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Lower Pleistocene leporids (Lagomorpha, Mammalia) in Western Europe: New data from the Bois-de-Riquet (Lézignan-la-Cèbe, Hérault, France)



Les léporidés (Lagomorpha, Mammalia) du Pléistocène inférieur d'Europe occidentale : l'apport du Bois-de-Riquet (Lézignan-la-Cèbe, Hérault, France)

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ABSTRACT

Plio-Pleistocene climate oscillations in the different regions of Western Europe substantially influenced the evolutionary history of European leporids. Distinguishing rabbits (*Oryctolagus*) from hares (*Lepus*) in the archeological and palaeontological record of Pleistocene Europe is complicated due to the variability of their size and morphology. Here, we present the first description of two Pleistocene leporid species from Bois-de-Riquet (Lézignan-la-Cèbe, Hérault) in southern France. The first, *Oryctolagus* cf. *giberti*, exhibits similar characteristics to rabbit species documented in Spain and, thus, for the first time is recorded outside the Iberian Peninsula. The second leporid is a hare represented by very limited number of non-diagnostic remains, which, unfortunately, precludes an exact species identification. Already known from Lower Pleistocene deposits in Central Europe and Spain, the presence of *Lepus* sp. in southern France sheds new light on the geographic extension of these species. In this respect, Bois-de-Riquet is an important paleontological site that can further our understanding of the evolutionary history and expansion of European leporids.

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L'histoire évolutive des léporidés européens actuels dans les différentes régions de l'Europe occidentale a été fortement dépendante des oscillations climatiques du Plio-Pléistocène. La distinction entre les différentes espèces de lapins (*Oryctolagus*) et de lièvres (*Lepus*) dans les gisements archéologiques et paléontologiques pléistocènes constitue une tâche délicate, tant leurs morphologies et leurs tailles demeurent très variables. Dans ce travail, deux espèces de léporidés du Pléistocène inférieur ont été décrites, pour la première fois en France, à partir du matériel du Bois-de-Riquet (Lézignan-la-Cèbe, Hérault). La première est

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une espèce de lapin, décrite comme *Oryctolagus cf. giberti*, présentant les caractères similaires à celle retrouvée en Espagne. Cela permet de mettre en évidence sa présence au-delà de la péninsule Ibérique à cette époque. Le second léporidé est un lièvre, dont la détermination spécifique n'a pas pu être effectuée en raison du très faible nombre de restes qui s'y rapportent et de leur caractère non diagnostique. Enregistré dans des gisements du Pléistocène inférieur d'Espagne et d'Europe centrale, la présence de *Lepus* sp. dans le Sud de la France permet de renouveler nos connaissances concernant leur extension géographique. À cet égard, le Bois-de-Riquet est un site paléontologique de première importance, permettant de discuter de l'histoire évolutive et de l'expansion des léporidés en Europe.

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1. Introduction

Leporidae are a family of small mammals currently divided into 11 genera and 16 species (Hoffmann and Smith, 2005), with European examples represented by hares (*Lepus*) and rabbits (*Oryctolagus*). Although species of both genera are abundant in palaeontological and archaeological sites across Western Europe, very little has been published concerning their evolutionary history. Moreover, they have too often been ignored in paleontological and palaeo-environmental studies because of their significant intra-group variability (De Marfà, 2009; López-Martínez, 1989) and capacity to adapt to environmental changes, respectively. Both of these leporids are also commonly left out of zooarchaeological studies due to their small size and low caloric value (Cochard, 2004a; Sanchis-Serra, 2010, 2012).

Modern rabbits and hares first appear in Europe during the Pleistocene, making it a key period for understanding their evolutionary history and phylogeny (Callou, 2003; De Marfà, 2009; Donard, 1982; El Guennoui, 2001; López-Martínez, 1989). However, the paucity of available data and the wide spatiotemporal distribution of these leporids has meant that both these aspects remain poorly understood. Prior to the Pliocene, several genera of leporids were already present in Europe, including *Alilepus*, *Hypolagus*, *Trischizolagus* and, more debatably, *Serengetilagus* (Flynn et al., 2014; López-Martínez, 2008). While *Alilepus* is currently considered the most probable common ancestor of numerous leporid genera, *Trischizolagus* is in all likelihood the most recent ancestor of both *Oryctolagus* and *Lepus* (López-Martínez, 2008; Patnaik, 2002). Furthermore, despite molecular data placing the divergence of *Oryctolagus* and *Lepus* between 12 and 11 Ma in Asia or North America (Ge et al., 2013; Matthee et al., 2004), this is not corroborated by what is currently known from the paleontological record. In fact, these two genera are only much later recorded in the fossil record, ~3.5 Ma for *Oryctolagus* in Western Europe and ~2.5 Ma for *Lepus* in North America (López-Martínez, 2008).

1.1. Origin and characteristics of European rabbits

The earliest rabbit species of the genus *Oryctolagus* has been identified from Pliocene deposits at Layna in Soria (Fig. 1F). This species, *Oryctolagus laynensis* (López-Martínez, 1977), was present in Spain between 3.5 and 2 Ma

(López-Martínez, 2008) and is characterized by archaic features, including a well-developed deltoid tuberosity, a short and robust ischium as well as a marked medial femoral trochanter.

The earliest rabbits known from France, *Oryctolagus lacosti* (Fig. 1E), date to the beginning of the Pleistocene (~2.5 Ma) and are known from Perrier in the Auvergne (De Marfà and Mein, 2007), Saint-Vallier in the Drôme (Guérin et al., 2004; Martín-Suárez and Mein, 2004) and Montoussé-5 in the Hautes-Pyrénées (Chaline et al., 2000; Clot, 1975). Their distribution expands around 2 Ma, when they first appear in Italy at Monte Peglia in the Umbria region (López-Martínez, 1980). However, the individuals from Monte Peglia were initially assigned to *Lepus* sp. (Van der Meulen, 1973). This species shares morphological characteristics typical of the genus *Oryctolagus*, such as a relatively closed coxal acetabular notch and a large mental foramen positioned in close proximity to the third lower premolar characterized by two large anteroconids and a deep anteroflexid with inwardly converging edges. This species stands out primarily due to its large size, which is similar to extant European hares (De Marfà and Mein, 2007). Although both emerged in the Pliocene and share a still unknown common ancestor, *Oryctolagus laynensis* and *O. lacosti* evolved independently of one another, initially in the Iberian Peninsula and then emerging in France and Italy, respectively (López-Martínez, 2008).

