. ratticepoides*, *Pliomys episcopalis*, *Apodemus* sp., *Micromys minutus*, *Eliomys quercinus*, *Allocricetus bursae*, *Marmota* sp., *Hystrix* sp., *Castor* sp.

5. Discussion

The stratigraphic distribution of the species of small mammals along the stratigraphic sequences of levels TD3/4 up to TD8, and levels TELRU, is shown in Fig. 2. Four main observations may be made:

(i) For the eight fossiliferous layers of TELRU, the composition of the microfaunal assemblage is stratigraphically uniform, there are no LO or HO along the section.
(ii) In comparing TELRU with TD, or the limit between FU1 and FU2, there is a clear faunal change in the microfaunal assemblages. At the top of TE14 there is the HO of 80% of the small mammal taxa from TELRU, while at the bottom of TD3/4, there is the LO of the 80% of the taxa from TD.
(iii) This conspicuous faunal turnover characterizes the upper and lower limit respectively, of FU1 and FU2 of Atapuerca (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010; Rodríguez et al., 2011).
(iv) The LO and HO of microfaunal taxa in TD, was used for the definition of the FU 2, 3, 4, 5 and 6 (Cuenca-Bescós and García, 2007). Nevertheless, the levels of TD lack the conspicuous faunal turnover as the one between FU1 and FU2, except for the limit between the FU6 and FU7, which marks the limit between the Middle Pleistocene and the Upper Pleistocene in Atapuerca.

Much information on distribution can be extracted from the PAMs of taxa throughout the stratigraphic sequences (Fig. 2, Table 2). We performed multivariate analyses of ordination for the evaluation of these differences using PAST (Hammer et al., 2001). For the Atapuerca localities the cluster analyses (CA) and the detrended correspondence analyses (DCA) (Fig. 3) clearly show the separation of the TELRU levels from the Gran Dolina levels, which are plotted separately in the CA and to the right of the scatter plot in the DCA. We analyse the TELRU levels TE7—TE14, although as they have identical faunal composition, *i.e.* no LO or HO occurs along the sequence, they are plotted in a single point. This is the reason we represent the eight levels with one label, TELRU. The analysis in Fig. 3 includes only the insectivores and rodents. Other small vertebrates from TELRU are also different from those in the Gran Dolina, as shown in Table 1.

Table 2
Presence–absence data matrix of the microfauna from the Early Pleistocene localities of Spain.

Age Ma	Guadix-Baza	Atapuerca	Catalunya	*Sorex* sp. 1	*Sorex (Drepanosorex) margaritodon*	*Sorex minutus*	*Asoriculus gibberodon*	*Beremendia fissidens*	*Dolinasorex glyphodon*	*Crocidura* sp.	*Crocidura kornfeldi*	*Galemys kormosi*	*Galemys* sp.	*T. Europaea*	*Erinaceus cf. praeglacialis*	*Erinaceus europaeus*	*Eliomys* sp.	*Hystrix* sp.	*Castor* sp.	*Marmota* sp.	*Sciurus* sp.	*Apodemus atavus*
		Gran Dolina 8								x			x	x		x	x					
		Gran Dolina 7		x		x								x			x			x		
0.78 ± 0.85		Gran Dolina 6				x			x	x			x	x		x	x	x	x	x		
		Gran Dolina 5				x			x	x				x		x	x	x		x		
		Gran Dolina 3/4				x			x	x				x		x	x			x		
			Cal Guardiola D5																			
			Vallparadis 3 (EVT 3)																			
0.83 ± 0.07			Vallparadis 7 (EVT 7)							x				x			x	x				
Jaramillo			Vallparadis 10 (EVT 10)																			
Pre-Jaramillo			Cal Guardiola D3														x					
			Cal Guardiola D2														x					
			Cal Guardiola D1															x				
			Vallparadis 12 (EVT12)														x	x				
c.a.1.4	Barranco León 5/D			x		x	x				x											
	Fuente Nueva 3						x															
		Sima del Elefante 14		x	x		x	x			x	x		x	x		x		x		x	
		Sima del Elefante 13		x	x		x	x			x	x		x	x		x		x		x	
		Sima del Elefante 12		x	x		x	x			x	x		x	x		x		x		x	
		Sima del Elefante 11		x	x		x	x			x	x		x	x		x		x		x	
		Sima del Elefante 10		x	x		x	x			x	x		x	x		x		x		x	
1.2 ± 0.16		Sima del Elefante 9		x	x		x	x			x	x		x	x		x		x		x	
		Sima del Elefante 8		x	x		x	x			x	x		x	x		x		x		x	
1.13 ± 0.16		Sima del Elefante 7		x	x		x	x			x	x		x	x		x		x		x	
	Venta Micena						x						x									
	Barranco Conejos			x		x						x					x					

Table 2 also shows the small mammal taxa present in other relevant localities of Early Pleistocene age of the Iberian Peninsula. Here, we will discuss some general aspects of relevant taxa from these localities.

