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The Vallparadís section (Terrassa, Iberian Peninsula) and the latest Villafranchian faunas of Europe

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ABSTRACT

The late Early to early Middle Pleistocene section from Torrent de Vallparadís is a 20 m-thick, composite section with multiple stratigraphic horizons, which have yielded close to 30,000 remains of large and small vertebrates, as well as macrobotanical remains of non-carbonized wood and a complete pollen record. This series is well correlated on the basis of magnetostratigraphic and small mammal biostratigraphic data, ranging from 1.2 to 0.6 Ma. There are only a few other European localities recording this time interval from a faunal, floral and stratigraphical perspective, so that the Vallparadís series provides a unique opportunity to investigate the faunal and environmental changes that occurred in south-western Europe during the Early to Middle Pleistocene transition. This time interval recorded at Vallparadís coincides with major climatic changes at a global scale (the Middle Pleistocene Transition), which had important effects on the composition of mammalian assemblages. The remains recovered from the latest Early Pleistocene layers of the Vallparadís section show that most of the components of the Villafranchian carnivore guild survived until close to the Brunhes-Matuyama boundary (probably until the interglacial stage 21), which might have significantly influenced the foraging strategies of early *Homo* in Europe. On the other hand, the remains of the straight-tusked elephant, *Elephas (Palaeoloxodon) antiquus*, from the latest Early Pleistocene layers of Vallparadís represent the earliest European record of this species, indicating that the dispersal of African elements into Europe during the Middle Pleistocene Transition began earlier than previously thought, at close to 1 Ma.

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1. Introduction

The faunal turnover that occurred around the Early/Middle Pleistocene transition in Europe involved the extinction of most Villafranchian faunal elements. These include many carnivorous taxa, such as the giant hyena *Pachycrocuta brevirostris*, the felids *Megantereon whitei*, *Acinonyx pardinensis*, *Panthera gombaszoegensis* and *Puma pardoides*, and the pack-hunting canid *Lycaon lycaonoides*, as well as the equids *Equus altidens* and *Equus sussenbornensis*. On the other hand, species of African origin arrived to Europe by this time, including the lion (*Panthera leo*), the leopard (*Panthera pardus*) and the spotted hyena (*Crocuta crocuta*), as well as the straight-tusked elephant (*Elephas (Palaeoloxodon) antiquus*) and the auroch (*Bos*

primigenius). Simultaneously, species of Asian origin, such as the steppe mammoth (*Mammuthus trogontherii*), the red deer (*Cervus elaphus*), an Indian bovid (*Hemibos galerianus*), the horse (*Equus ferus*) and probably the wild boar (*Sus scrofa*), among others, are first recorded in Europe by this time (Martínez-Navarro et al., 2009a,b). In the paleontological literature, this faunal turnover is known as the 'C. crocuta event' (Martínez-Navarro, 2010; see also Palombo et al., 2008, for additional discussion). This major faunal renewal occurred during a time span ranging from 1.1 to 0.6 Ma, thus roughly coinciding in time with the major global climatic changes that are known as the Middle Pleistocene Transition (MPT; Clark et al., 2006) or Mid-Pleistocene Revolution (MPR; Maslin and Ridgwell, 2005), which spanned between 1.25 and 0.7 Ma. Before the onset of this faunal turnover, climate was dominated by 41 ky obliquity orbital cycles, whereas towards its end, this mode had shifted to a highly non-linear system dominated by 100 ky periodicity with asymmetric glacial/interglacial cycles (Clark et al., 2006; Almqvist-Labin, in

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press). These changes had an important effect on seasonality, affecting the type and the structure of the vegetation cover. In the Mediterranean area, temperature and humidity decreased slightly, and the short alternations between deciduous forests and open landscapes were substituted by longer alternations between steppe and deciduous forests (Suc and Popescu, 2005; Bertini, in press; Palombo, in press). This time interval of major climatic changes and intense faunal renewal, elapsing over nearly 600 ky, is known regarding large mammal biochronology as the Epivillafranchian Biochron or Villafranchian–Galerian transition (Kahlke, 2007; Rook and Martínez-Navarro, 2010).

Regarding early European hominins, the latest Early Pleistocene humans might have taken advantage from these unstable climatic conditions and changing mammalian guilds (Palombo, in press). Several latest Early Pleistocene and early Middle Pleistocene localities have yielded human and/or lithic remains. Some of these localities, such as Vallonnet (de Lumley et al., 1988) and Soleilhac (Bonifay and Mergoïl, 1988) in France, and Trinchera Elefante of Atapuerca in Spain (Carbonell et al., 2008), show a typically Villafranchian mammalian assemblage together with Mode I artifacts. On the other hand, other localities, such as the lower layers of Trinchera Dolina in Spain (Falgüères et al., 1999) and the Pakefield site in Great Britain (Parfitt et al., 2005), display Galerian elements associated to Mode I lithic artifacts and, in the case of the Spanish locality, evidences of primary and early access to the carcasses (Diéz et al., 1999). From a biochronological viewpoint, both groups of localities can be distinguished by the presence of the short-faced hyena *P. brevirostris* in the first group, and that of the spotted hyena *C. crocuta* in the second. Recently, Martínez-Navarro et al. (2007, 2009a,b, 2010) (see also Martínez-Navarro and Rabinovich, in press) established a parallelism between the dispersal into Eurasia of the Acheulian culture (Mode II tools) and the dispersal of the genus *Bos*. They occur together in the Israeli localities of Ubeidiya (ca 1.2–1.5 Ma), which has yielded a primitive Acheulian assemblage, and Gesher Benot Ya'akov (ca 0.7–0.8 Ma), which shows a more developed Acheulian technology. In Europe, this association is first recorded at Venosa Notarchirico (Cassoli et al., 1999; Piperno, 1999), coinciding with the more stable climatic conditions that characterize the end of the Middle Pleistocene Transition.

Unfortunately, there are only a few European localities recording this crucial moment of life history on Earth from a faunal, floral and stratigraphical perspective. Most Epivillafranchian localities in Europe, such as Vallonnet in France (Moullé, 1992), Untermassfeld in Germany (Kahlke, 1995) and Colle Curti in Italy (Coltorti et al., 1998), correspond to the Jaramillo or a pre-Jaramillo paleomagnetic subchron, and do not provide multiple fossiliferous levels recording this transition through a long and continuous stratigraphic sequence. On the contrary, the 20 m-thick Vallparadís composite section in Terrassa (Vallès-Penedès Basin, NE Iberian Peninsula) displays multiple fossiliferous levels, which have yielded abundant macro and micromammal remains (Berástegui et al., 2000; Alba et al., 2008a; Madurell-Malapeira et al., 2009a). Furthermore, these mammalian remains are associated to macrobotanical remains and an accurate pollen record (Postigo Mijarra et al., 2007), and the several fossiliferous levels can be accurately dated thanks to detailed litho and magnetostratigraphic correlation (Madurell-Malapeira et al., 2009a). The Vallparadís section includes the Cal Guardiola and Vallparadís sites excavated during the last 15 years (Alba et al., 2008a,b; Madurell-Malapeira et al., 2009a,b), spanning from slightly before the base of the Jaramillo subchron to the early Middle Pleistocene. As such, this section documents the latest Villafranchian faunas of Europe, associated with the earliest Galerian elements such as *E. (P.) antiquus*, *Sus* sp. and *Ursus deningeri*. Here we describe the geological, paleomagnetic, faunal and floral evidence from this succession, in order to improve the current knowledge of

the Villafranchian–Galerian transition and the faunal and environmental changes that preceded the arrival of the Acheulian culture into Europe.

2. Regional and geological setting

The Vallparadís composite section includes the paleontological sites of Cal Guardiola and Vallparadís, which are situated in the western and eastern bank, respectively, of the Torrent de Vallparadís, within the town of Terrassa (el Vallès Occidental, Catalonia, Spain) (Fig. 1). These deposits are located in the Vallès-Penedès Basin, a narrow half-graben trending NE-SW, parallel to the Catalan margin. This basin is bounded along its NW margin by the master normal fault, which is Neogene in age (Cabrera and Calvet, 1996). Minor and parallel faults also bound the basin towards its SE margin. The basin infill is made up of Neogene and Quaternary clastic sediments resulting from the erosion of metasedimentary and igneous Paleozoic rocks, and terrigenous and carbonate Mesozoic sequences of the Prelittoral Range. These sediments mainly constitute alluvial fan and alluvial plain deposits, related to the NW and SE active basin margins. The more significant sedimentary thickness is located along NW margin of the basin, coinciding with the presence of the master normal fault (Agustí et al., 1997; Berástegui and Losantos, 2001).

