

## The Epivillafranchian and the arrival of pigs into Europe

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### Abstract

Suids are found in Europe before and during the Olduvai magnetostratigraphic subchron, including the Fonelas P-1 site in the Guadix Basin (Andalusia, Southern Spain, ~2.0 Ma), in which the remains have been ascribed to *Potamochoerus magnus*, and many other localities that record the presence of *Sus strozzi* (e.g., Saint Vallier and Senèze in France). However, there is no pig record in the biochronological range comprised between the post Tasso Faunal Unit, which marks the base of the Late Villafranchian (~1.8 Ma), and their arrival in Western Europe at layer TE9 from Sima del Elefante, Atapuerca, Northern Spain (~1.2 Ma), where pigs are recorded under the name of *Sus* sp., and at the sites of Untermassfeld (Germany), Vallonnet (France) and layer EVT12 of Vallparadís Estació (Spain), dated 1.1-1.0 Ma (MIS31), which suid

remains have been ascribed to *Sus scrofa priscus* in the first site and to *Sus* sp. in the other two. Later, the genus *Sus* is recorded everywhere in Europe as a ubiquitous member of the Epivillafranchian/Galerian and posterior faunas. When pigs are in an ecosystem, they use to be abundant in the large mammal community given their opportunistic feeding behavior and high reproductive success. Their short gestation periods and elevated offspring numbers allow them to colonize new and varied environments and territories faster than other ungulates, which use to display a *K*-reproductive strategy, with a single pup per birth. For this reason, suids are usually preserved in the fossil assemblages after their dispersal and colonization of a geographic region. The arrival of suids phylogenetically related to *Sus* gr. *scrofa* into Europe marks the end of the Late Villafranchian and the beginning of the Epivillafranchian, which is approximately dated at ~1.2 Ma. Given that suids are omnivorous, generalist mammals with bunodont teeth that do not tolerate very low temperatures, this suggests that their colonization of Europe can be related to a change in the ecosystems and climate. In addition, the arrival of suids postdates the earliest arrival of hominins into Western Europe, which is documented at the Orce sites of Barranco León-D and Fuente Nueva-3 (~1.5-1.2 Ma). In these sites, rich faunal assemblages, abundant lithic artifacts and one human tooth have been unearthed after more than twenty years of excavations, but no evidence of pigs has yet been detected.

*Keywords: Suidae, Early Pleistocene, Europe, Orce, Pirro Nord, Dmanisi*

## **1. Introduction**

The Villafranchian is a biochronological unit of large mammals, which includes the Late Pliocene and most of the Early Pleistocene in Europe. This land mammal stage is characterized by the succession of a number of faunal turnovers marked by the extinction of species and the arrival of new immigrants (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Martínez-Navarro, 2010; Rook and Martínez-Navarro, 2010). It is currently divided in the Early Villafranchian for the Late Pliocene, the Middle Villafranchian for the early Early Pleistocene (Gelasian), until the base of the Olduvai paleomagnetic normal event, and the Late Villafranchian, which comprises a large part of the late Early Pleistocene (Calabrian) and ends around 1.2 Ma, below the base of the normal paleomagnetic event Jaramillo (see Rook and Martínez-Navarro, 2010; Madurell-Malapeira et al., 2014; Palombo, 2014; Bellucci et

al., in press; and references therein). For a discussion on the dynamics of faunal turnover in the pre-Jaramillo small mammals, see Cuenca-Bescós et al. (in press). The Villafranchian is succeeded by the Epivillafranchian or Early Galerian stage, which includes the time span from the latest pre-Jaramillo, around 1.2 Ma, until the post-Jaramillo, around 0.8 Ma (for its definition and discussion, see in this issue Bellucci et al., in press).

In this context, the earliest arrival of humans into Western Europe is a much debated topic, with an important amount of information pointing to a dispersal of hominins from the Caucasus to Europe in a chronology earlier than Jaramillo, as recorded at the sites of Orce in southern Spain (Martínez-Navarro et al., 1997; Arribas and Palmqvist, 1999; Oms et al., 2000; Palmqvist et al., 2005; Espigares et al., 2013; Toro-Moyano et al., 2013; Álvarez et al., in press), Atapuerca TE-9 in northern Spain (Carbonell et al., 2008; Lorenzo et al., in press.), Lezignan-la-Cèbe in southern France (Crochet et al., 2009; Bourguignon et al., 2014), Pirro Nord in southern Italy (Arzarello et al., 2009), Kozarnika Cave, Bulgaria (Sirakov et al., 2010), or Kocabaş in the Denizli basin, Turkey (Lebatard et al., 2014). In spite of this, it is worth noting that there are a few researchers who do not consider the fossil faunal assemblages and the inferred biochronologic data for these sites, thus claiming that humans did not arrive in western Europe until a post-Jaramillo age (Muttoni et al., 2010, 2013). However, this interpretation is in contrast with the radiometric ages estimated for the Orce sites,  $1.43 \pm 0.38$  Ma for BL-D (Toro-Moyano et al., 2013) and  $1.19 \pm 0.21$  Ma for FN-3 (Duval et al., 2012) using the combined U-series/ESR method,  $1.50 \pm 0.31$  Ma for FN-3 from cosmogenic nuclides (Álvarez et al., in press), and also for TE-9,  $1.22 \pm 0.16$  Ma from cosmogenic nuclides (Carbonell et al., 2008), which clearly point in all cases to a pre-Jaramillo chronology (see discussion on these age estimates in Palmqvist et al., 2015).

In this study, we discuss (1) the importance of the absence of fossil record of suids in Europe during an important part of the Late Villafranchian; (2) the reproductive ecology of suids compared to other ungulate groups; (3) the chronology of the arrival of *Sus gr. scrofa* in a pre-Jaramillo age; (4) the potential biases posed by the fragmentary and geographically limited nature of the biochronological record of Early Pleistocene large mammals in Europe; and (5) the significance of the archaeological and paleoanthropological record of the Orce and Pirro Nord sites in a chronology that predates the arrival of pigs in Western Europe during the Epivillafranchian.