During the Early Pleistocene, the presence and diversity of species that are indicators of warm and moist–humid climate, such as the red toothed shrews, *Asoriculus gibberodon*, *Beremendia fissidens*, *Sorex margaritodon*, the bats *Miniopterus schreibersii* and *R.* gr. *euryale/mehelyi,* aves such as *Carduelis,* rodents such as the *Castor* sp, the *Castillomys*, among others, may be correlated with the generally warm period prior to the Jaramillo Subchron. The Caudata, the, small penduline tit (*Remiz*), *Galemys*, *Castor*, and otters, among other vertebrates are strongly related to permanent water, in streams and/or ponds, lakes. In Spain, the primate *Macaca*, present in Atapuerca only in TELRU (Cuenca-Bescós and García, 2007) is characteristic of this time interval (although it is found in the older and younger Jaramillo levels of Vallparadis and Cal Guardiola, Minwer-Barakat et al., 2011). Some taxa from TELRU, such as *Asoriculus gibberodon*, *Castillomys*, and *Ungaromys* are "old taxa" that have their FAD at the Pliocene/Pleistocene boundary. Others, such as *Allophaiomys,* have their FAD at the beginning of the Biharian, and their LAD at the end of the late Biharian (Maul, 1990, 2001; Maul et al., 1998; Masini and Sala, 2007; Cuenca-Bescós et al., 2010a,b, 2013; Minwer-Barakat et al., 2011). The LAD of *Allophaiomys* coincides with the upper limit of the interval prior to Jaramillo as in Vallparadis (Minwer-Barakat et al., 2001; Duval et al., 2011). The pre-Jaramillo section of Vallparadis shares with TELRU the presence of *Allophaiomys lavocati* (Table 1). The Early Pleistocene levels of Gran Dolina, on the other hand, have several taxa in common with the post Jaramillo levels of Vallparadis and Cal Guardiola (D5, EVT 3, EVT 7) such as *Mimomys savini*, *Iberomys huescarensis* and *Stenocranius gregaloides* (Table 1).

In addition, the small mammal assemblage remains almost vertically unchanged along the sequence of TELRU, in other words, the fauna is the same within TE7–TE14, which suggests that the time span is relatively short. Therefore, this may support the hypothesis of rapid and discontinuous sedimentation in the site. However, the changes in the microfaunal compositions of TD reveal a longer time span for the sedimentation of the levels TD3/4–TD8. The paleoenvironmental changes along the sequence in TD may support this hypothesis (Cuenca-Bescós et al., 1995, 2005, 2011; López-Antoñanzas and Cuenca-Bescós, 2002; Blain et al., 2009); *i.e.* level TD6 with *H. antecessor* is warmer than the underlying TD5 (Blain et al., 2013).

Consequently, even if the Jaramillo subchron has not been unambiguously identified in the Atapuerca sedimentary record, the great difference in the microfaunal associations from each site strongly suggests that there is an important chronological gap between each unit. Although the available burial cosmogenic ages available for TELRU cannot help to securely conclude about the younger than-Jaramillo subchron age of the deposits given the error range at 2 sigma, some chronological evidence may nevertheless be derived from the study of the small mammal faunas. By a simple comparison with the Early Pleistocene levels