A new species, *Oryctolagus giberti*, has recently been identified in the Lower Pleistocene levels of Cueva Victoria in Murcia (Fig. 1D). Dated to around 1.4 Ma, it could represent a potential transitional species between *O. laynensis* and extant wild rabbits, *Oryctolagus cuniculus* (De Marfà, 2008). This species is present uniquely in the Iberian Peninsula until the early Middle Pleistocene (De Marfà, 2009). The only possible member of this species known beyond the Iberian Peninsula is an example from Vallonnet in the Alpes-Maritimes (*Oryctolagus* gr. *laynensis-cuniculus*). Unfortunately, the poorly preserved bones of this fossil rabbit precluded a precise species identification (Nocchi and Sala, 1997b). *Oryctolagus giberti* is smaller than extant rabbits but does share several modern characters, including a biometric relationship between the length of the palatal bridge and width of the choanas as well as a very similar p3 morphology to *O. cuniculus*. However, *O. giberti* retains a suite of ancestral morphological features of *O. laynensis* such as a pronounced deltoid tuberosity, a short and robust ischium and a heavily-developed medial femoral trochanter.

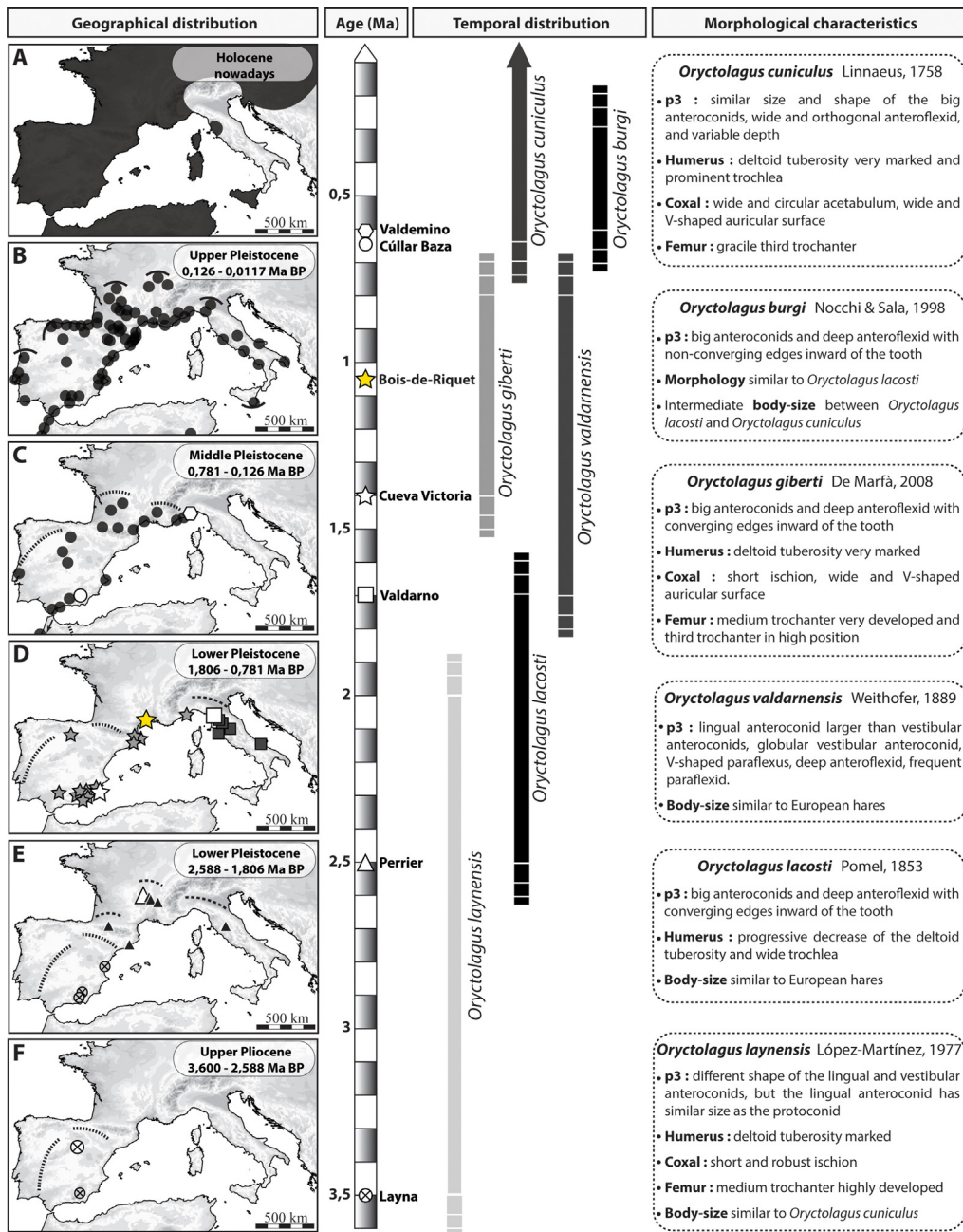


Fig. 1. (Color online.) Paleobiogeographic and temporal distribution of the genus *Oryctolagus* based on published data alongside the discriminant morphological characteristics of each species. A. Current distribution of European rabbit (from Flux, 1994, modified). B. Location of Upper Pleistocene deposits yielding *Oryctolagus cuniculus* remains (circles). Circular arcs represent the maximum distribution during this period (from Callou, 2003). C. Location of Middle Pleistocene deposits yielding *O. cuniculus* (circles) and *Oryctolagus burgi* (hexagon). D. Location of Lower Pleistocene deposits containing *Oryctolagus giberti* (stars) and *Oryctolagus valdarnensis* (squares). E. Location of Lower Pleistocene deposits containing *Oryctolagus lacosti* (triangles) and *Oryctolagus laynensis* (crossed circle). F. Location of Late Pliocene deposits with *O. laynensis* (crossed circle). In maps C to F, the dotted lines represent the likely limit of maximum distribution during each period. The white symbols indicate deposits where these species were first identified.