## 2. The absence of suids during the Late Villafranchian of Europe

The lack of record of a taxon in a fossil assemblage is not an evidence of its absence from the original paleocommunity, as it may result from taphonomic causes and/or environmental circumstances (as the latter often determine the taphonomic context in which the skeletal remains are preserved). However, the consistent absence of suids from any of the rich large mammals assemblages unearthed from the Late Villafranchian sites of Europe with chronologies between 1.8 and 1.2 Ma, including Dmanisi in Georgia (Vekua, 1995; Lordkipanidze et al., 2007), Kocabaş in Turkey (Lebatard et al., 2014), Apollonia 1 in Greece (Kostopoulos, 1997), Argentario and Pirro Nord in Italy (Sardella et al., 2008; Arzarello et al., 2009; Martínez-Navarro et al., 2012), Sainzelles in France (Thouveny and Bonifay, 1984), or the Spanish sites of Orce (Venta Micena, FN-3 and BL-D) (Martínez-Navarro and Palmqvist, 1995; Martínez-Navarro et al., 1997, 2011; Oms et al., 2000; Palmqvist et al., 2005; Toro-Moyano et al., 2013), and Incarcál (Ros-Montoya et al., 2012). (Figs. 1 and 2), and their presence during the Epivillafranchian and the early Middle Pleistocene in many European sites (e.g., Le Vallonnet, Hérault and Pech de L'Azé in France, Untermassfeld in Germany, Vallparadís Section EVT12, EVT7 and CGRD7, and layer TE-9 from Atapuerca sima del Elefante in Northern Spain) is a strong argument that should not be avoided, as the presence or absence of pigs is most probably a reliable biochronological marker for this part of the Early Pleistocene in the European continent.

In contrast, suids are abundantly preserved in Europe before and during the Olduvai subchron at the Olivola and Tasso Faunal Units in the base of the Late Villafranchian, just before ~1.8 Ma, including the Fonelas P-1 site in the Guadix Basin (Southern Spain), dated to 2.0 Ma, where suid remains were ascribed to *Potamochoerus magnus* (Arribas et al., 2009), and at many other localities in the continent in which the fossil remains are currently ascribed to *Sus strozzi* (for review, see Rook and Martínez-Navarro, 2010; Bellucci et al., in press) (Figs. 1 and 2). However, no record of suids is consistently found in Europe during the chronological time span comprised between the post Tasso Faunal Unit and TE9 from Atapuerca Sima del Elefante (~1.2 Ma), where suid remains are ascribed to *Sus* sp. (Carbonell et al., 2008), and at the sites of Untermassfeld (Germany), Vallonnet (France) and layer EVT12 of Vallparadís Estació (Northeastern Spain), dated 1.0-1.1 Ma (MIS31), where pig remains have been

classified as *Sus scrofa priscus* in the first locality and as *Sus* sp. in the other two (Gúerin and Faure, 1997; Moullé et al., 2006; Madurell-Malapeira et al., 2010, 2014). Later, the genus *Sus* is recorded everywhere in Europe as a ubiquitous member of the Epivillafranchian/Early Galerian and posterior faunas.

*Sus strozzi* has been reported by the presence of a teeth (an upper second molar) in a Late Villafranchian site of the Ellera basin (Italy), tentatively dated at about 1.6-1.5 Ma (Pazzaglia et al., 2013), which assemblage is composed of typical Villafranchian taxa (e.g., *Stephanorhinus etruscus*, *Hippopotamus* cf. *antiquus*, *Leptobos* sp. and *Axis* sp.). Unfortunately, the exact geographic and stratigraphic origin of these remains is unclear and only their provenance from the Ellera basin is certain, due to the presence of original historical labels associated to each specimen (Pazzaglia et al., 2013). Moreover, the single talus attributed to *S. etruscus* is fragmentary and thus cannot be discarded its attribution to *S. hundsheimensis*. Similarly, *Leptobos* is typical of chronologies earlier than the Olduvai normal paleomagnetic subchron in Europe, but not later. The form of *Bison* that arrives into Europe, recorded at Dmanisi at 1.8 Ma (previously named *Dmanisibos georgicus*, in Vekua, 1995), is a direct descendant of *Leptobos* (Martínez-Navarro et al., 2007, and references therein) and its arrival is coincident with the disappearance of *Leptobos*. Thus, *Leptobos* is recorded at the Tasso Faunal Unit, but not later, and the material described from the Ellera Basin is absolutely fragmentary and can be perfectly attributed to *Bison* instead of *Leptobos*. Finally, *Hippopotamus* is abundant in Europe after its record at Venta Micena around 1.6-1.5 Ma, but the records of this taxon earlier than this chronology are very doubtful, as those from the Upper Valdarno (see Napoleone et al., 2003) or from Coste San Giacomo (Bellucci et al., 2012). Therefore, it is impossible to know the chronology of this fauna with these elements. Also, a current revision on the fauna from the Epivillafranchian site of La Boella in Catalonia (northeastern Spain), where the presence of *Sus strozzii* has been recently cited (Vallverdú et al., 2014), suggests that the fossil remains of Suidae from this site must be included in *Sus* gr. *scrofa*.

In any case, the relatively low preservational completeness and the geographic limitations of the European record of large mammals can pose some problems to the biochronological interpretation proposed in this work. In fact, there are few paleontological localities with thousands of skeletal remains from hundreds of individuals unearthed after decades of systematic excavation, for example Fonelas P-1,

Saint Vallier, Venta Micena, Untermassfeld, Vallonnet, or Vallparadís Section. However, even in these unique assemblages many craniodental and postcranial specimens are severely damaged by the hyenas (e.g., see Arribas and Palmqvist, 1998; Kahlke and Gaudzinski, 2005; Espigares, 2010; Palmqvist et al., 2011) or altered by other taphonomic processes and agents (e.g., fluvial transport and weathering). For this reason, it is often difficult to identify some ungulate taxa preserved in the sites, as illustrated by the recent description of a bovine species in Venta Micena by the first time in Europe (*Hemibos* aff. *gracilis*) from skeletal remains that were previously attributed to other taxa (Martínez-Navarro et al., 2011). Given these limitations of the Pleistocene record, it is not surprising that suids remains have not been identified by the moment in a number of large mammals assemblages of Epivillafranchian age (e.g., Het Gat in the Netherlands, Huéscar-1 in Spain, Durfort in France, Colle Curti, Redicicoli and Madonna della Strada in Italy, and Megapolis-Marathousa in Greece; see review in Bellucci et al., in press). These assemblages are composed of comparatively lower numbers of specimens than the ones cited above. For this reason, the absence of pig remains in them can merely result from incomplete sampling of these localities (i.e., low observational completeness).