Apodemus aff. Sylvaticus	*Castillomys crusafonti*	*Castillomys rivas*	*Micromys minutus*	*Allocricetus* sp.	*Mimomys* sp.	*Mimomys oswaldoreigi*	*Mimomys savini*	*Pliomys cf. simplicior*	*Pliomys episcopalis*	*Tibericola vandermeuleni*	*Allophaiomys pliocaenicus*	*Allophaiomys ruffoi*	*Allophaiomys lavocati*	*Allophaiomys burgondiae*	*Allophaiomys nutiensis*	*Ungaromys* sp.	*Victoriamys chalinei*	*Microtus seseae*	*Microtus ratticepoides*	*Iberomys huescarensis*	*Terricola arvalidens*	*Stenocranius gregaloides*	*Arvicola jacobaeus*	*Arvicola mosbachensis*	S	Authors
x				x			x											x	x	x	x				12	Cuenca-Bescós et al., 1999, 2010a,b, 2011
x				x			x		x									x			x				11	Cuenca-Bescós et al., 1999, 2010a,b, 2011
x			x	x			x		x								x	x		x	x	x			20	Cuenca-Bescós et al., 1999, 2010a,b, 2011
x			x	x			x		x								x	x		x	x	x			18	Cuenca-Bescós et al., 1999, 2010a,b, 2011
x			x	x			x		x								x	x		x	x	x			17	Cuenca-Bescós et al., 1999, 2010a,b, 2011
x							x										x			x	x				5	Minwer-Barakat et al., 2008, 2011, 2012
																					x			x	2	Minwer-Barakat et al., 2008, 2011, 2012
x							x													x		x			8	Minwer-Barakat et al., 2008, 2011, 2012
							x													x					2	Minwer-Barakat et al., 2008, 2011, 2012
x							x						x												4	Minwer-Barakat et al., 2008, 2011, 2012
							x																		2	Minwer-Barakat et al., 2008, 2011, 2012
x																									2	Minwer-Barakat et al., 2008, 2011, 2012
							x													x					4	Minwer-Barakat et al., 2008, 2011, 2012
		x					x						x												7	Agustí et al., 1999, 2010
							x						x												3	Agustí et al., 1999, 2010
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
		x						x					x	x	x	x							x		18	Cuenca-Bescós et al., 2013
												x													3	Agustí et al., 1999
	x	x			x	x				x															9	Agustí et al., 1999

(TD3/4 to the base of TD7) of the nearby site of Gran Dolina whose microfauna is more similar to that of the post-Jaramillo levels of the site of Vallparadís (levels EVT12-7), as well as the new TT-OSL, 846 ± 57 ka dating of the level TD6 of Gran Dolina by Arnold et al. (2014) it can be thus reasonably assumed an age older than the Jaramillo paleomagnetic subchron of the TELRU unit.

Fig. 4 shows a comparison, using the PAMs of taxa of the Atapuerca sites with other Spanish localities of late Early Pleistocene age from the Guadix–Baza basin, BC, FN3, BLD, VM, and from the Vallparadís – Cal Guardiola composite section, such as D3–D5 and EVT12-3 (Minwer-Barakat et al., 2011). There is a strong ordering of the localities in two groups along the axis 1. To the left, one group of data include the sites of TELRU, D3, BLD, FN, BC, and VM. The chronology of all these sites has been established by a magneto-bio-stratigraphy and some of them have been also dated by numerical methods: all these data strongly suggest an age older than 1 Ma for all these sites (e.g. Carbonell et al., 2008; Cuenca-Bescós et al., 2010; Madurell-Malapeira et al., 2010; Duval et al., 2011, 2012; Arnold et al., 2014). Within this group, VM and BC both show high values along axis 2. This might be linked to the chronology of the sites, VM and BC being the oldest localities of the group. To the right, a second group of data includes the localities of TD3/4–TD8, EVT12-7 and D5, whose chronologies are clearly younger than 1 Ma (Falguères et al., 1999; Duval et al., 2011, 2012; Arnold et al., 2014). No apparent subdivision can be done within this group.

Interestingly, this division into two different groups may be thus directly correlated to the chronology of the sites: group 1 includes all the sites older than the age of the Jaramillo subchron, whereas group 2 is made by the sites younger than the age of the Jaramillo Subchron. This clear separation suggests that the Jaramillo Subchron may be used as a landmark for Early Pleistocene small mammal biochronology in Spain.

6. Conclusions

Dating Early Pleistocene localities in Spain, as well as in Europe, is quite challenging because the first humans, their FAD, appears during the Early Pleistocene. As so far there is no ideal method that can be used alone to provide an accurate and irrefutable chronology, the solution lies rather in the combination of different, but complementary, approaches for complementing their chronological framework. Magnetostratigraphy provides geomagnetic polarities that can be correlated to specific chrons or subchrons when associated to biostratigraphic data. In contrast, chronometric dating methods such as ESR, TCN and Luminescence may provide numerical ages, but the precision afforded is not as good as that of the Ar–Ar method (Ludwig and Renne, 2000), which may sometimes generate some debates around crucial questions linked to the chronology of the first hominin settlements in Europe (Muttoni et al., 2013; Toro-Moyano et al., 2013; García et al., 2014). In that regard, the results of the present study show that biochronology may be a useful additional tool to further refine the chronology of