The Quaternary sediments from Cal Guardiola and Vallparadís correspond to the Pleistocene alluvial fan system of Terrassa (Berástegui and Losantos, 2001), which overlies a marked Miocene paleorelief. The sediments in the Cal Guardiola site consist of a 7 m-thick unit of massive conglomerates and gravels in a matrix-supported fabric. The clasts attain block size and are rounded or sharp depending on their lithology. The beds are about 1 m-thick and rich in fossils of animals and plants. The fossils are mainly concentrated in a black unit (D2) interbedded with the above-mentioned conglomerates and gravels (Berástegui et al., 2000). In the Vallparadís site, there is a 14 m-thick succession mainly composed of conglomerates and mudstones, which are arranged in two units separated by an erosive angular unconformity. The lower unit (layers 6, 7, 8, 9, 10, 11 and 12) is made up of clast-supported, rounded, polymictic and poorly sorted conglomerate beds that hardly attain 1 m of thickness. The conglomerates are intercalated

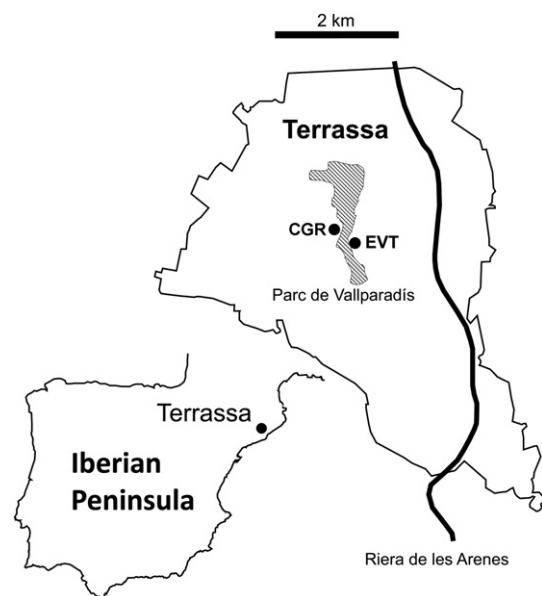


Fig. 1. Location map of the two sites of the Torrent de Vallparadís section, Cal Guardiola and Vallparadís, next to the city of Terrassa, and situation of the latter within the Iberian Peninsula.

A correlation of the Vallparadís section magnetostratigraphy with the time scale (Gradstein et al., 2004) can be established (Fig. 2), which is supported on biostratigraphic grounds by the large and small mammal fossil assemblages found in different stratigraphic intervals (Fig. 3) (Madurell-Malapeira et al., 2009a). To sum up, on the basis of magnetostratigraphic and biostratigraphic data, the composite section of Vallparadís, formed by the local Cal Guardiola and Vallparadís stratigraphic sequences, spans from before the Jaramillo paleomagnetic subchron to the early Middle Pleistocene. This time span can be divided into four intervals (Figs. 2 and 3): (R1) pre-Jaramillo times, only recorded in the Cal Guardiola sequence (layers D1, D2 and D3), with a reversed paleomagnetic polarity (Fig. 2); (N1) the Jaramillo subchron, only recorded in the Vallparadís sequence (bottom of layer 8, and layers 9, 10, 11 and 12), with a normal polarity; (R2) post-Jaramillo, Matuyama times, with a reversed polarity, recorded both at Vallparadís (bottom of layer 3 and layers 4, 5, 6, 7, and the top of layer 8) and Cal Guardiola (layers D4, D5, D6, D7 and D8); and (N2) early Middle Pleistocene times, only recorded in the topmost of the Vallparadís sequence (layers 2 and 3), with a normal polarity.

4.2. Macrovertebrates

The Vallparadís sequence includes more than ten layers from which large mammal remains have been recovered in an excellent state of preservation. Within these horizons, layers D2 and D7 of Cal Guardiola and layers 12, 10, 7 and 3 of Vallparadís are the richest. The faunal composition of these layers can be grouped into two different associations: the Early Pleistocene layers, which have yielded a typically Villafranchian assemblage; and the Middle Pleistocene layers, where all the identified species show Galerian affinities. The following species have been recorded from the Early Pleistocene layers (Alba et al., 2008a; Madurell-Malapeira et al., 2009a,b, 2010; J.M.-M.'s unpublished data) (Figs. 3 and 4): *Macaca sylvanus* cf.

florentina, *P. brevisrostris*, *Meles meles*, *U. deningeri*, *L. lycaonoides*, *Canis mosbachensis*, *Vulpes praeglacialis*, *Homotherium latidens*, *M. whitei*, *P. gombaszoegensis*, *P. pardoides*, Felidae indet., *Lynx* sp., *E. (P.) antiquus*, *E. altidens*, *Stephanorhinus hundsheimensis*, *Hippopotamus antiquus*, *Sus* sp., *Dama vallonmentensis*, *Praemegaceros verticornis*, *Bison* sp. and *Caprini* indet. In its turn, from the early Middle Pleistocene layers, the following taxa have been identified (Aurell-Garrido et al., 2009, 2010; Madurell-Malapeira et al., 2009a; J.M.-M.'s unpublished data) (Figs. 3 and 4): *Vulpes* sp., *E. (P.) antiquus*, *Equus* cf. *hydruntinus*, *E. cf. ferus*, *Stephanorhinus* sp., *C. elaphus* and *Bison* sp.

4.3. Microvertebrates

Small mammal remains from the Vallparadís section are not very abundant, although several taxa can be identified. Thus, in the Early Pleistocene levels of the Vallparadís section, the following different genera of Arvicolidae, Muridae, Gliridae and Hystricidae are recorded (R.M.B.'s unpublished data): *Allophaiomys*, *Mimomys*, *Iberomys*, *Stenocranius*, *Apodemus*, *Eliomys* and *Hystrix* (Figs. 3 and 5). Regarding the Middle Pleistocene levels, the following two genera of Arvicolidae can be identified (R.M.B.'s unpublished data): *Terricola* and *Arvicola* (Figs. 3 and 5). Finally, with regard to paleotherpetological remains, the following taxa have been identified from the late Early Pleistocene (post-Jaramillo) levels of the Cal Guardiola section: *Bufo bufo*, *Bufo calamita*, *Rana* cf. *temporaria*, Lacertidae indet. and *Natrix* cf. *natrix* (Blain, 2005).

4.4. Wood and pollen remains

During the field excavation of the layer D2 (pre-Jaramillo) of the Cal Guardiola local section in 1997, several fossil wood fragments were recovered. One hundred of these wood fragments were analysed, together with 16 pollen and 18 coprolite samples, by Postigo

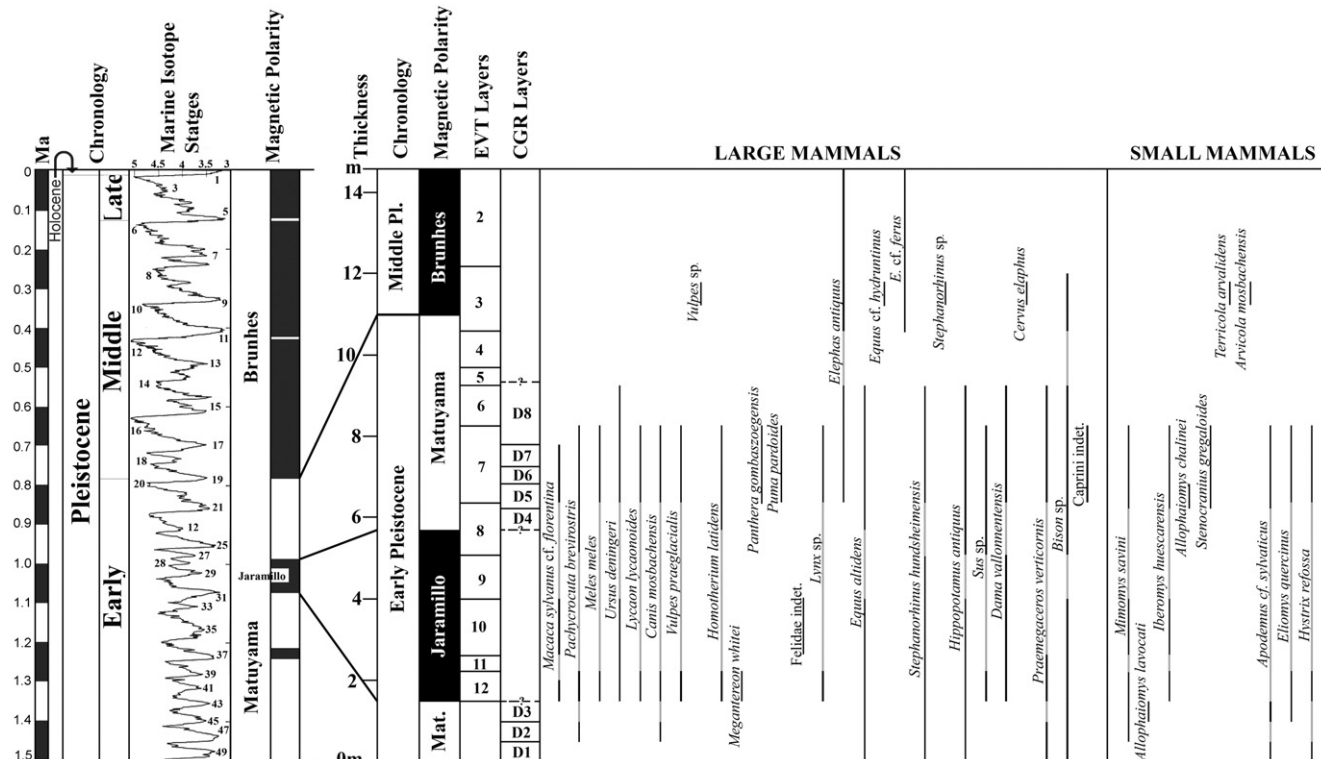


Fig. 3. Chronological range of the large and small mammals recorded from the Torrent de Vallparadís section. Dark lines represent the layers where the species are identified, while the gray lines depict the estimated range according to available information.