Given their opportunistic feeding behavior and high reproductive potential, when suids are present in an ecosystem they use to be abundant in the extant community of large mammal species, which results in good opportunities for their remains of being preserved in the fossil assemblage generated from this community. Specifically, the demographic potential of suids is unique among ungulates, because they follow an *r*-selection-like reproductive strategy, with elevated offspring numbers. This is exemplified by data in Figure 3, which shows that suids have higher litter sizes (and, correspondingly, higher teat numbers) than all other ungulates, traits in which suids resemble the reproductive ecology of fissiped carnivores. Given that tayassuids, the American sister family of suids, do not differ in litter size and teat number from other ungulates (Fig. 3), this suggests that the elevated litter size of suids is an evolutionarily derived trait exclusive of suids. In addition, all suid species plot below the regression lines derived in ungulates for length of gestation period (Fig. 4A) and neonate body mass (Fig. 4B) on adult body mass, with several species situated below the lower 95% confidence intervals of these regressions. This indicates that suids have comparatively shorter gestation periods and lower values of neonate mass than other ungulates of

similar body size, aspects in which they behave also as terrestrial carnivores. In contrast, interbirth interval (Fig. 4C), weaning age (Fig. 4D) and age of sexual maturity (Fig. 4E) scale in suids as expected for ungulates of their body size, with most species plotting between the upper and lower 95% intervals of the regression lines, aspects that distinguish ungulates from terrestrial carnivores, in which weaning age is comparatively longer (data not shown). The combination of reproductive traits of suids probably means that their extraordinary capability of reproduction allows them to colonize new and varied environments and territories faster than other ungulates, which use to display a *K*-reproductive strategy, with a single pup per birth, a long gestation period and a neonate well developed (Figs. 3-4). For this reason, suids are usually abundantly preserved in the fossil assemblages. As in the case of rodents, the biostratigraphy of the Neogene-Quaternary of Africa is largely based on suids (White and Harris, 1977; Harris and White, 1979; Cooke, 1978, among others; Bishop, 2010, and references there in). However, although suid remains are well represented in the African and Asian archaeological and paleontological sites, including those from the Levantine Corridor as 'Ubeidiya (Geraads et al., 1986), dated 1.3-1.6 Ma (Martínez-Navarro et al., 2009, 2012), they are apparently not present in the European continent during the period comprised between 1.8 and 1.2 Ma.

### **3. Discussion and conclusions**

It could be argued that the absence of pigs in those European sites with chronology included in the time span between 1.8 and 1.2 Ma may be related to preservational biases of the mammalian fossil record, as discussed above. However, we can affirm that after a long period of systematic excavations at sites such as Dmanisi, which has provided a huge collection of large mammals remains, including an abundant record of ungulates, carnivores and also hominins, no pigs have ever been found. Similarly, at the sites of Orce, after more than 30 years of fieldwork and continuous research in the triangle formed by the region of Orce-Fuente Nueva-Venta Micena, and systematic excavation of 370m<sup>2</sup> at Venta Micena, 140m<sup>2</sup> at Barranco León, and 106 m<sup>2</sup> at Fuente Nueva-3, no pig remains have ever been found among the more than 27,000 large mammal fossils unearthed from these sites. We must also consider that the stratigraphic series of Orce probably preserves the best record of Early Pleistocene fauna in the European subcontinent.

The extinction or the arrival of suids in a given territory can be a major biochronological marker, and the data discussed suggests that their sudden appearance in the European continent marks the end of the Late Villafranchian and the beginning of the Epivillafranchian, which has been approximately dated at ~1.2-1.1 Ma (see Rook and Martínez-Navarro, 2010). In addition, most suids are omnivorous, generalist species with bunodont (round cusped) teeth that do not tolerate very low temperatures, which suggests that their colonization of Europe could be related to a change in the ecosystems and climate probably as a consequence of the great climatic shifts associated with the 'Mid-Pleistocene Revolution' (Maslin and Ridgwell, 2005; Clark et al., 2006). The faunal composition of TE9, which preserves the earliest presence of suids (*Sus gr. scrofa*) in a pre-Jaramillo age, indicates that it may record a warm event, as suggested by the abundant presence of "giant" shrews (Rofes and Cuenca-Bescós, 2009), an event that would have also allowed the dispersal of suids in Europe.

Following this reasoning, the arrival of suids at the sites of Atapuerca TE9 (Carbonell et al., 2008), Untermassfeld (Guerin and Faure, 1997), Vallonnet (Moullé et al., 2006) and Vallparadís Estació EVT12 (Madurell-Malapeira et al., 2010; 2014) marked the beginning of the faunal assemblages typical of the European Epivillafranchian, and they became a permanent and well recorded species in most archaeopaleontological sites of the continent until the present. For this reason, the presence of *Sus gr. scrofa* should be considered as a major bioevent in addition to those recently proposed for the definition of the Epivillafranchian biochrone in Europe (i.e., the first appearance of *Praemegaceros verticornis*, *Bison menneri* and *Crocota crocuta*; Bellucci et al., in press).

Finally, it is also worth indicating that the arrival of suids is subsequent to the dispersal of humans in Europe and its surrounding areas, as recorded in Spain at the Orce sites of BL-D (dated ~1.4 Ma by Toro-Moyano et al., 2013) and FN-3 (dated ~1.5-1.2 Ma after Duval et al., 2012 and Álvarez et al., in press), in Italy at the Pirro Nord locality (dated within the *Allophaiomys ruffoi* zone, in a chronology ranging from 1.6 to 1.3 Ma after López-García et al., 2015), and in Turkey at the Kocabaş site, dated in the 1.3–1.1 Ma range by Lebatard et al. (2014). The lack of coexistence between the hominin populations that first dispersed in Europe with an Oldowan technology and suids can be tentatively interpreted in terms of competitive displacement, because the opportunistic trophic behavior of both groups would probably exceed the permissible degree of niche



overlap in the Late Villafranchian ecosystems. However, further studies are required to address this issue.

#### *Acknowledgments:*

We thank Mathieu Duval for inviting us to participate in the ESF EarthTime-EU initiative “The Early-Middle Pleistocene transition: Significance of the Jaramillo subchron in the sedimentary record” and to contribute to this special issue. This work is part of a project authorized and funded by the 'Consejería de Educación, Cultura y Deportes' of the Junta de Andalucía (contract Exp. B090678SV18BC) and has also been supported by grants of the Spanish Ministry of Economy and Competitiveness CGL2010-15326/BTE, CGL2011-28681, CGL2011- 30334/BTE, project P11-HUM-7248 from Junta de Andalucía, grant HAR2010-19957/HIST, Generalitat de Catalunya GENCAT 2009 SGR 324 and 2009 SGR 754 GRC, and a personal grant to T. M. by the Atapuerca Foundation. Last but not least, we gratefully acknowledge the constructive remarks provided by three anonymous reviewers.