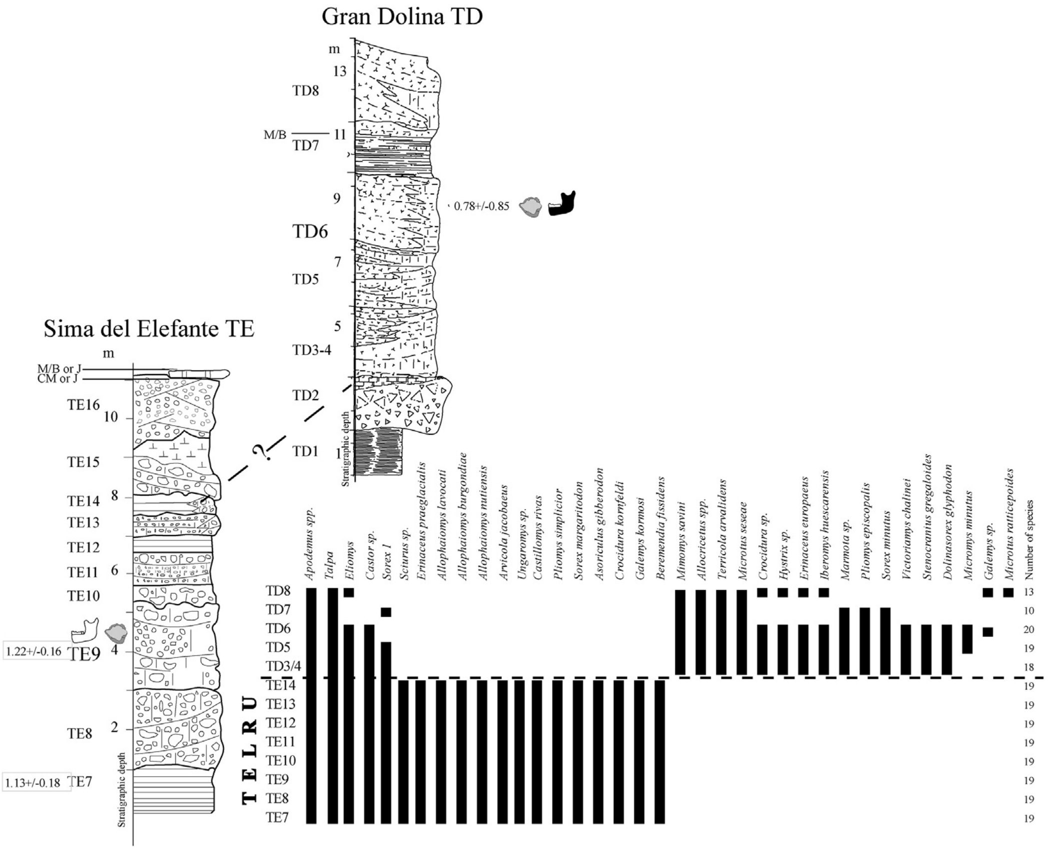

Fig. 2. Stratigraphy and distribution of Eulipotyphla and Rodentia from the Early Pleistocene localities of the Sierra de Atapuerca, Burgos, Spain: Sima del Elefante (TE) and Gran Dolina (TD). Schematic stratigraphic columns of the Figures of the lithostratigraphic units and paleomagnetic data are drawn after several authors (Parés and Pérez-González et al., 1995; Carbonell et al., 2008; Falgueres et al., 2013). Numerical ages (in Ma) are discussed in the text. Correlation between levels TE14 and TD3/4 is based upon the microfaunal change explained in the text. M/B, Matuyama–Brunhes boundary; CM, Cobb Mountain subchron; J, Jaramillo subchron. The drawings of the human mandible and the stone tool indicate the layers TE9 and TD6 where they appear. To the left the distribution of some microfaunal taxa in both localities, with the presence–absence of the Eulipotyphla and Rodentia from TE and TD. Presence is represented with the black line, absence is in white. The number of species (S) in the right column shows the high diversity of these small mammals in the sequence, which diminishes only in TD7 and TD8. Note that TD6 has the highest S. The basis of the correlation line is solely biostratigraphic, because the significant microfaunal taxa suggest that the TELRU levels of Sima del Elefante are below the lower levels TD3/4 of Gran Dolina (levels TD2 and TD1 do not contain fossil faunal remains. We have sampled TD1 during the last two years and have found no microfossils. Levels TE15, TE16 and TE17 of Sima del Elefante are sterile.

these localities, by providing not only relative chronological information between the sites, but also giving some important indications about a pre or post-Jaramillo age.