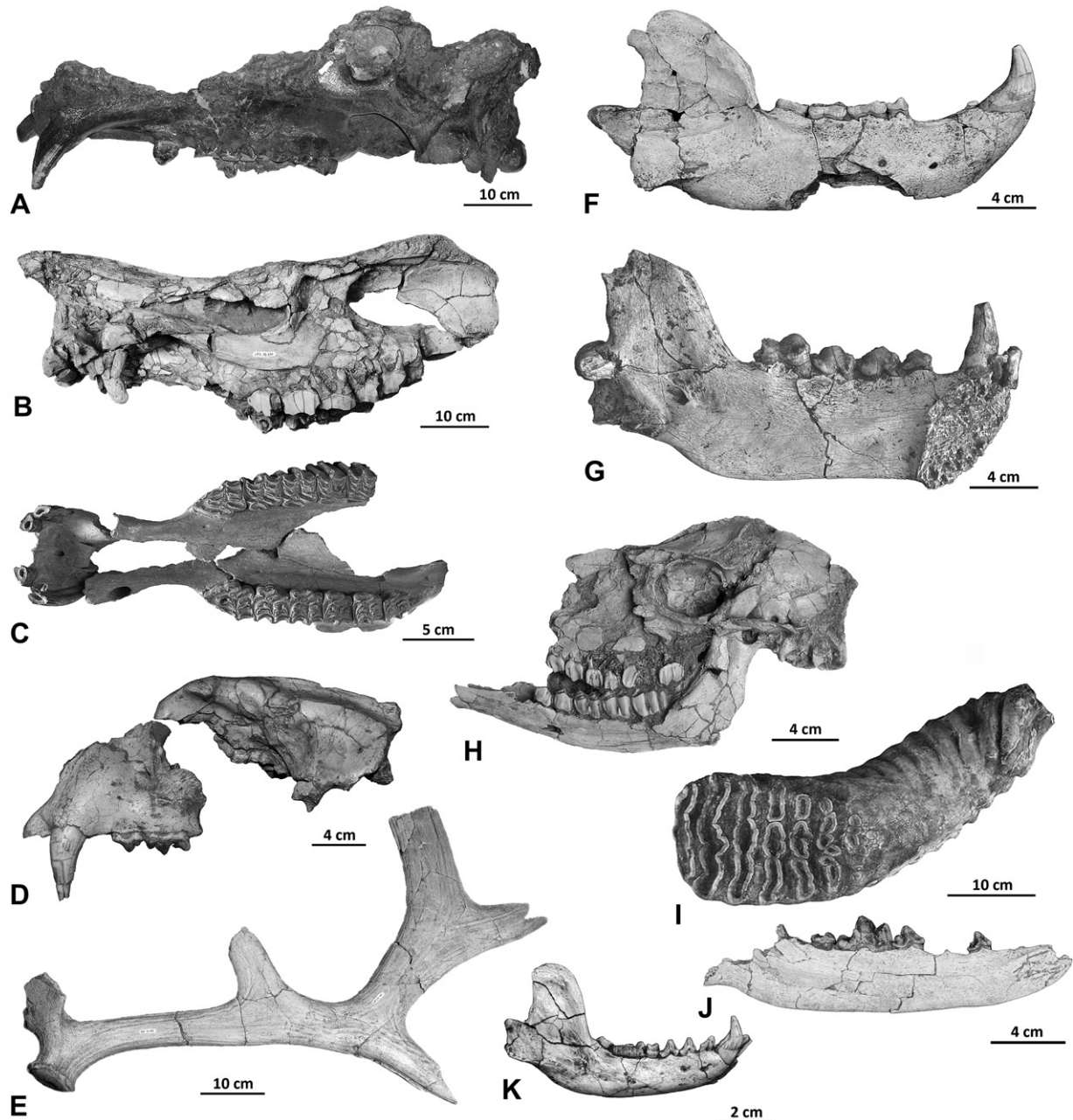


Fig. 4. Large mammal remains from the Torrent de Vallparadís section. A: *Hippopotamus antiquus* cranium from the D2 layer of Cal Guardiola in lateral view (IPS14960), B: *Stephanorhinus hundsheimensis* cranium from the D7 layer of Cal Guardiola in lateral view (IPS13371), C: *Equus* cf. *ferus* maxilla and pre-maxilla from the layer 3 of Vallparadís in occlusal view (EVT0540), D: *Panthera gombaszoegensis* partial cranium from the layer 7 of Vallparadís in lateral view (EVT20122 + EVT20156), E: *Praemegaceros verticornis* antler from the D7 layer of Cal Guardiola (IPS13370), F: *Ursus deningeri* right hemimandible of layer D7 of Cal Guardiola in buccal view (IPS14950), G: *Pachycrocuta brevirostris* left hemimandible from the layer 12 of Cal Guardiola in lingual view (EVT24641), H: *Dama vallonnetensis* cranium from the layer D7 of Cal Guardiola in lateral view (IPS14911), I: *Elephas (Palaeoloxodon) antiquus* right M2 from the layer 7 of Vallparadís in occlusal view (EVT3206), J: *Lycaon lycaonoides* left hemimandible from the layer 7 of Vallparadís in lingual view (EVT23434), K: *Meles meles* right hemimandible from the layer 12 of Vallparadís in buccal view (EVT23914).

Mijarra et al. (2007). Eleven taxa (from 7 different angiosperm families) were identified from the fossil wood remains: *Acer* aff. *pseudoplatanus*, *Quercus* subgen. *Quercus*, *Aesculus* aff. *hippocastanum*, *Ulmus* sp., *Acer* aff. *campestre*, *Fraxinus* aff. *angustifolia*, *Populus* sp., *Salix* sp., *Lingustrum vulgare*, *Acer* sp., *Cornus sanguinea* and *Quercus* sp. The analysis of pollen and coprolite samples permitted Postigo Mijarra et al. (2007) to identify the following taxa basically from the analysed coprolites of D2 layer of Cal Guardiola: *Phillyrea* sp., evergreen *Quercus*, *Viburnum opulus*, cf. *Fraxinus*, *Pinus* sp., *Pinus* type *haploxylon*, Cupressaceae indet., Cistaceae indet., *Tamarix* sp., *Castanea* indet., *Ephedra* sp., *Abies* sp., *Juglans* sp., *Carya* sp., *Rhamnus* sp.,

Buxus sp., *Vitis* sp., Taxodiaceae indet., *Chamaerops* indet., *Hedera* sp., *Celtis* sp., Thymelaeaceae indet., *Pistacia* sp., *Erica* sp., *Betula* sp., *Carpinus* sp., *Platanus* sp., and *Corylus* sp.

5. Discussion

5.1. Large mammal fauna

The large mammal record of the Vallparadís section includes 27 species of carnivores, artiodactyls, perissodactyls and proboscideans (Figs. 3 and 4).