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*Figure captions:*

**Figure 1.** Geographical situation of selected Early and Middle Pleistocene sites included in the study. Middle Villafranchian (Black circles), 1, Puebla de Valverde; 2, Fuente Nueva-1; 3, Fonelas P-1; 4, Perrier; 5, Saint-Vallier; 6, Montopoli; 7, Coste San Giacomo; 8, Varshets; 9, Dafnero. Late Villafranchian (Black squares), 10, Venta Micena, Barranco León and Fuente Nueva-3; 11, Olivola; 12, Pirro Nord; 13, Sainzelles; 14, Ceyssaguet; 15, Apollonia-1; 16, Dmanisi. Epivillafranchian (White circles), 17, Atapuerca TE9; 18, Vallparadís Section; 19, Colle Curti; 20, Vallonnet; 21,



Untermassfeld; 22, Kozarnika; 23, Kocebas. Galerian (White squares), 24, Isernia; 25, Ponte Galeria; 26, Valdemino; 27, Mauer; 28, Aragón; 29, West Runton; 30, Pakefield.

Figure 2. Chronological range of selected Early and early Middle Pleistocene European large mammals (including suids) correlated with the geomagnetic polarity scale, the marine isotopic stages and Mammal ages. Abbreviations: Ata, Atapuerca; EVT, Vallparadís Estació; CGR, Cal Guardiola, Ata-TE9, Atapuerca Trinchera Elefante 9, Ata-TD6, Atapuerca Trinchera Dolina 9.

**Figure 3.** Litter size (A) and teat number (B) in ungulates (species ordered by body size in the X-axis). Data from the PanTHERIA database (Jones et al., 2009).

**Figure 4.** Least-squares linear regressions (solid lines) for the relationship between mean adult body mass (X-axis) and gestation length (A), neonate body mass (B), interbirth interval (C), weaning age (D) and age of sexual maturity (E) (Y-axes) in ungulate species. Striped lines indicate the 95% confidence intervals above and below the regression line. Variables log-transformed. Data from the PanTHERIA database (Jones et al., 2009).

Figure 1  
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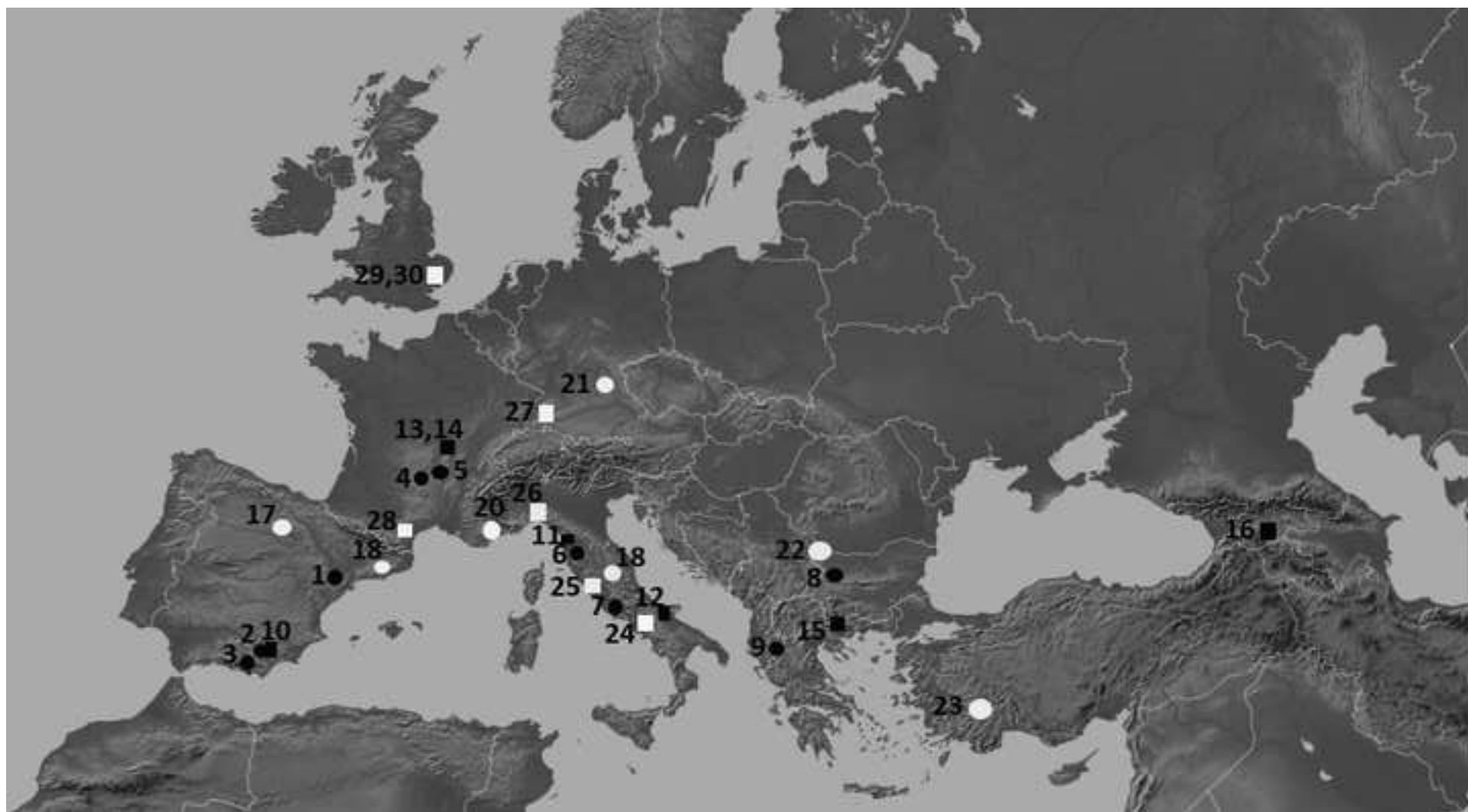