Fig. 1. (Couleur en ligne.) Distribution paléobiogéographique et temporelle du genre *Oryctolagus* à partir des données paléontologiques et caractéristiques morphologiques discriminantes de chaque espèce. A. Distribution actuelle du lapin européen (d'après Flux, 1994, modifié). B. Localisation des dépôts du Pléistocène supérieur fournissant des restes d'*Oryctolagus cuniculus* (cercles). Les arcs circulaires représentent la distribution maximum pendant cette période (d'après Callou, 2003). C. Localisation des dépôts du Pléistocène moyen fournissant *O. cuniculus* (cercles) et *Oryctolagus burgi* (hexagone). D. Localisation des dépôts du Pléistocène inférieur contenant *Oryctolagus giberti* (étoiles) et *Oryctolagus valdarnensis* (carrés). E. Localisation des dépôts du Pléistocène inférieur contenant *Oryctolagus lacosti* (triangles) et *Oryctolagus laynensis* (cercle avec croix). F. Localisation des dépôts du Pliocène terminal à *O. laynensis* (cercle avec croix). Sur les cartes C à F, les lignes en pointillé représentent la limite probable de distribution maximum au cours de chaque période. Les symboles blancs indiquent les gisements dans lesquels ces espèces ont été identifiées pour la première fois.

From Angelone and Rook, 2012; De Marfà, 2008; López-Martínez, 1977, 1989; Nocchi and Sala, 1997a; Pomel, 1853.

Another contemporaneous species, *Oryctolagus valdarnensis*, is present on the Italian Peninsula (Fig. 1D) at the sites of Valdarno (Angelone and Rook, 2012) and Montagnola Senese in Tuscany (Fondi, 1972), at Pietrafitta in the Umbria region (Argenti and Kotsakis, 2009) and Pirro Nord in the Apulia region (Angelone, 2013). This very large rabbit, similar to European hares, shows a “p3 with lingual anteroconid larger than lingual one, often globular labial anteroconid, V-shaped paraflexus, deep, U-shaped anteroflexid, frequent paraflexid” (Angelone and Rook, 2012: p. 167).

During the Middle Pleistocene, a new species, *Oryctolagus burgi*, appears at Valdemino in Liguria around 0.605 Ma (Fig. 1C; Nocchi and Sala, 1997a; Sala and Masini, 2007). Present between 0.8 and 0.1 Ma and limited to this region of the Italian peninsula (López-Martínez, 2008), this species, while morphologically similar to *O. lacosti*, was somewhat smaller but not as small as *O. cuniculus* (Fig. 1B). Characteristic of *O. burgi* is the morphology of the third lower premolar, which has similarly-sized anteroconids and an anteroflexid with parallel, non-convergent inward edges (Nocchi and Sala, 1997a).

The Middle Pleistocene also marks the appearance of the modern European rabbit, *O. cuniculus* (~0.6 Ma). First emerging in the southern Iberian Peninsula at Cúllar de Baza (Fig. 1C; López-Martínez, 1989), this adaptable species quickly spread throughout Mediterranean Western Europe and North Africa (Callou, 2003; El Guennouni, 2001; López-Martínez, 1989). Its current distribution and population differentiation (Fig. 1A), although influenced by Holocene climate patterns, is largely due to human-assisted transport and colonization during historic periods (Callou, 2003).

1.2. Origins of the European hares

The genus *Lepus* most likely emerged in North America around 2.5 Ma (Ge et al., 2013; López-Martínez, 2008), and Averianov and Tesakov (1997) suggest a direct phylogenetic link with the genus *Trischizolagus*, which went extinct during the Early Pleistocene. Hares are known from Lower Pleistocene contexts in Central Europe (Fladerer, 1987; Kretzoi, 1956; Paunović and Jambrešić, 1997), Germany (Maul, 2001), Italy (Van der Meulen, 1973) and Spain (De Marfà, 2009; Galobart et al., 2003; Mazo et al., 1985). The limited number of remains coupled with an incomplete speciation event (López-Martínez, 1980) has, however, complicated identifying distinct *Lepus* species during this period.

Different species of European hare gradually emerged from the Middle Pleistocene onwards. The Iberian hare (*Lepus granatensis*) was first documented at Cúllar de Baza (López-Martínez, 1989) and appears to be consistently present on the Iberian Peninsula (Sesé and Sevilla, 1996). The mountain hare (*Lepus timidus*) and European hare (*Lepus europaeus*) appeared almost simultaneously in both Western and Central Europe (Guérin and Patou-Mathis, 1996). Despite occupying different habitats, both species alternately inhabited Western Europe depending on climatic conditions (Donard, 1982) or the degree of interspecific competition (López-Martínez, 1980; Thulin,

2003). While Mountain hare are known from high Alpine contexts (Mitchell-Jones et al., 1999), they primarily occupy middle to high latitudes from Fennoscandia to Siberia as well as Ireland, Poland and the United Kingdom (Flux and Angermann, 1990). European hares, on the other hand, emerged sometime during the Holocene and evolved across much of continental Europe (Corbet, 1986; Fickel et al., 2008; Stamatis et al., 2009).

Alongside this broader-ranging species, Europe is home to two other hare species; the broom hare (*Lepus castroviejoi*) and Corsican hare (*L. corsicanus*), which are distributed in the central Cantabrian mountains (Palacios, 1976) and southern Italy (Palacios, 1996), respectively. These two geographically isolated species would have emerged from the endemic evolution of a common ancestor (Alves and Melo-Ferreira, 2007; Alves et al., 2008; Llorente-Rodríguez, 2010; Palacios, 1996), which likely occupied a large area of southwestern Europe during the Pleistocene prior to the expansion of *L. europaeus* (Palacios, 1996). Fossil finds of Corsican hares are known from the Upper Pleistocene levels of Romanelli Cave and Melpignano in the Apulia region of southern Italy (Trocchi and Riga, 2005).

Finally, the African hare (*Lepus capensis*) has been identified in several Pleistocene deposits in Spain (Alcalde et al., 1981; Altuna, 1990; Daura et al., 2005; Fa et al., 2013; Sanchis-Serra and Fernández-Peris, 2011) and may suggest, like in the case of *O. cuniculus*, a passage across the Strait of Gibraltar during the Pleistocene. However, the presence of African species in Spain warrants some caution as southern European hares, considered conspecific and assigned to *Lepus capensis* by Petter (1961), may actually represent *L. europaeus* or *L. granatensis*.