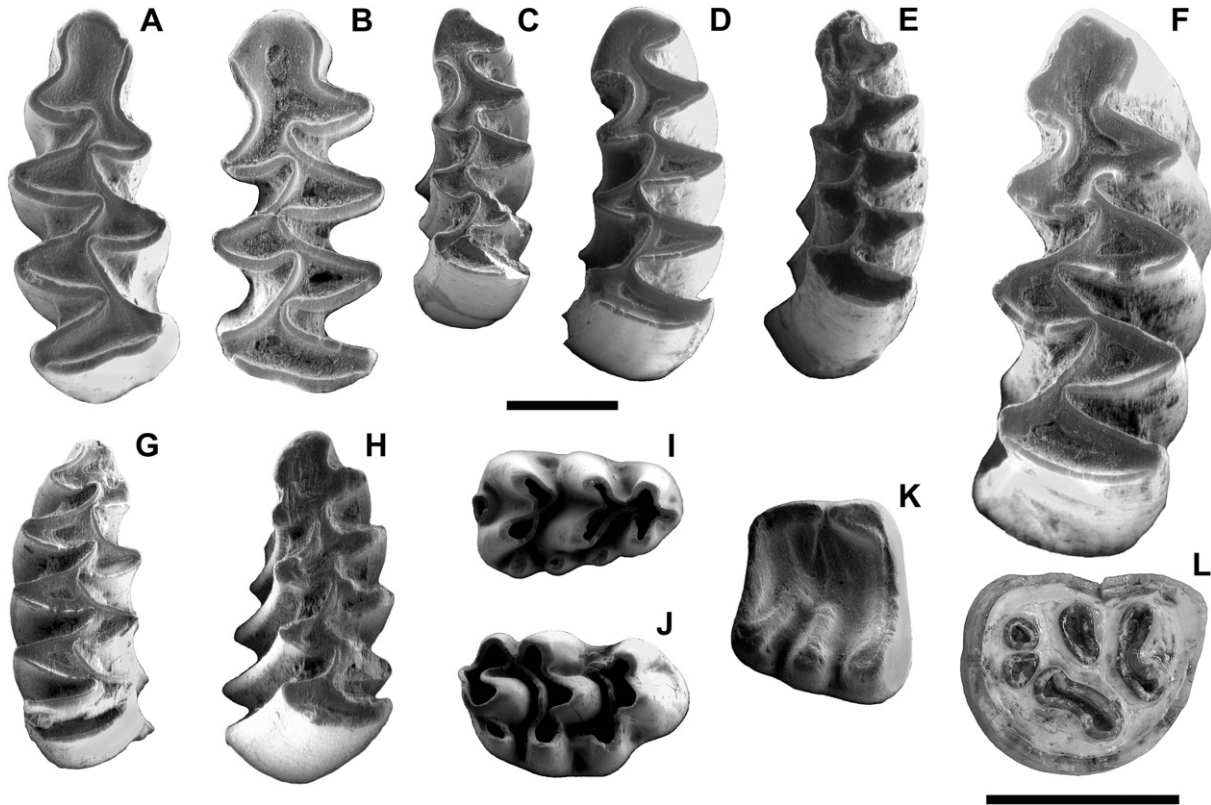


Fig. 5. Small mammals from the Torrent de Vallparadís section. A: right m1 of *Mimomys savini* from the D2 layer of Cal Guardiola (IPS21047), B: left m1 of *Mimomys savini* from the layer 12 of Vallparadís (IPS49430), C: left m1 of *Allophaiomys lavocati* from the D3 layer of Cal Guardiola (IPS50226), D: left m1 of *Allophaiomys chalinei* from the D5 layer of Cal Guardiola (IPS50214), E: left m1 of *Stenocranius gregaloides* from the D5 layer of Cal Guardiola (IPS50162), F: left m1 of *Arvicola mosbachensis* from the layer 3 of Vallparadís (IPS49558), G: right m1 of *Iberomys huescarensis* from the layer 10 of Vallparadís (IPS49459), H: left m1 of *Terricola arvalidens* from the layer 3 of Vallparadís (IPS49569), I: right m1 of *Apodemus cf. sylvaticus* from the layer 7 of Vallparadís (IPS49509), J: right M1 of *Apodemus cf. sylvaticus* from the layer 7 of Vallparadís (IPS49533), K: left m1–2 of *Eliomys quercinus* from the layer 12 of Vallparadís (IPS49450), L: left P4 of *Hystrix refossa* from the layer 7 of Vallparadís (IPS54944). All teeth are depicted in occlusal view. Central scale bar, for A–K, equals 1 mm. Right bottom scale bar, only for L, equals 10 mm.

In the late Early Pleistocene levels, the most abundant material corresponds to large-bodied species, such as *H. antiquus*, *Stephanorhinus hundsheimensis* and *E. altidens*. Small to medium-sized herbivores are poorly represented, and only dentognathic remains and antlers of *Dama vallonnetensis* are abundant among non mega-herbivores. The scavenging activity of *P. brevirostris* is documented extensively by nearly 850 coprolites, as well as by the remains of the three former species, which include a large amount of broken fossil bones, sometimes without epiphyses, and further showing gnaw marks and bite impacts. This scavenging activity by hyenids is outside the scope of this paper; nevertheless, it is worth noting that it shows several points in common with the evidences of the activity of *P. brevirostris* in the Early Pleistocene site of Venta Micena in Orce (Spain) (Arribas and Palmqvist, 1998; Madurell-Malapeira et al., 2009a).

The large mammals recovered from the late Early Pleistocene levels of the Vallparadís section have in most instances a clearly Villafranchian character. Most of the recorded species are also recorded in other Early Pleistocene (late Villafranchian) localities throughout Europe, including Venta Micena, Barranco León D, Fuente Nueva 3, Incarcál or Cueva Victoria in Spain, Vallonnet in France, Piro Nord, Colle Curti and Upper Valdarno in Italy, Apollonia in Greece and Untermassfeld in Germany (Koufos et al., 1992; Moullé, 1992; Kahlke, 1995; Galobart, 1996; Gliozzi et al., 1997; Martínez-Navarro et al., 2003; Palmqvist et al., 2005; Sardella et al., 2006; Blain et al., 2008; Petrucci, 2008). Nevertheless, the evidence provided by the localities of Vallparadís and Cal Guardiola expand the biochronological range of several of these Villafranchian species

to Jaramillo or post-Jaramillo times. This is the case of the dirk-toothed cat *M. whitei*, previously never recorded from Jaramillo times, and also other carnivores such as *P. brevirostris*, *L. lycanoides*, *P. gombaszoegensis* and *P. pardoides* (from reversed polarity levels), which had been only poorly and/or doubtfully recorded from post-Jaramillo times in Europe. For example, Lewis et al. (in press) recently identified *P. brevirostris* and *P. gombaszoegensis* from the West Runton (Norfolk, UK) early Middle Pleistocene layers; however, the identification of these larger carnivores in that site would probably require further research and more specimens (particularly dentognathic ones) in order to be confirmed.

On the other hand, the record of the above-mentioned five species of carnivores in the Vallparadís section represents the latest occurrence of these Villafranchian carnivores in Europe, at least as recorded in a well-calibrated and accurately dated sequence. These species of Villafranchian affinities recorded from the Vallparadís section are for the first time associated with three species of Galerian character: *E. (P.) antiquus*, *U. deningeri* and *Sus* sp. The straight-tusked elephant, *E. (P.) antiquus*, had been never previously recorded from the Early Pleistocene in Europe in reversed magnetostratigraphic polarity layers. Until recently, the earliest record of *E. (P.) antiquus* in Europe corresponded to the site of Huéscar-1 (southern Iberian Peninsula), with an age of 0.8–0.9 Ma (Mazo, 1989). Davies (2002) attributed the proboscidean from this locality to *M. trogontherii*, whereas more recently Ros-Montoya (2010) showed that it actually corresponds to the latest *Mammuthus meridionalis* of Europe. In the Vallparadís section, *E. (P.) antiquus* is only recorded in the post-Jaramillo, reversed polarity levels, thus

roughly coinciding with the chronology of the *Mammuthus* remains from Húscar 1. This evidence therefore confirms the coexistence of two different proboscidean species during the late Early Pleistocene in Europe. These two species probably displayed similar generalist foraging strategies (Lister, 2004), which might have ultimately prompted the extinction of *M. meridionalis* as a result of direct competition with *E. (P.) antiquus* after a short coexistence interval during the late Early Pleistocene, as evidenced by the proboscidean record from Huéscar-1 and the Vallparadís section. These considerations suggest that *E. (P.) antiquus* may be the earliest immigrant of African origin to be recorded in Europe during the Early Pleistocene–Middle Pleistocene turnover, prior to the dispersal of other true Galerian African immigrants, such as *C. crocuta*, *P. leo*, *P. pardus* and *B. primigenius*, among others.