Figure 3  
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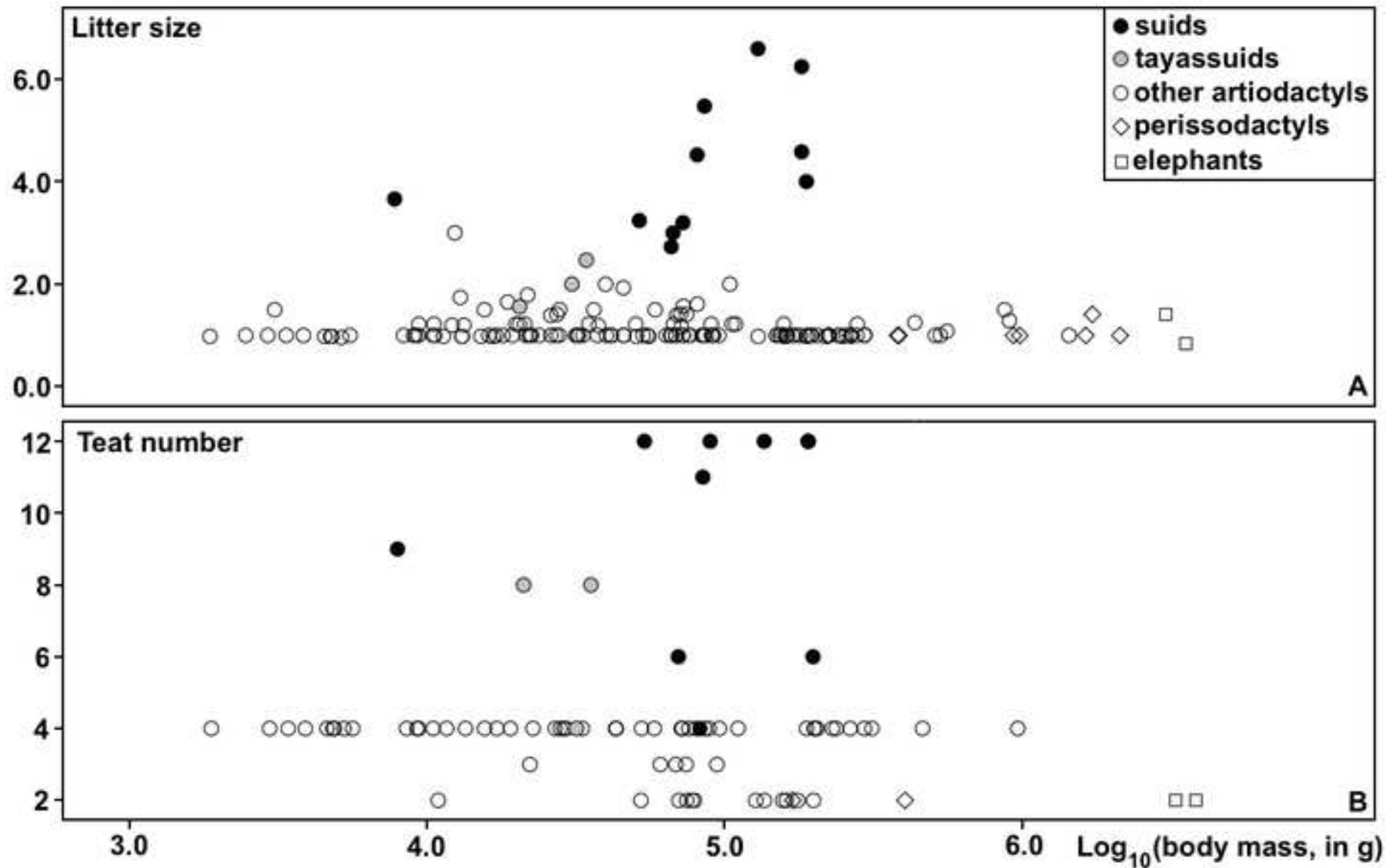
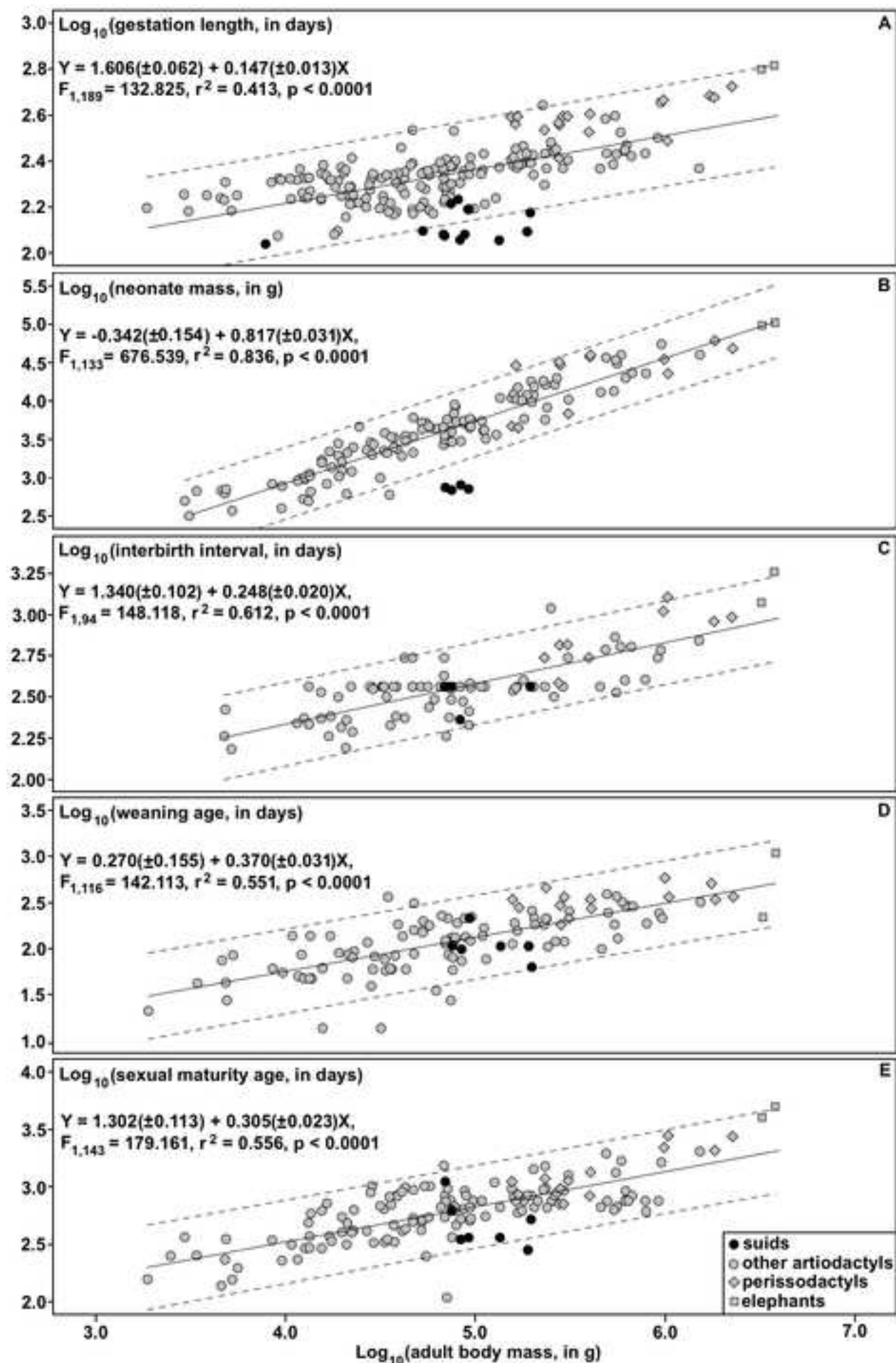