The lack of paleontological data complicates establishing a robust evolutionary history for the genus *Lepus* during the Pleistocene. Currently, only molecular studies of extant hares have succeeded in drawing clear phylogenetic relationships and reconstructing speciation events (Alves et al., 2003).

1.3. The Bois-de-Riquet leporids

It is now clear that both these leporid genera are absent from France during the second part of the Early Pleistocene (1.8 to 0.78 Ma BP). This hiatus may result from:

- the concentration of leporids in the Iberian and Italian peninsula as a function of paleoecological constraints;
- a lack of paleontological data from the rest of Western Europe, or at least the Mediterranean periphery, which is rich in leporid remains before and after this period.

The Bois-de-Riquet (Lézignan-la-Cèbe, Hérault) leporid assemblage is important for addressing at least part of this question, as palaeontological studies of both fossil micro-mammals and microfauna from the site date the bone accumulation to between 1.2 and 1 Ma (Bourguignon et al., submitted for publication). Furthermore, the large number of leporid remains from the site ($n > 1280$) makes it one of the largest palaeontological collections of this family currently known in Western Europe.

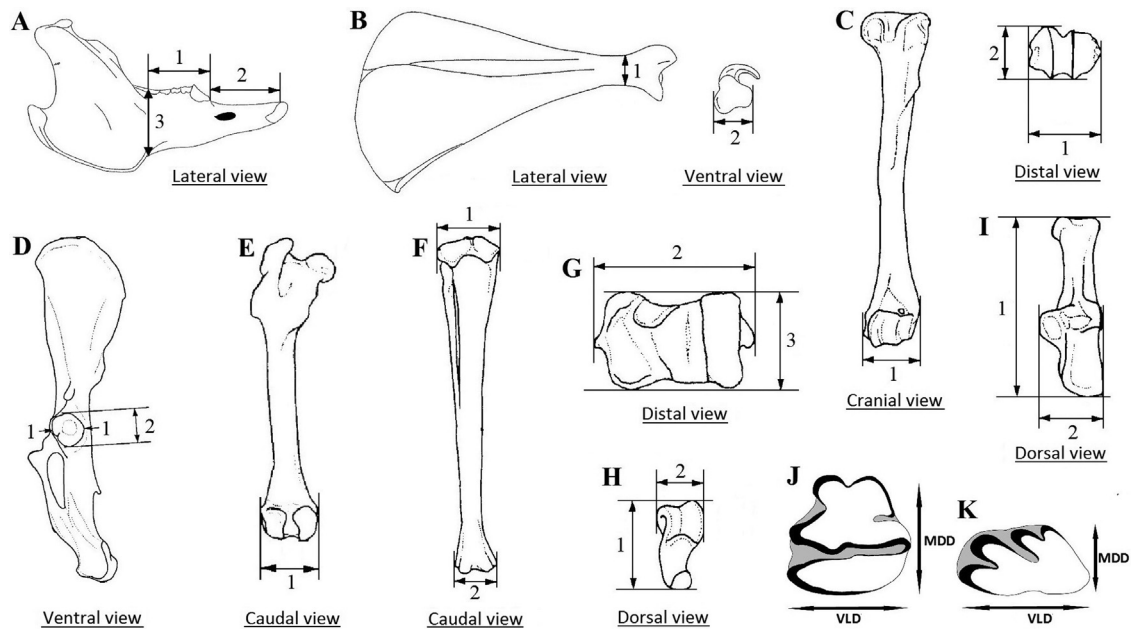


Fig. 2. Selected measures for biometric analysis (from Donard, 1982, modified). **A.** Right mandible (1: length of the dental series; 2: length of diastema; 3: height of the mandible). **B.** Right scapula (1: DAP of the neck [Sca-SLC]; 2: DCG [Sca-BG]). **C.** Left humerus (1: DT distal [Hum-Bd]; 2: DAP distal). **D.** Left coxal (1: DT acetabulum; 2: DAP acetabulum). **E.** Left femur (1: DT distal [Fem-Bd]). **F.** Left tibia (1: DT proximal [Tib-Bp]; 2: DT distal [Tib-Bd]). **G.** Left tibia (2: DT distal [Tib-Bd]; 3: DAP distal [Tib-Dd]). **H.** Left talus (1: length [Tal-GL]; 2: DT trochlea). **I.** Left calcaneus (1: length [Cal-GL]; 2: DT [Cal-GB]). **J.** Left p3. **K.** Left P2. Codes used by Von Den Driesch (1976) are mentioned in square brackets.

Fig. 2. Mesures sélectionnées pour l'analyse biométrique (d'après Donard, 1982, modifié). **A.** Mandibule droite (1 : longueur de la série dentaire ; 2 : longueur du diastème ; 3 : hauteur de la mandibule). **B.** Scapula droite (1 : DAP du col [Sca-SLC] ; 2 : DCG [Sca-BG]). **C.** Humérus gauche (1 : DT distal [Hum-Bd] ; 2 : DAP distal). **D.** Coxal gauche (1 : DT acetabulum ; 2 : DAP acetabulum). **E.** Fémur gauche (1 : DT distal [Fem-Bd]). **F.** Tibia gauche (1 : DT proximal [Tib-Bp] ; 2 : DT distal [Tib-Bd]). **G.** Tibia gauche (2 : DT distal [Tib-Bd] ; 3 : DAP distal [Tib-Dd]). **H.** Talus gauche (1 : longueur [Tal-GL] ; 2 : DT cochlea). **I.** Calcaneus gauche (1 : longueur [Cal-GL] ; 2 : DT [Cal-GB]). **J.** p3 gauche. **K.** P2 gauche. Les codes utilisés par Von Den Driesch (1976) sont mentionnés entre crochets.

The significance of the Bois-de-Riquet material lies mainly in the fact that it is the first time that both *Oryctolagus* and *Lepus* have been documented in France from the second half of the Lower Pleistocene, with the possible exception of Vallonet (see above). The location of the site is also informative as it lies between the Iberian and Italian peninsulas, where the lineages of modern (*O. laynensis* – *O. giberti* – *O. cuniculus*), as well as French and Italian rabbits (*O. lacosti* – *O. valdarnensis* – *O. burgi*), first emerged and subsequently evolved. The same is true for the genus *Lepus*, as Bois-de-Riquet is positioned between the modern ranges of Iberian, central European and Italian hares. The Bois-de-Riquet assemblage is therefore ideal for exploring the dispersal dynamics of the genus *Lepus* in Europe.