Regarding the remains of *U. deningeri*, those from Cal Guardiola represent, together with the Vallonnet bears, the first representatives of the cave bear lineage (Madurell-Malapeira et al., 2009b). Other similarly-aged ursid remains from the late Early Pleistocene of Europe, namely those from Trinchera Dolina and Sima del Elefante in Atapuerca (Spain), together with those from Untermassfeld, have been classified as *Ursus dolinensis* or *U. cf. dolinensis*, respectively (García, 2003, 2004; Carbonell et al., 2008). The origin and dispersal of cave bears and their relationships with brown bears remains controversial (Olive, 2006; Palombo et al., 2008), but on the basis of currently available data, the ursid remains from the Vallparadís section and Vallonnet may represent the earliest true Galerian carnivores recorded from Europe (correlated with the Jaramillo subchron). Finally, remains of *Sus* have been recorded from several late Early Pleistocene European sites: *Sus* sp. from the pre-Jaramillo layers of Sima del Elefante (Carbonell et al., 2008); *S. scrofa* from Trinchera Dolina TD6 (van der Made, 1999); *S. scrofa prisca* from Untermassfeld (Güerin and Faure, 1997); and *Sus* sp. from Le Vallonnet (Moullé, 1992). The suid remains from the Vallparadís section come from both Jaramillo and post-Jaramillo levels, and are thus younger than the Sima del Elefante remains. In the future, the suid remains from the Vallparadís section may shed light into the taxonomy and dispersal events of Epivillafranchian suids, by clarifying the time of arrival of *S. scrofa* into Europe, as well as testing whether Epivillafranchian suids are a transitional form similar to *Sus lydekkeri* (Moullé et al., 2006), a distinct species, or a subspecies of *S. scrofa*.

On the basis of the data reported above, from a biochronological viewpoint, the late Early Pleistocene levels of the Vallparadís section record the beginning of the Early–Middle Pleistocene faunal turnover, by showing the persistence of some Villafranchian elements together with the first appearance of some Galerian newcomers. The uppermost levels of the Early Pleistocene of EVT and CGR, with a reversed polarity, still show a similar mixture of Villafranchian and Galerian elements, but do not record yet the presence of other Galerian elements, such as the spotted hyena (*C. crocuta*) and the red deer (*C. elaphus*). The two latter species are probably first recorded from the TDW4 layer of Trinchera Dolina in Atapuerca (Spain), with an estimated age close to 800 ka. This reinforces the contention that the uppermost Early Pleistocene levels of the Vallparadís section are older than the lower levels (TDW4) of the Trinchera Dolina, thus probably representing the last Epivillafranchian faunas in Europe prior to the arrival of *C. crocuta*.

In the Middle Pleistocene levels of Vallparadís, the recovered remains show an opposite taphonomical pattern to those from the Early Pleistocene levels. Thus, the remains from the former levels are almost always well preserved and complete, without evidence of hyenid activity and without coprolites. The most abundant species in all the Middle Pleistocene levels of EVT are equids, even including several partial skeletons. Regarding the Middle Pleistocene mammalian assemblage recorded from the Vallparadís local section,

there are many differences as compared to the Early Pleistocene levels. No species of Villafranchian character persist in these levels, and for the first time in the Vallparadís sequence three new Galerian species are recorded: the horses *E. cf. ferus* and *E. cf. hydruntinus*, and the red deer *C. elaphus*. The first dispersal of caballoid species into Europe has been established at around 0.9 Ma (Caloi, 1997), and the stenoian horses probably became extinct during the Early–Middle Pleistocene transition, although stenoian horses were tentatively cited recently inform the early Middle Pleistocene (Lister et al., in press). Be that as it may, the earliest record of caballoid equids in the Vallparadís section correspond to the early Middle Pleistocene layers 2 and 3, whereas no stenoian have been reported from the Middle Pleistocene layers. Up to now, the oldest record of the small stenoian equid *E. hydruntinus* corresponded to the Lunel-Viel Cave (France), with an approximate age of 0.4 Ma (Bonifay, 1991), the species being widely distributed throughout Eurasia until the Holocene (Antunes, 2006). Consequently, the occurrence of *E. cf. hydruntinus* in the layer 3 of EVT may represent the oldest record of this species in Europe (Aurell-Garrido et al., 2009). Regarding the origin of the true caballoid equids, it remains a controversial issue. Some authors considered that *E. ferus* evolved in Europe from an indeterminate large-sized species of the *Equus bressanus*–*E. sus-bornensis* lineage (Gromova, 1949; Prat, 1968; Alberdi and Ruíz-Bustos, 1989). Azzaroli (1990, 1995), on the contrary, supported a North American origin of *E. ferus*. Although the remains from Vallparadís layer 3 correspond to a robust middle-sized *E. ferus*, a subspecific identification is not possible, thus precluding an accurate biostratigraphical interpretation. Finally, the presence of *C. elaphus* in the Middle Pleistocene levels of Vallparadís agrees with the earliest record of this taxon in the TDW4 level (ca 800 ka) of the Trinchera Dolina in Atapuerca (van der Made, 1999). The absence of this species from the late Early Pleistocene layers of Vallparadís confirms the contention that these layers predate the first arrival of *C. crocuta* into Europe.

5.2. Small mammal fauna

During the excavations carried out in the Vallparadís section, almost all available levels were sampled for microvertebrate remains. Unfortunately, small mammal teeth are less abundant than large mammal remains, although in most instances they enable an identification to the species level that permits us to make biochronological inferences. At the bottom of the Vallparadís sequence, the layer D1 of Cal Guardiola is the lowermost one that has yielded micromammal remains, including only a few specimens of *Apodemus cf. sylvaticus* and *Hystrix refossa*. The lowest layer in which arvicoline remains have been identified is Cal Guardiola D2; despite the scarcity of the material (only two molars of *Mimomys savini* have been determined), this layer can be clearly assigned to the Biharian, since the lower and upper boundaries of this Mammal Age are determined by the FAD and LAD of *M. savini* (Fejfar et al., 1998). In its turn, the presence of *Allophaiomys lavocati* in the layer D3 of Cal Guardiola indicates that it belongs to the *A. lavocati* zone defined by Cuenca-Bescós et al. (2010), which permits us to correlate it with the Sima del Elefante Lower Red Unit, and the localities of Barranco León D and Fuente Nueva 3, for which an age between 1.2 and 1.4 Ma has been proposed (Cuenca-Bescós et al., 2010; Agustí et al., 2010). Therefore, the reversed polarity detected in this layer must correspond to the pre-Jaramillo Matuyama Chron.

The layers 10 and 12 of Vallparadís are very poor in small mammal remains. Nevertheless, the identification of *Iberomys huescarensis* indicates that they correspond to the upper part of the Early Pleistocene (see Cuenca-Bescós et al., 1999, 2010). The layers 7 of Vallparadís and D5 of Cal Guardiola have yielded a more complete micromammal assemblage, which includes the arvicolines *M. savini*,

Stenocranius gregaloides, *I. huescarensis*, and *Allophaiomys chalinei* (only in D5), besides other rodents with no biostratigraphical significance (*A. cf. sylvaticus*, *Eliomys quercinus*, *H. refossa*). This fauna is very similar to that of the levels TD 3–6 of Gran Dolina in Atapuerca (Cuenca-Bescós et al., 1995, 1999, 2010); the presence of *I. huescarensis* and *A. chalinei* also enables their correlation with the localities of Cueva Victoria, Casablanca 3, Huéscar-1, Puerto Lobo and Loma Quemada (Alcalde et al., 1981; Agustí and Galobart, 1986; Agustí et al., 2010). The layers 10, 12, 7 of EVT and D5 of CGR can be assigned to the *A. chalinei* zone of Cuenca-Bescós et al. (2010), despite the absence of *A. chalinei* in some of them, since this biozone is defined by the association of *I. huescarensis*, *S. gregaloides*, *A. chalinei* and *M. savini*. The differences observed between the respective assemblages from these several layers are attributable to the paucity of material, lacking any biochronological significance. Paleomagnetic data, however, allow us to further precise the age of these levels: EVT layers 10 and 12, with a normal polarity, can be assigned to the Jaramillo Subchron (1.07–0.99 Ma), whereas EVT layer 7 and CGR layer D5, with a reversed polarity, correspond to the post-Jaramillo Matuyama Chron (0.99–0.78 Ma). These levels are older than those from other European localities corresponding to the early Brunhes (such as Rifreddo, West Runton, Prezletice, Beftia 7 and levels TD7–8a of Gran Dolina), which still contain *M. savini* and *S. gregaloides* (Masini et al., 2005; Maul et al., 2007; Cuenca-Bescós et al., 2010; Maul and Parfitt, in press).