Figure 4

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Reviewers 2 and 3 comments and our response (penciled in green for Reviewer 2 and in grey for Reviewer 3, for ease of recognition):

## REVIEWER 2:

### GENERAL COMMENTS

Martínez-Navarro et al. report the absence of suids in the Late Villafranchian record of Europe and suggest their reappearance may be used as a biochronological marker for the Epivillafranchian. This is a very interesting work that naturally raises two main questions: (i) is this absence of suids real, or simply an artifact due to a poor palaeontological record?; (ii) does this absence have a biochronological meaning ?

Although it seems indeed that there are some evidence pointing in the direction indicated by the authors, the manuscript is unfortunately overall not totally convincing, as the conclusions are not entirely supported by the data presented. Again, the authors may be right, but they need to provide additional data. Several factors may potentially impact the relevance of their conclusions, and each of them should openly and fairly be discussed in the manuscript: (i) the fragmented and geographically limited palaeontological record, (ii) a possible taphonomic bias, (iii) the role of biogeography, (iv) the uncertainty on the age of the sites and (v) the potential outliers.

We have tried to answer all of these questions, and have included in the manuscript the new information suggested by the reviewer (i.e., taphonomic aspects related to completeness of the large mammals record, problems with age determinations, etc.).

#### 1. A fragmented and geographically limited biochronological record

Perhaps the most striking observation is the fragmented aspect of the Early Pleistocene mammal record in Europe, with a very limited number of sites. The authors mention only a very a few Late Villafranchian sites in the manuscript (e.g. Dmanisi, Apollonia 1, Argentario and Pirro Nord, Sainzelles, Orce and Incarcal), and even less have been reported in Fig.1. Is there any reason why only these sites have been selected? A quick look at Madurell-Malapeira et al (2014), Palombo (2014) [Fig. 1] and Rook and Martínez-Navarro (2010) [Fig. 3] suggest that several other Late Villafranchian sites may be included in the present study. If possible, I would encourage the authors to expand their dataset by including more the Late Villafranchian sites in Europe (or Southern Europe, see later). If specific criteria are used to select/eliminate the sites included in the study (e.g. richness of the fossil record, imprecise chronology, etc.), they should at least be mentioned.

Actually, the palaeontological record presented in the MS includes only one Late Villafranchian site that is not located in South Western Europe (Dmanisi). All the other sites are from Greece, France, Italy, and mostly from Spain. Consequently, it does not seem very relevant to extrapolate a conclusion for the whole European continent: the authors should thus limit their discussion and interpretation to the South Western Europe and avoid using the term “Europe”

(otherwise the discussion should include all the Late Villafranchian sites of the continent). Changes should be made accordingly in the text as well as in the title and Fig. 1.

To support their demonstration, the authors should add to the manuscript:

- (i) A map locating all the sites mentioned in the text in order to see their geographical distribution. Those that do not document suids should be highlighted.
- (ii) A table with the detailed biochronological record including selected faunal assemblages for Italy, Spain and France (i.e. a significantly extended version of Fig. 1).

As suggested by the reviewer, we have included a map and a new table (figures 1 and 2) with this information and more sites are discussed now in the text.

## 2. The taphonomic bias

As mentioned by the reviewer #1, the large mammal record may be significantly affected by a taphonomic bias. However, the authors convincingly address this issue with the examples of the Orce sites and Dmanisi, for which the extensive and systematic excavations carried out over many years, and combined with the richness of the paleontological record, seem indeed to indicate that suids were really absent. However, it is unclear whether this argument may be also applied to the other sites like Pirro Nord or others, as all of them may not have been subject to extensive excavations or have a very limited fossil record. This should be mentioned in the MS.

(see in point 3)

## 3. The role of biogeography

Suids may simply be absent at a given site because biogeographical conditions were not favorable at that time. To address this question, it seems the Guadix-Baza record may be used as a reference, as the authors emphasise “that the stratigraphic series of Orce probably preserves the best record of Early Pleistocene fauna in the European subcontinent.” If it can be demonstrated that suids were present in the basin before and after VM, BL and FN, then the biogeographic argument would lose some weight. This has been briefly mentioned by the authors with Fonelas P1 and Cúllar, but there are many other sites that may be integrated in the discussion, e.g. Huescar-1, Huelago, la Solana del Zamborino, Fuente Nueva-1, Barranco Conejos, etc. The list is probably incomplete. Perhaps the Guadix-Baza record may be also included in a dedicated column as part of Fig.1.

In which concerns these two points, we have included the following paragraph:

“In any case, the relatively low preservational completeness and the geographic limitations of the European record of large mammals can pose some problems to the biochronological interpretation proposed in this work. In fact, there are few paleontological localities with thousands of skeletal remains from hundreds of individuals unearthed after decades of systematic excavation, for example Fonelas P-1, Saint Vallier, Venta Micena, Untermassfeld, Vallonnet or Vallparadís Section. However, even in these unique assemblages many craniodental and postcranial specimens were severely damaged by the hyenas (e.g., see

Arribas and Palmqvist, 1998; Kahlke and Gaudzinski, 2005; Espigares, 2010; Palmqvist et al., 2011) or were altered by other taphonomic processes and agents (e.g., fluvial transport and weathering). For this reason, it is often difficult to identify some ungulate taxa preserved in the sites, as illustrated by the recent description of a bovine species in Venta Micena by first time in Europe (*Hemibos* aff. *gracilis*) from skeletal remains that were previously attributed to other taxa (Martínez-Navarro et al., 2011). Given these limitations of the Pleistocene record, it is not surprising that suids remains have not been identified by the moment in a number of large mammals assemblages of Epivillafranchian age (e.g., Het Gat in the Netherlands, Huéscar-1 in Spain, Durfort in France, Colle Curti, Redicicoli and Madonna della Strada in Italy, and Megapolis-Marathousa in Greece; see review in Bellucci et al., in press). These assemblages are composed of comparatively lower numbers of specimens than the ones cited above. For this reason, the absence of pig remains in them can merely result from incomplete sampling of these localities (i.e., low observational completeness)".