2. Materials and method

Genus and, when possible, species attributions were determined for the Bois-de-Riquet leporids using three analyses commonly applied in palaeontology. Data for the western European fossil record comes primarily from the literature and covers the entire Pleistocene period (ca. 2.6 to 0.02 Ma). Comparisons with Holocene populations were limited as these likely underwent recent human-induced

changes (Callou, 2003). All dental and post-cranial skeletal elements have been described, measured and compared with previously published data (Fig. 2; Donard, 1982; Von Den Driesch, 1976), and the terminology employed for describing the post-cranial elements is that published by Barone (1986).

The morphology of skeletal remains and relevant characters were used to group similar populations. We also used two-dimensional geometric morphometrics based on the protocol established by De Marfà (2009) to analyze the third lower premolar (p3), the tooth showing the highest degree of morphological differentiation in leporids. Landmark based geometric morphometrics is more robust than a simple two-dimensional method or descriptive analyses (Bookstein, 1991). Landmarks locations were digitized from photographs using the tpsDig2 software (thin plate splines; © 2005 Rohlf) and compiled with tpsUtil (© 2005 Rohlf). Principal Component Analysis (PCA) using the tpsRelw software (© 2005 Rohlf) was produced. In order to ensure reproducibility and standardize the photos, the p3 were fixed vertically with respect to the camera lens. The landmarks represent the points of maximum curvature for the (1) anteroflexid, (2) vestibular anteroconid, (3) protoflexid, (4) protoconid, (5) hypoconid, (6) entoconid, (7) paraflexid and (8) lingual anteroconid (Fig. 3).

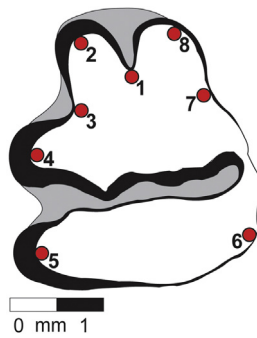


Fig. 3. (Color online.) Position of the eight landmarks.
Fig. 3. (Couleur en ligne.) Position des huit points repères.
 From De Marfà, 2009, modified.

Despite the relatively limited number of publications concerning leporids that use geometric morphometrics (De Marfà, 2009; Patnaik, 2002), the reliability of such analyses have been widely demonstrated for Pleistocene samples (e.g., Bignon et al., 2005; Boudadi-Maligne, 2010; Cucchi, 2005; De Marfà, 2009; Harvati, 2003). For example, De Marfà (2009) demonstrated the efficiency of the method for separating *Oryctolagus* and *Lepus*. However, unlike De Marfà, who based his reference collection on modern leporids, we chose to rely mainly on Pleistocene populations, integrating modern specimens only to compare their morphological variability with the fossil populations.

Our reference collection comprised 88 Pleistocene leporids held at the de la Préhistoire à l'Actuel: Culture, Environnement, Anthropologie (PACEA) and Laboratoire Méditerranéen de Préhistoire Europe–Afrique (LAMPEA) laboratories (Table 1). However, as no published photographs of the p3 from Lower Pleistocene specimens were available, this sample essentially informed the osteometric and morphological analysis to ensure reliability in species identification. Finally, prior to the palaeontological analysis and in order to better understand the leporid population represented in the Bois-de-Riquet assemblage, it was important to identify the origin of the accumulation and

Table 1

Detail of numbers used for 2D morphometric geometric. All individuals belong to *Oryctolagus cuniculus*, except for the Bois-de-Riquet.

Tableau 1

Détail des effectifs utilisés pour la géométrie morphométrique 2D. Tous les individus appartiennent à *Oryctolagus cuniculus*, excepté pour le Bois-de-Riquet.

Site, locality	Chronology	n
Abri Murat, Lot	0.011 Ma BP	4
Arbri Morin, Gironde	0.012 Ma BP	13
Bois-de-Riquet, Hérault	1.000 Ma BP	21
Coudoulous 1, Lot	0.140 Ma BP	22
Igue du Gral, Lot	0.013 Ma BP	3
Igue des Rameaux, Tarn-et-Garonne	0.150 Ma BP	5
Les Canalettes, Aveyron	0.075 Ma BP	23
Lunel-Viel 1, Hérault	0.500 Ma BP	18
PACEA laboratory	Modern populations	14

any taphonomic factors affecting its integrity (Bourguignon et al., 2012; Pelletier, 2013).

3. Results

3.1. Taphonomy

The palaeontological study of the Bois-de-Riquet leporids included 1286 skeletal remains. All skeletal elements are present except for the carpal bones. Based on the number of p3s in the assemblage, at least 30 individuals are present. However, this assessment likely underestimates the true number as it does not take into account the stratigraphic subdivisions.

As body size generally limits prey selection (e.g., Blondel, 1967; Brugal and Fosse, 2004; Cochard, 2008; Denys et al., 1987; Dickman, 1988), the skeletal profile, percentage of complete bones and number of digested elements provide important information concerning the primary agents of accumulation (Blasco and Fernández-Peris, 2012; Cochard, 2004a,b,c, 2007, 2008; Cochard et al., 2012; Hockett, 1991; Lloveras et al., 2008a,b, 2009, 2010, 2012; Mallye et al., 2008; Sanchis-Serra, 2000). No skeletal elements were found in anatomical connection, and the relatively low percentage of complete bones (20.0%) combined with traces of digestion (13.8%) and tooth marks (5.4%) indicate a medium-sized carnivore (*Canis* or *Vulpes*) to be responsible for the Bois-de-Riquet leporid accumulation.

Moreover, the lack of a correlation between % nNRD (percentage of the remains determined) and bone density values for *O. cuniculus* (Pavao and Stahl, 1999) demonstrate the absence of a differential preservation due to sediment conditions and destructive chemical processes. Bones surface preservation and the skeletal part profile argue against the secondary transport of elements by water action (Dodson, 1973). Furthermore, it is more than likely that synsedimentary processes, namely sediment compaction, may have affected some elements such as vertebrae and skull fragments.