Finally, the layer 3 of Vallparadís must correspond to the Toringian on the basis of the presence of *Arvicola mosbachensis*. Traditionally, the upper boundary of the Biharian (and, consequently, the lower boundary of the Toringian) was defined by the LAD of *Mimomys* (and the FAD of the genus *Arvicola*). However, the very recent definition of *Arvicola jacobaeus* from the Early Pleistocene Red Lower Unit of Sima del Elefante in Atapuerca (Cuenca-Bescós et al., in press) put into question the validity of this limit. In any case, accepting that the FAD of *A. mosbachensis* (= *Arvicola cantianus*, according to Maul et al., 2000) marks the beginning of the Toringian, the assignation of the layer 3 to this Mammal Age and to the “*A. cantianus*” zone (Fejfar et al., 1998) is clearcut. The locality of Isernia, with transitional forms between *M. savini* and *A. mosbachensis*, has been dated by radiometric methods at around 0.6 Ma (Coltorti et al., 2005; Maul and Parfitt, in press); consequently, an age younger than 0.6 Ma can be estimated for the layer 3 of Vallparadís. This level cannot be included in the *Iberomys brecciensis* zone defined by Cuenca-Bescós et al. (2010), which is defined by the ranges of *I. brecciensis* and *Terricola atapuerquensis* (the latter one only found in Atapuerca), although a similar (Middle Pleistocene) age can be assumed. This level from Vallparadís can be correlated with other Middle Pleistocene Spanish sites containing *A. mosbachensis*, like Cúllar-Baza (Agustí et al., 2010), and with other European localities in which the association of *A. mosbachensis* and *Terricola arvalidens* has been identified, such as Medzhybozh (Rekovets et al., 2007) and Mauer (Wagner et al., in press).

5.3. Amphibians and squamate reptiles

The record of amphibians and squamate reptiles from the Vallparadís section merely includes about 40 remains from the upper part (post-Jaramillo) of the Cal Guardiola local section (Units D4–D8). More than 80% of these fossils correspond to the Anura, whereas the remaining ones are Lacertilia and Serpentes (Blain, 2005). Agustí et al. (2009) recently studied the record of amphibians and squamate reptiles from the Late Pliocene to the early Middle Pleistocene of the Iberian Peninsula, including among others Blain's (2005) data for Cal Guardiola. Agustí et al. (2009) attribute to the upper part of the Cal Guardiola local section a post-Jaramillo age, although predating the TDW4 and TD6 levels of the Gran Dolina of Atapuerca, according to

the microvertebrate available data. According to these authors, the Cal Guardiola locality, together with Almenara-Casablanca-3 (Castelló, Spain), would be placed in a climatic phase characterized by a sharp temperature decrease (including mean annual temperature, mean temperature of the warmest month and mean temperature of the coldest month), which is associated with an increase of the mean annual precipitation. Agustí et al. (2009) correlate this ‘cold’ phase with the isotopic stage OIS22, and attribute the lack of human presence in both Cal Guardiola and Almenara-Casablanca-3 to the above-mentioned sharp cooling.

5.4. Wood and pollen samples

The analysis of the fossil wood and pollen from the Unit D2 from the Cal Guardiola local sequence (Postigo Mijarra et al., 2007) reflect warm-temperate and humid conditions, indicating that the area sustained a river or rivermarsh ecosystem with a variety of plant environments; these include aquatic macrophytes, several taxa of plants characteristic of river margins and banks, and a mixed deciduous forest over the damp soils near the river, further indicating the presence of a Mediterranean shrubland and forest on the sunny slopes away from the riverside, as well as some grasslands in more open dry areas. The inferred warm climatic conditions and the preponderance of hippopotamid remains in the Unit D2 of Cal Guardiola is consistent with a fluvial/lacustrine main depositional environment, while the existence of a more diverse panoply of different environments nearby further agrees with the recorded high diversity of large-sized ungulates at Cal Guardiola (Berástegui et al., 2000).

5.5. Biochronological, paleoecological and paleoclimatic implications

The evidence reported in this paper from the Torrent de Vallparadís section expands the biochronological range of most Villafranchian carnivores until close to the Brunhes-Matuyama boundary. This is highly significant, because the presence of large predators is one of the main factors that probably affected the dispersal of humans across the Mediterranean area during the late Early Pleistocene. To this respect, food acquisition must have been one of the key problems for these first human populations to overcome in an environment subject to periodic glaciations. Several authors suggested that the survival of these hominids during the cold season, in the absence of vegetal resources, probably induced the development of scavenging strategies focused on ungulate carcasses (Martínez Navarro and Palmqvist, 1995; Arribas and Palmqvist, 1998; Palombo, in press). The availability of these carcasses depends to a large extent on the internal structure of the carnivore guild and the intrinsic relationships between top predators. To this regard, some scholars suggested that the presence of stable populations of sabertooth felids in the late Early Pleistocene of Europe, and specifically the activity of the dirk-toothed cat *Megantereon*, probably opened an ecological niche for scavengers. This role was probably played by both *Pachycrocuta* and early *Homo*, since *Megantereon*, given its great killing capabilities and peculiar dental characteristics, was probably unable to consume all of the meat that it obtained by hunting large ungulates (Turner, 1992; Martínez Navarro and Palmqvist, 1995; Palmqvist et al., 1996, 2005). These human populations had to compete directly for these carcasses with very powerful carnivores, such as sabertooth felids, *Pachycrocuta* and probably also pack-hunting lycaons, the jaguar *P. gombaszoegensis* and the puma-like cat *P. pardoides*, among others. Although several previous studies have shown that these early human populations were able to process carcasses (Selvaggio, 1998; Dominguez-Rodrigo and Pickering, 2003, and

references therein), the evidence provided by late Early Pleistocene localities with human presence, such as Vallonnet, Fuente Nueva 3 and Barranco León D, demonstrates that most of the reported scavenging activity in the preserved bones from these localities does in fact correspond to the short-faced hyenid *Pachycrocuta* (Echassoux, 2004; Espigares et al., 2008; Espigares, 2010).

We show here on the basis of the Vallparadís section that the above-mentioned conditions of the carnivore guild remained stable until close to the Brunhes-Matuyama boundary, which probably implies the maintenance of difficulties for humans when trying to obtain food resources. Even though Agustí et al. (2009) correlated the uppermost Early Pleistocene layers of the Vallparadís section with the glacial isotopic stage 22, on the basis of data reported here, it is more parsimonious to correlate the latest Early Pleistocene horizons of EVT and CGR with the interglacial stage 21. This is supported by the abundance of *H. antiquus* in these horizons. This fossil hippo, closely related to the extant species, is unlikely to have tolerated very cold temperatures resulting in the freezing of the rivers where they inhabited (Eltringham, 1999; Madurell-Malapeira, 2006), such as the cold temperatures typical of a glacial stage. All these data are also in agreement with the ESR-U-series data obtained for two horse teeth recovered from the layer 7 of the Vallparadís locality (Martínez et al., 2010), which yielded an estimated age of 0.83 ± 0.07 Ma, thus corresponding to the post-Jaramillo and pre-Brunhes part of the Vallparadís local section. After the interglacial stage 21, the carnivore guild would have begun to change, so that the concomitant difficulties that humans must have been obligated to face would have also changed. Thus, correlated with the isotopic stages 20 or 19, the lower levels of Trinchera Dolina in Atapuerca (Spain) display the earliest evidences in Europe of the presence of *C. crocuta* and *C. elaphus*, which are further associated to lithic artifacts and human remains (García and Arsuaga, 1999). The archeozoological study of this horizon shows that humans had primary and early access to carcasses and that there was only a very limited impact of carnivores, indicating that meat consumption was under the control of humans (Diéz et al., 1999). The probable decrease in carnivorous competitors after the OIS 21 (no secure records of *Megantereon*, *P. pardoides*, *L. lycaonoides* and *A. pardinensis* are available after this date) probably benefited hominin strategies for obtaining food resources.

After OIS 21, the record of Villafranchian elements progressively decreases, while the record of the new Galerian elements concomitantly increases. The earliest European lions are recorded from Pakefield (Great Britain) slightly before the Matuyama-Brunhes boundary (Parfitt et al., 2005). Shortly later, the first Indian Bovini (*H. galerianus*) is recorded in the Italian site of Ponte Galeria (Martínez-Navarro and Palombo, 2004). Then, when the Middle Pleistocene climatic transition is coming to an end, and climatic conditions are more or less stable, the latest-arriving Galerian elements make its first appearance in Europe. This is the case of *P. pardus*, recorded at ca 0.6 Ma from Valdemino Cave in Italy (Nocchi and Sala, 1997), whereas the earliest record of *M. trogontherii* probably corresponds to the similarly-aged German site of Süssenborn (Kahlke and Mania, 1994). Finally, when almost all the Villafranchian species had disappeared from Europe, and nearly all the Galerian newcomers were already recorded in the Mediterranean area, the Acheulian technology made its first appearance in Europe accompanied by the earliest representatives of *B. primigenius* at Venosa Notarchirico in Italy (Cassoli et al., 1999; Piperno, 1999).