#### 4. Existing age uncertainties

The existing age uncertainties for most of the sites are not discussed at all, whereas many localities mentioned in the manuscript have either not been dated at all (Apollonia-1, Sainzelles, Argentario?), or have only magnetostratigraphic constraints (Pirro) or imprecise numerical age results (BL, FN). Perhaps the only exception is Dmanisi. If numerical ages are quoted, associated errors should be given or if not, mentioned as approximated values. The age uncertainties on the sites should be acknowledged and briefly discussed to see in which extent they may impact the conclusions of the work.

We have discussed this, as follows:

In this context, the earliest arrival of humans into Western Europe is a much debated topic, with an important amount of information pointing to a dispersal of hominins from the Caucasus to Europe in a chronology earlier than Jaramillo, as recorded at the sites of Orce in southern Spain (Martínez-Navarro et al., 1997; Arribas and Palmqvist, 1999; Oms et al., 2000; Palmqvist et al., 2005; Espigares et al., 2013; Toro-Moyano et al., 2013; Álvarez et al., in press), Atapuerca TE-9 in northern Spain (Carbonell et al., 2008; Lorenzo et al., in press.), Lezignan-la-Cèbe in southern France (Crochet et al., 2009; Bourguignon et al., 2014), Pirro Nord in southern Italy (Arzarello et al., 2009), Kozarnika Cave, Bulgaria (Sirakov et al., 2010), or Kocabaş in the Denizli basin, Turkey (Lebatard et al., 2014). In spite of this, it is worth noting that there are a few researchers who do not consider the fossil faunal assemblages and the inferred biochronologic data for these sites, thus claiming that humans did not arrive in western Europe until a post-Jaramillo age (Muttoni et al., 2010, 2013). However, this interpretation is in contrast with the radiometric ages estimated for the Orce sites,  $1.43 \pm 0.38$  Ma for BL-D (Toro-Moyano et al., 2013) and  $1.19 \pm 0.21$  Ma for FN-3 (Duval et al., 2012) using the combined U-series/ESR method,  $1.50 \pm 0.31$  Ma for FN-3 from cosmogenic nuclides (Álvarez et al., in press), and also for TE-9,  $1.22 \pm 0.16$  Ma from cosmogenic nuclides (Carbonell et al., 2008), which clearly point in all cases to a pre-Jaramillo chronology (see discussion on these age estimates in Palmqvist et al., 2015).



## 5. Potential outliers

Several sites may potentially present evidence against the conclusions defended by the authors. However, these should not be ignored, but rather openly discussed. For example the discussion about the fauna from the Ellera basin in answer to the reviewer #1 should be included in the MS. The same applies for Ubeidiya and the possible occurrence of *Sus strozzi* mentioned by the authors. There is another example with the work by Palombo and Valli (2003) [Table 1], where the presence of *Sus strozzi* has been reported in France from MN17a to MNQ20 (see below), whereas the evidence in appendix may show the opposite. The authors may have some disagreements regarding the stratigraphic position, age attribution or taxonomical attributions presented in previous studies and should share them with the scientific community.:

We have included the information on the Ellera basin and from the Spanish site of La Boella:

“It should be noted, however, that *Sus strozzi* has been reported by the presence of a teeth (an upper second molar) in a Late Villafranchian site of the Ellera basin (Italy), tentatively dated at about 1.6-1.5 Myr (Pazzaglia et al., 2013), which assemblage is composed of typical Villafranchian taxa (e.g., *Stephanorhinus etruscus*, *Hippopotamus* cf. *antiquus*, *Leptobos* sp. and *Axis* sp.). Unfortunately, the exact geographic and stratigraphic origin of these remains is unknown and only their provenance from the Ellera basin is sure, due to the presence of original historical labels associated to each specimen (Pazzaglia et al., 2013). Moreover, the single talus attributed to *S. etruscus* is fragmentary and thus cannot be discarded its attribution to *S. hundsheimensis*. Similarly, *Leptobos* is typical of chronologies earlier than the Olduvai normal paleomagnetic subchron in Europe, but not later. The form of *Bison* that arrives into Europe, recorded at Dmanisi at 1.8 Ma (previously named *Dmanisibos georgicus*, in Vekua, 1995), is a direct descendant of *Leptobos* (Martínez-Navarro et al., 2007, and references therein) and its arrival is coincident with the disappearance of *Leptobos*. Thus, *Leptobos* is recorded at the Tasso Faunal Unit, but not later, and the material described from the Ellera Basin is absolutely fragmentary and can be perfectly attributed to *Bison*, better than to *Leptobos*. Finally, *Hippopotamus* is abundant in Europe after its record at Venta Micena around 1.5-1.6 Ma, but the records of this taxon earlier than this chronology are very doubtful, as those from the Upper Valdarno (see Napoleone et al., 2003) or from Coste San Giacomo (Bellucci et al., 2012). Therefore, it is impossible to know the chronology of this fauna with these elements. Also, a current revision on the fauna from the Epi-Villafranchian site of La Boella, in Catalonia, northeastern Spain, where it was cited the presence of *Sus strozzi* (Vallverdú et al., 2014), suggest that the *Suidae* fossil remains from this site have to be included in *Sus* gr. *scrofa*”.

In addition to the points previously raised, I would have two additional general comments/questions:

## 6. A marker for the beginning of the Epivillafranchian ?

The authors state that “the arrival of suids in a given territory is a major biochronologic marker, and their sudden appearance in the European continent marks the end of the Late Villafranchian and the beginning of the Epivillafranchian”. However:

(i) in previous studies some authors have positioned FN-3 and BL in the Epivillafranchian biochron (Bellucci et al., 2015).

As we defend in the manuscript (and discuss more in-depth now the evidence that favors our interpretation), we consider that FN-3 and BL-D correspond to the Late Villafranchian and not to the Epivillafranchian.

(ii) In addition there are some apparent inconsistencies between the two studies, Bellucci et al. mentioning suids in Untermassfeld and Vallparadís (Table 1), whereas the authors also added TE9 and Le Vallonnet. Why these differences?