Bone color is homogeneous for the entire leporid assemblage and is identical to that of the large mammals remains, such as *Pachycrocuta brevirostris*, *Bison* sp. and *Praemegaceros* sp. (Bourguignon et al., 2012, submitted for publication), species that first appear in Europe during the Plio-Pleistocene around 1 Ma (Guérin and Patou-Mathis, 1996). Overall, the Bois-de-Riquet assemblage has not been affected by bioturbation and the leporid accumulation can be securely associated with the Pleistocene fauna present in the deposit.

3.2. Systematic palaeontology

Morphological and morphometric analyses of the leporid remains clearly demonstrate the majority presence of *Oryctolagus* ($n = 350$, MNI = 27), accompanied by much smaller numbers of elements attributable to *Lepus* ($n = 18$, MNI = 3). Rabbits and hares clearly differ both in terms of size and anatomical characteristics specific to each genus (Callou, 1997; Donard, 1982). The remaining 918 bones (molariform teeth other than P2 and p3, phalanges, ribs,

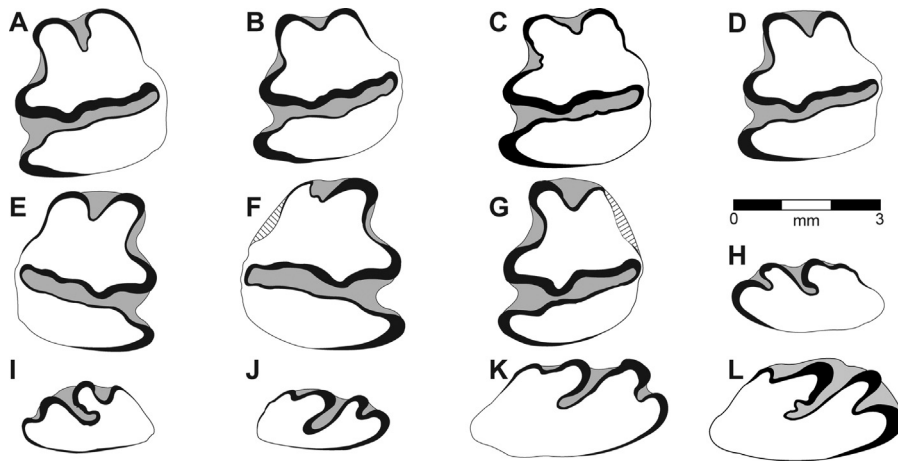


Fig. 4. Leporid teeth from Bois-de-Riquet. **A–D.** Left p3 of *Oryctolagus* cf. *giberti* (BDR10 α 7AB – MP0544; BDR12 X37A – MP1050; BDR10 α 7AB – MP0533; BDR12 Y36D – MP0421). **E.** Right p3 of *Oryctolagus* cf. *giberti* (BDR10 β 7A – MP0474). **F.** Right p3 of *Lepus* sp. (BDR12 X37A – MP0829). **G.** Left p3 juvenile of *Lepus* sp. (BDR10 α 7AB – MP0229). **H–I.** Left P2 of *Oryctolagus* cf. *giberti* (BDR12 X36D – MP0864; BDR10 W33 – MP0066). **J.** Right P2 of *Oryctolagus* cf. *giberti* (BDR10 α 7AB – MP0232). **K–L.** Right P2 of *Lepus* sp. (BDR12 Z34A – MP0959; BDR12 Y36D – MP0700).

Fig. 4. Dessins des dents de léporidés du Bois-de-Riquet. **A–D.** p3 gauche d'*Oryctolagus* cf. *giberti* (BDR10 alpha7AB – MP0544; BDR12 X37A – MP1050; BDR10 alpha7AB – MP0533; BDR12 Y36D – MP0421). **E.** p3 droite d'*Oryctolagus* cf. *giberti* (BDR10 beta7A – MP0474). **F.** p3 droite de *Lepus* sp. (BDR12 X37A – MP0829). **G.** p3 gauche de *Lepus* sp. juvénile (BDR10 alpha7AB – MP0229). **H–I.** P2 gauche d'*Oryctolagus* cf. *giberti* (BDR12 X36D – MP0864; BDR10 W33 – MP0066). **J.** P2 droite d'*Oryctolagus* cf. *giberti* (BDR10 alpha7AB – MP0232). **K–L.** P2 droite de *Lepus* sp. (BDR12 Z34A – MP0959; BDR12 Y36D – MP0700).

vertebrae) could not be determined to species due to their fragmentary state or the lack of diagnostic elements and clear metrical differences.

3.2.1. *Oryctolagus* cf. *giberti*

Class MAMMALIA Linnaeus, 1758

Order LAGOMORPHA Brandt, 1855

Family LEPORIDAE Gray, 1821

Genus *Oryctolagus* Lilljeborg, 1874

Species *Oryctolagus* cf. *giberti* De Marfà, 2008

3.2.1.1. Diagnostic elements. The p3 have a subtriangular occlusal surface (Fig. 4A–E) with a relatively shallow anteroflexid compared to *O. burgi* and *O. cuniculus* (Fig. 5Ae–f) as well as inwardly converging edges. The ellipsoidal vestibular anteroconid is generally smaller than the rectangular lingual anteroconid, as is the case in *O. valdarnensis* and *O. giberti* (Fig. 5Ac–d). The protoflexid forms an obtuse angle, and the protoconid is similar to the vestibular anteroconid and the hypoconid. The hypoflexid is deep and occupies almost the entire width of the tooth. It has two inflexions on its mesial edge that can be smooth or slightly undulating. The lingual edge has a well-developed paraflexid and distinct entoconid, reminiscent of *O. valdarnensis* and *O. giberti* (Fig. 5Ac–d).

In terms of size, these teeth fall outside the range of the *Oryctolagus* from Sima del Elefante, Caune de l'Arago, Lunel-Viel and Lazaret, and are closer to the *O. giberti* sample from Cueva Victoria and Fuente Nueva 3 (Table 2 and Fig. 6). The Bois-de-Riquet population tends to stand out from larger forms such as *O. lacosti* and *O. valdarnensis*.

Morphometric analysis of the p3 reveals differences between the Bois-de-Riquet population ($n=21$) and the 102 other teeth in the reference collection of taxonomically

known fossil and modern populations. The PCA incorporated eight landmarks (Fig. 7) and shows a clear separation between the *O. cuniculus* populations from the end of the Late Pleistocene (Abri Morin, Abri Murat and Igue du Gral) and the early Late Pleistocene (Les Canalettes) and Middle Pleistocene (Igue des Rameaux, Coudoulous I and Lunel-Viel). The Bois-de-Riquet sample, while clearly

Table 2

Measurements for *Oryctolagus* from Bois-de-Riquet. Number of elements (n), minimum and maximum values or each measurement, and mean and standard deviations (σ).