Our study presents the revised faunal list of each Early Pleistocene level from the localities of Gran Dolina and Sima del Elefante, in Atapuerca. Both localities have very likely the richest associations of small mammal species in the Quaternary of Europe (Table 2, S column).

Perhaps the most striking observation in our study is the lack of similarities between the assemblages from each site, which can only be explained by a chronological gap between them. If Jaramillo subchron has not been directly identified at Atapuerca, the existing chronostratigraphical framework combined with similarities of the assemblages between Gran Dolina and Vallparadís indicate with some confidence that TELRU levels have a pre-Jaramillo age. Consequently, the Early Pleistocene levels of both Atapuerca sites

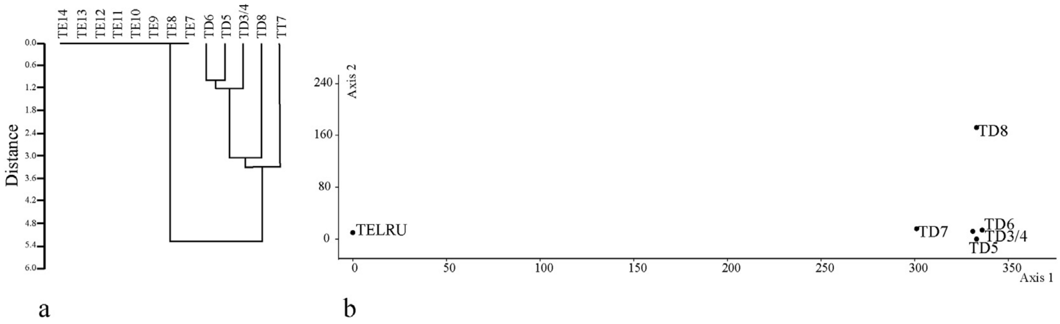

Fig. 3. a. Cluster analysis (hierarchical clustering by Euclidean distance, items are taxa that occurs in each fossiliferous layer) of the Early Pleistocene localities of Atapuerca, TELRU and TD3–TD8. b DCA of TE and TD.

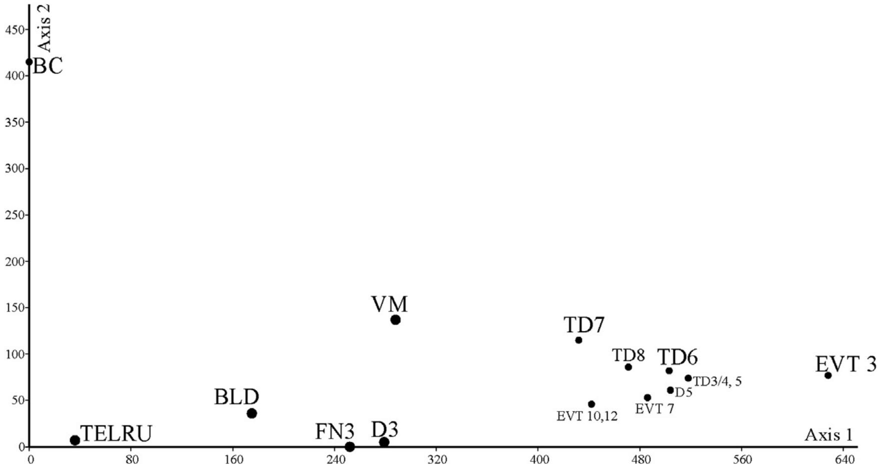

Fig. 4. DCA of the localities of Atapuerca and other Early Pleistocene localities from Spain: Vallparadis and Orce. 92% of the variance is explained in the first axis (0.9299). Axis 1 reflects the faunal composition of localities which are around the Jaramillo subchron in age, and Axis 2 indicates localities which are quite different such as Barranco Conejos (BC, see Table 2).

TE and TD are the only sequence from Spain that allows the study of a continuous stratigraphic succession of the interval prior to the Jaramillo subchron in terrestrial sequences. The faunal distribution of the levels from TE and TD shows the faunal turnover of small mammals at the end of the pre-Jaramillo interval that is recorded in other, though isolated localities throughout Europe. Biostratigraphy of the Early Pleistocene from Europe, based mainly in the few isolated localities of the pre-Jaramillo time interval, is reinforced by faunal succession of the Atapuerca sites.

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