6. Conclusions

The late Early to early Middle Pleistocene section from Torrent de Vallparadís records ca 600 ky of faunal evolution in south-western Europe in multiple stratigraphic horizons that are well-calibrated on the basis of magnetostratigraphic and small mammal

biostratigraphic data. The time interval recorded in this section coincides with highly significant climatic changes at a global scale (the MPT), which had important effects on the composition of mammalian assemblages and, as a consequence, probably in the relationships of European early *Homo* with their environment. The persistence of most components of the Villafranchian carnivore guild until close to the Brunhes-Matuyama boundary (probably until the interglacial stage 21), as shown here, would have had an important effect in determining the strategies of early *Homo* for obtaining food resources. After the Early to Middle Pleistocene boundary, typically Galerian large mammals (such as the spotted hyena, the leopard, the lion, the red deer and the straight-tusked elephant, among others) are commonly recorded in Europe, whereas Villafranchian carnivores, with the exception of *Homo-therium* (Reumer et al., 2003), have doubtful and sparse records. The extinction of most European Villafranchian carnivores must have benefited early *Homo* populations, as evidenced in the lower layers of the Gran Dolina of Atapuerca (Diéz et al., 1999), where the humans had primary and early access to the carcasses, therefore indicating that meat consumption was under their control. Finally, ca 0.6 Ma, once Villafranchian carnivores are lacking, and the African incoming carnivores typical of the Galerian are distributed throughout Europe, the earliest Acheulian tools are recorded in Venosa Notarchirico in association with the earliest remains of *B. primigenius* (Cassoli et al., 1999; Piperno, 1999; Martínez-Navarro, 2010). From this time onwards, once global climatic shifts had already ended, human settlements become common in Europe (Dennell, 2003; Palombo, in press). Finally, the presence of *E. antiquus* in the reversed magnetic polarity levels of the Vallparadís section is also noteworthy. This species of African origin represents the earliest Galerian element recorded in Europe, thus evidencing the presence of an open window for the dispersal of African species into Europe at ca 1 Ma.

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Appendix. Supplementary data

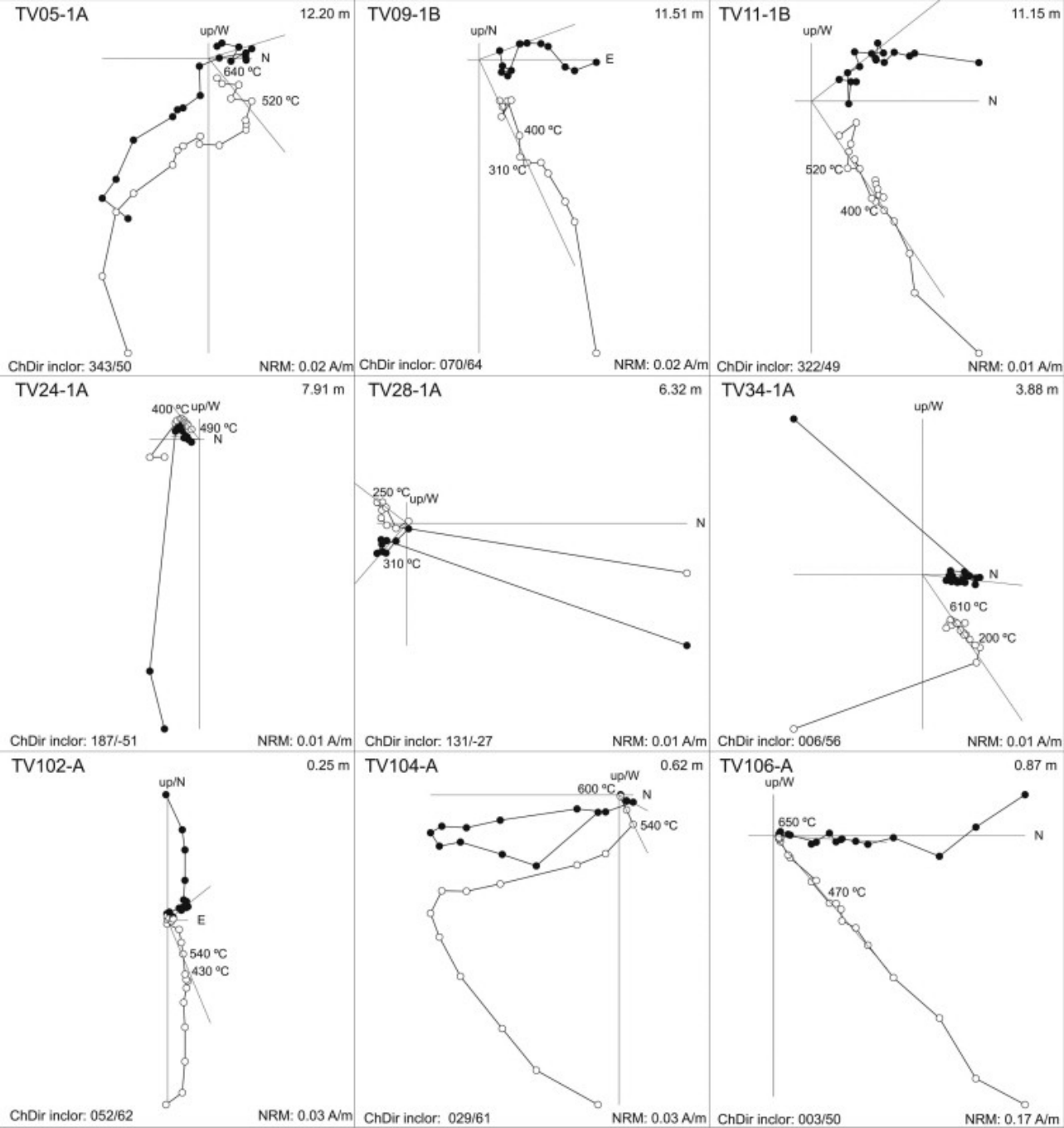
Supplementary data related to this article can be found online at doi:10.1016/j.quascirev.2010.09.020.