Well, if Bellucci et al. do not include TE9 and Le Vallonnet in their study, maybe the reviewer has to ask them. As we discuss in the text, the presence of *Sus gr. scrofa* is published by the authors that have been or are working in these sites. Both localities have a very important paleontological and archaeological record.

(iii) I think the authors are providing a major contribution to the definition of the Epivillafranchian by adding a third major bioevent in addition to the two previously proposed by Bellucci et al. (*Praemegaceros verticornis* e *Bison menneri* FO and *Crocota crocuta* FO).

We have added this paragraph:

“For this reason, the presence of *Sus gr. scrofa* should be considered as a major bioevent in addition to those recently proposed for the definition of the Epivillafranchian biochrone in Europe (i.e., the first appearance of *Praemegaceros verticornis*, *Bison menneri* and *Crocota crocuta*; Bellucci et al., in press)”.

These 3 points would deserve a brief discussion in the MS.

7. Abundance of the suids remains?

The authors state “suids are usually abundantly preserved in the fossil assemblages” and “when suids are present in an ecosystem they use to be abundant in both the extant community of large mammal species and the fossil assemblages generated from their remains”, whereas in the answer to the reviewer they mention “suids are not normally dominant in the fossil assemblages, with the exception, sometimes, of the African Plio-Pleistocene sites. In Europe, they are not abundant but, when they were present in the past ecosystems, their remains were normally identified in the sites”. There is an apparent contradiction here that should be clarified.

We have extended the following paragraph:

“Given their opportunistic feeding behavior and high reproductive potential, when suids are present in an ecosystem they use to be abundant in the extant community of large mammal species, which results in good opportunities for their remains of being preserved in the fossil assemblage generated from this community. Specifically, the demographic potential of suids is unique among ungulates, because they follow an *r*-selection-like reproductive strategy, with elevated offspring numbers”.

Additionally, although there is an interesting discussion about the r-selection like reproductive strategy of suids based on actual species, it should be pushed one step further by demonstrating that this abundance can actually be really observed in fossil assemblages: do data collected from fossil assemblages confirm such an observation? The abundance of suid remains vs other large mammal taxa should be illustrated by showing MNI or MNR values at different sites in Europe.

This is a short manuscript and we cannot revise and include all of this information. In the paragraph on the taphonomic biases, we discuss that the absence of suids in the Epivillafranchian European sites is normally related to localities with defective record and small collections. Where there are large excavations, such as Atapuerca TE9, Vallparadís, Untermassfeld, Vallonnet, or La Boella, the record of pigs is normally good.

#### OTHER POINTS

☐ Abstract: the abstract is excessively long and should be reduced at least by half.

The abstract is following the instructions of Quaternary International.

☐ Section “The absence of suids during the Late Villafranchian of Europe”, First paragraph: for each site mentioned, a corresponding reference including the details of the faunal assemblage should be provided.

Yes, we have included now the references.

☐ Section The absence of suids during the Late Villafranchian of Europe, 2nd paragraph: change “is found at Europe” to “is found in Europe”

It has been changed.

☐ Section The absence of suids during the Late Villafranchian of Europe, last sentence: change “they are not definitively present in the European continent during the period comprised between 1.8 and 1.2 Ma” to “they are apparently not present in South Western Europe during the period comprised between ~1.8 and ~1.2 Ma.”

We have changed “definitively” by “apparently”.

☐ The authors mention several times that the arrival of the genus Homo predates that of the suids in Europe. What does this mean, i.e. what is the implication of such an observation?

We have included this paragraph at the end of the discussion:

“The lack of coexistence between the hominin populations that first dispersed in Europe with an Oldowan technology and suids can be tentatively interpreted in terms of competitive displacement, because the opportunistic trophic behavior of both groups would probably exceed the permissible degree of niche overlap in the Late Villafranchian ecosystems. However, further studies are required to address this issue”.

☐ Fig. 1

- 1st column: heading should be "Age (Ma)",
- 1st column: use "." Instead of ","
- What is Orce FN-1 ? Fonelas P1, Fuente Nueva-1?
- The Epivillafranchian biochron should definitely be included in the third column as this forms the core of the study.

#### REFERENCES

Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M. P., Alba, D. M. and Aurell-Garrido, J. A. (2014). Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events.

Palombo, M. R. (2014). Deconstructing mammal dispersals and faunal dynamics in SW Europe during the Quaternary. *Quaternary Science Reviews* 96(0): 50-71.

Palombo, M. R. and Valli, A. M. F. (2003-2004). Remarks on the biochronology of mammalian faunal complexes from the Pliocene to the Middle Pleistocene in France. *Geologica Romana* 37: 145-163.

Rook, L. and Martínez-Navarro, B. (2010). Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International* 219(1–2): 134-144.

#### REVIEWER 3:

Reviewer #3: In the abstract I suggest partially eliminate the paragraph concerning the biology of extant *Sus scrofa*, and change slightly. Later in the text it is ok.

In the introduction about Jaramillo faunas in Spain, add also the discussion about Jaramillo small mammal faunas from Cuenca-Bescós et al., 2015: Cuenca-Bescos G, Blain H-A; Rofes J, Lozano-Fernández I; López-García JM; Duval, M, Galan J., Nuñez-Lahuerta, C. 2015. 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. *Quaternary International*. (ref. JQI4940 PII: S1040-6182(14)01015-5. DOI: 10.1016/j.quaint.2014.12.059).

In the conclusions, we also agree in that the TE9 may be a warmer event, allowing the entrance of suids, as well as the abundant presence of "giant" schrews (Rofes and Cuenca-Bescós, 2009 (Rofes J; Cuenca-Bescós G. 2009. First record of *Beremendia fissidens* (Mammalia Soricidae) in the Pleistocene of the Iberian Peninsula with a review of the biostratigraphy biogeography and palaeoecology of the species. *Comptes Rendus Palevol* 8 21-37.).

We have included the following paragraphs and the references cited by the reviewer.

In the introduction:

“For a discussion on the dynamics of faunal turnover in the pre-Jaramillo small mammals, see Cuenca-Bescós et al., in press”.

In the Discussion and conclusions:

“In fact, the faunal composition of TE9, which records the earliest presence of suids (*Sus gr. scrofa*) in a pre-Jaramillo age, indicates that it may record a warm event, as suggested by the abundant presence of "giant" shrews (Rofes and Cuenca-Bescós, 2009), which would also allow the dispersal of suids in Europe”.