Tableau 2

Mesures réalisées sur les différentes parties anatomiques des *Oryctolagus* du Bois-de-Riquet. Sont figurés le nombre de mesures (n), les valeurs minimums et maximums pour chaque mesure, la moyenne, ainsi que l'écart-type associé.

Measurements (mm)	n	Min	Max	Mean	σ
Dental series length	3	13.29	15.09	14.41	0.9773
Diastema length	3	15.14	18.40	17.00	1.6766
Height mandible	3	13.34	14.87	13.86	0.8720
DCG scapula	3	6.83	7.94	7.24	0.6092
DT distal humerus	7	8.86	9.79	9.27	0.3642
DAP distal humerus	8	5.24	7.08	6.38	0.6211
DAP acetabulum coxal	5	7.85	9.05	8.30	0.4646
DT acetabulum coxal	5	6.70	8.65	7.45	0.7491
DT distal femur	2	14.11	14.15	14.13	0.0283
DT proximal tibia	3	14.76	15.78	15.11	0.5832
DT distal tibia	7	10.01	12.71	11.14	0.9238
DAP distal tibia	7	6.18	7.52	6.75	0.4558
Calcaneus length	6	21.05	24.84	23.04	1.2606
DT calcaneus	9	8.79	9.95	9.34	0.5003
Talus length	4	11.39	12.41	12.03	0.4552
DT talus trochlea	4	5.11	6.38	5.77	0.5908
VLD p3	29	2.20	3.25	2.77	0.2655
MDD p3	29	2.30	3.45	2.90	0.3094
VLD P2	21	1.70	3.30	2.62	0.4833
MDD P2	21	0.95	1.80	1.37	0.2453

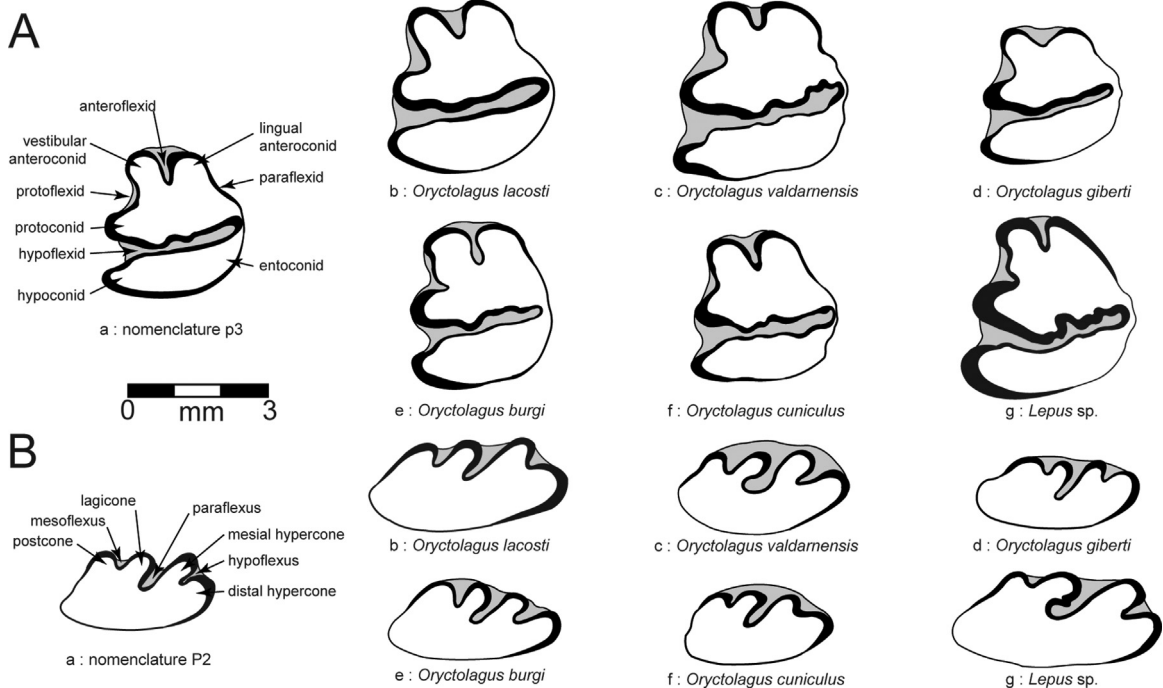


Fig. 5. Distinctive dental characteristics of different leporid species from Western Europe Pleistocene on left p3 (A) and right P2 (B), in occlusal view. **A–a:** p3 dental terminology (from Palacios and López-Martínez, 1980); **A–b:** *Oryctolagus lacosti* p3 of Perrier (FSL-211647, from De Marfà and Mein, 2007); **A–c:** *Oryctolagus valdarnensis* p3 of Valdarno (IGF 10129, from Angelone and Rook, 2012); **A–d:** *Oryctolagus giberti* p3 of Cueva Victoria (from De Marfà, 2008); **A–e:** *Oryctolagus burgi* p3 of Valdemino (Val 91 A/B, from Nocchi and Sala, 1997a); **A–f:** *Oryctolagus cuniculus* p3 of Pont d'Ambon c.3 (from Donard, 1982); **A–g:** *Lepus* sp. p3 of Sima del Elefante (from De Marfà, 2009); **B–a:** P2 dental terminology (from Palacios and López-Martínez, 1980); **B–b:** *Oryctolagus lacosti* P2 of Perrier (FSL-211646, from De Marfà and Mein, 2007); **B–c:** *Oryctolagus valdarnensis* P2 of Valdarno (IGF 10130, from Angelone and Rook, 2012); **B–d:** *O. giberti* P2 of Cueva Victoria (from De Marfà, 2008); **B–e:** *O. burgi* P2 of Valdemino (Val 91 A21/B/1, from Nocchi and Sala, 1997a); **B–f:** *O. cuniculus* P2 of Pont d'Ambon c.3 (from Donard, 1982); **B–g:** *Lepus* sp. P2 of Sima del Elefante (from De Marfà, 2009).