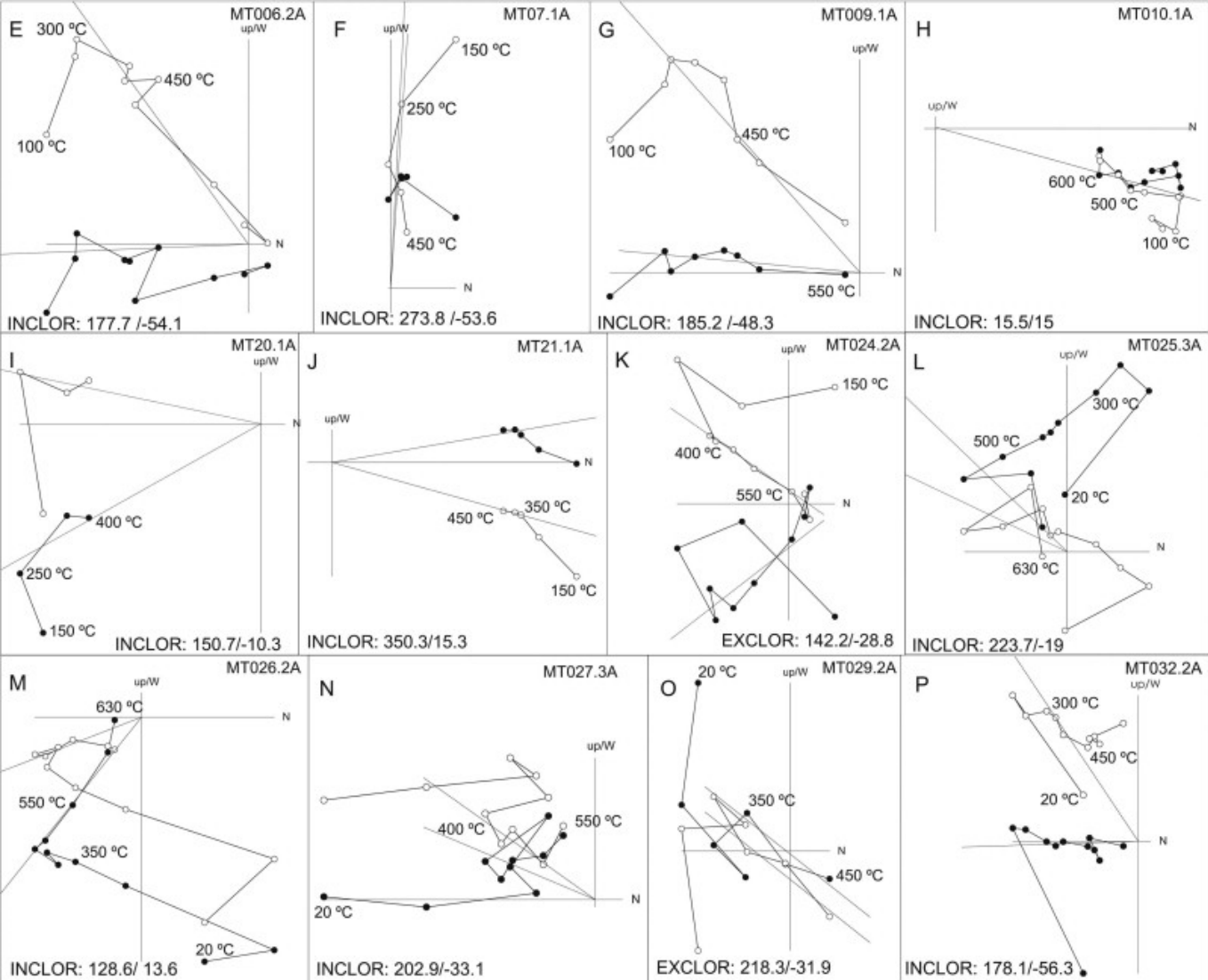
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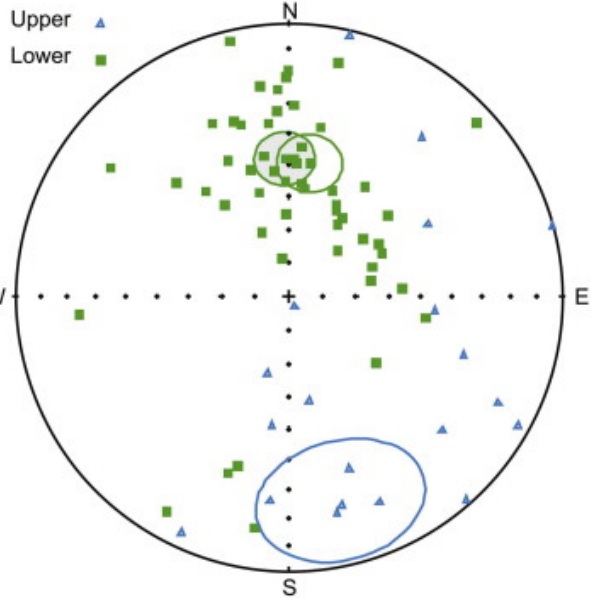
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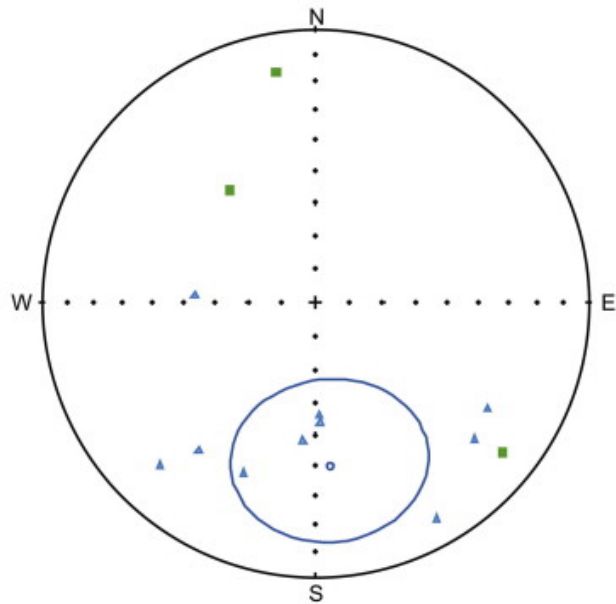




Vallparadís



Cal Guardiola



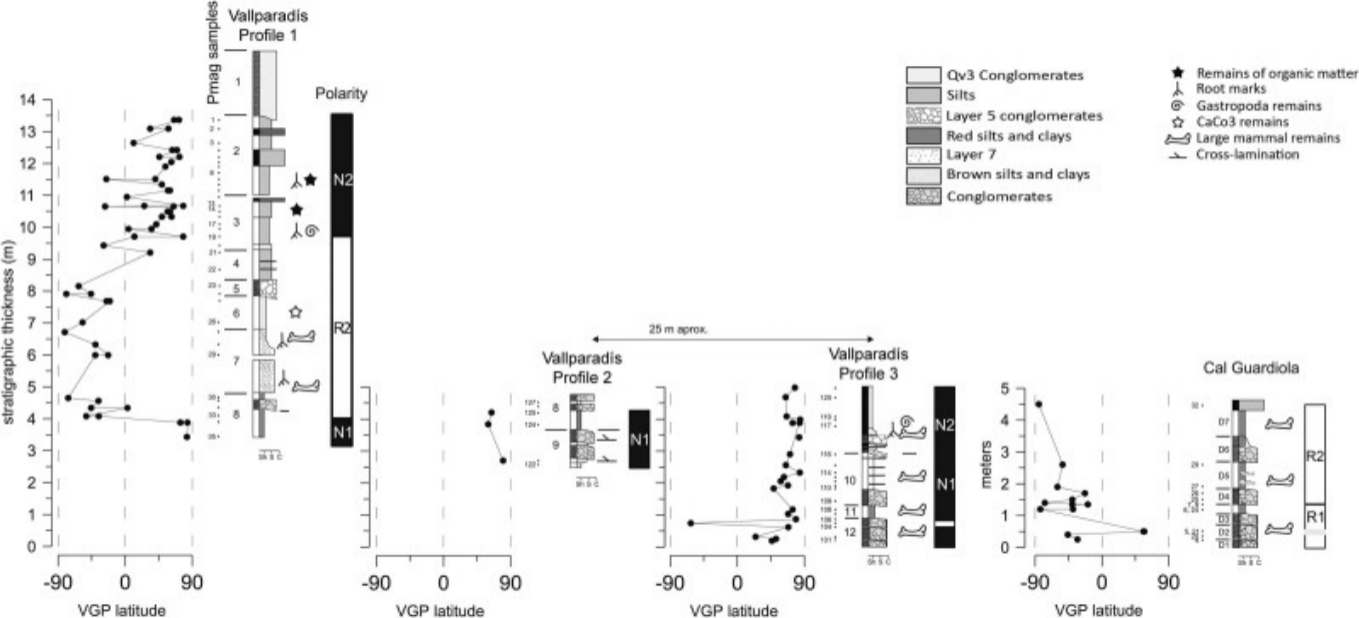


Table S1. Distribution of mammalian species from the several layers of the Torrent de Vallparadís section (Terrassa, Iberian Peninsula).

Layer	Cal Guardiola							Vallparadís							
	D1	D2	D3	D5	D6	D7	12	11	10	9	8	7	6	3	2
Primates															
<i>Macaca sylvanus</i> cf. <i>florentina</i>						X	X		X			X			
Carnivora															
<i>Pachycrocuta brevirostris</i>		X				X	X	X			X	X	X		
<i>Meles meles</i>							X					X			
<i>Ursus deningeri</i>					X	X	X	X	X			X	X		
<i>Lycaon lycaonoides</i>							X					X			
<i>Canis mosbachensis</i>		X				X	X					X			
<i>Vulpes praeglacialis</i>						X	X					X			
<i>Vulpes</i> sp.														X	
<i>Homotherium latidens</i>						X	X					X			
<i>Megantereon whitei</i>							X								
<i>Panthera gombaszoegensis</i>						X						X			
<i>Puma pardoides</i>												X			
Felidae indet.									X						
<i>Lynx</i> sp.							X					X			
Proboscidea															
<i>Elephas antiquus</i>					X	X						X	X	X	X
Perissodactyla															
<i>Equus altidens</i>	X	X	X		X	X	X	X	X	X	X	X	X		
<i>Equus</i> cf. <i>hydruntinus</i>														X	
<i>Equus</i> cf. <i>ferus</i>														X	X
<i>Stephanorhinus hundsheimensis</i>	X	X	X		X	X	X	X	X	X		X	X		
<i>Stephanorhinus</i> sp.														X	
Artiodactyla															
<i>Hippopotamus antiquus</i>	X	X	X	X	X	X	X	X	X		X	X	X		
<i>Sus</i> cf. <i>scrofa</i>						X	X				X	X			
<i>Dama vallonetensis</i>				X	X	X	X	X	X	X		X	X		
<i>Cervus elaphus</i>														X	
<i>Praemegaceros verticornis</i>	X	X		X	X	X	X	X				X	X		
<i>Bison</i> sp.	X	X	X			X	X	X	X		X	X	X	X	
Caprini indet.						X						X			
Rodentia															
<i>Mimomys savini</i>		X	X	X			X		X			X			
<i>Allophaiomys lavocati</i>			X												
<i>Iberomys huescarensis</i>				X			X		X			X			
<i>Allophaiomys chalinei</i>				X											
<i>Steocranius gregaloides</i>				X								X			
<i>Terricola arvalidens</i>														X	
<i>Arvicola mosbachensis</i>														X	
<i>Apodemus</i> cf. <i>sylvaticus</i>	X		X	X								X			
<i>Eliomys quericinus</i>			X				X					X			
<i>Hystrix refossa</i>	X						X					X			