Fig. 5. Caractères dentaires distinctifs des différentes espèces de léporidés pléistocènes d'Europe occidentale, sur la p3 gauche (A) et la P2 droite (B) en vue occlusale. **A–a:** terminologie dentaire de la p3 (d'après Palacios et López-Martínez, 1980). **A–b:** p3 d'*Oryctolagus lacosti* de Perrier (FSL-211647, d'après De Marfà et Mein, 2007). **A–c:** p3 d'*Oryctolagus valdarnensis* de Valdarno (IGF 10129, d'après Angelone et Rook, 2012). **A–d:** p3 d'*Oryctolagus giberti* de la Cueva Victoria (d'après De Marfà, 2008). **A–e:** p3 d'*Oryctolagus burgi* de Valdemino (Val 91 A/B, d'après Nocchi et Sala, 1997a). **A–f:** p3 d'*Oryctolagus cuniculus* de Pont d'Ambon c.3 (d'après Donard, 1982). **A–g:** p3 de *Lepus* sp. de la Sima del Elefante (d'après De Marfà, 2009). **B–a:** terminologie dentaire de P2 (d'après Palacios et López-Martínez, 1980). **B–b:** P2 d'*O. lacosti* de Perrier (FSL-211646, d'après De Marfà et Mein, 2007). **B–c:** P2 d'*Oryctolagus valdarnensis* de Valdarno (IGF 10130, d'après Angelone et Rook, 2012). **B–d:** P2 d'*O. giberti* de la Cueva Victoria (d'après De Marfà, 2008). **B–e:** P2 d'*Oryctolagus burgi* de Valdemino (Val 91 A21/B/1, d'après Nocchi et Sala, 1997a). **B–f:** P2 d'*O. cuniculus* de Pont d'Ambon c.3 (d'après Donard, 1982). **B–g:** P2 de *Lepus* sp. de la Sima del Elefante (d'après De Marfà, 2009).

different from both modern rabbits and our Late Pleistocene sample, is more difficult to distinguish from the Middle Pleistocene *O. cuniculus* populations. The deformation grids show these differences are particularly well expressed at the paraflexid.

In terms of the post-cranial skeleton, the humerus has a narrow bicapital groove in its distal portion. The convexity of the greater tubercle is prominent, and the deltoid crest occupies more than one third of the bone's length proximal-distally and disappears abruptly (Fig. 8A–e). These characters are typical of *O. giberti* (Fig. 8A–b). The deltoid crest is slightly less clear in *O. cuniculus* and gradually reduces in *O. lacosti* and hares. The average transverse diameter of the distal epiphysis in the Bois-de-Riquet individuals falls within the variability of the Pleistocene *Oryctolagus* (Table 3) and differs from both large rabbit species (*O. valdarnensis* or *O. burgi*) and the different hares in the sample (Table 5).

The acetabular notch of the coxal bone is deep and relatively more closed than in *O. cuniculus* (Fig. 8B). The semi-lunar surface is larger in *O. giberti* than in other leporid species (Fig. 8B–b), and the auricular surface is wide and V-shaped. The ventral edge of the ventro-caudal iliac spine is prominent. While the acetabulum dimensions falls within the variability of Middle Pleistocene rabbits from southern France, they are slightly larger than *O. giberti* from Cueva Victoria (Table 3).

The cranio-medial surface of the greater trochanter is narrow, and the third trochanter is higher than in other members of the genus *Oryctolagus* (Fig. 8C). In caudal view, the trochanteric fossa is narrow and deep. The distal fragments are mostly incomplete or belong to immature individuals. The dimensions of the two femurs are more comparable to those of *O. giberti* and *O. cuniculus* than *O. valdarnensis* or *O. burgi* (Table 3).

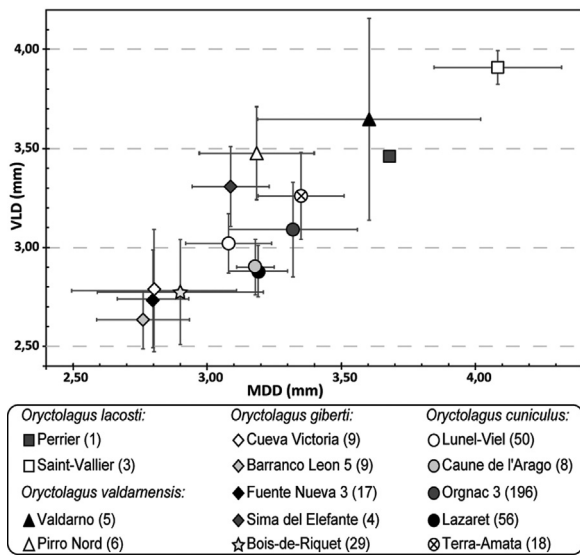


Fig. 6. (Color online.) Biometric relationship between mesio-distally diameter (MDD) and vestibular-lingually diameter (VLD) of p3 (in mm) in *Oryctolagus cf. giberti* from Bois-de-Riquet and other Pleistocene fossil leporids: *O. giberti* of Sima del Elefante, Cueva Victoria, Fuente Nueva 3 and Barranco Leon 5 (data from De Marfà, 2009); *Oryctolagus lacosti* of Perrier and Saint-Vallier (data from De Marfà, 2009); *Oryctolagus valdarnensis* of Valdarno (data from Angelone and Rook, 2012) and Pirro Nord (data from Angelone, 2013); *Oryctolagus cuniculus* of Lunel-Viel, Lazaret, Caune de l'Arago, Terra-Amata and Orgnac 3 (data from Desclaux, 1992; Donard, 1982; El Guennouni, 2001). The bars show the standard deviations for each series with the number of specimens in brackets.

Fig. 6. (Couleur en ligne.) Relation biométrique entre le diamètre méso-distal (MDD) et le diamètre vestibulo-lingual (VLD) des p3 (en mm) chez *Oryctolagus cf. giberti* du Bois-de-Riquet et d'autres léporidés fossiles du Pléistocène: *O. giberti* de la Sima del Elefante, Cueva Victoria, Fuente Nueva 3 et Baranco Leon 5 (données d'après De Marfà, 2009); *Oryctolagus lacosti* de Perrier et Saint-Vallier (données d'après De Marfà, 2009); *Oryctolagus valdarnensis* de Valdarno (données d'après Angelone et Rook, 2012) et Pirro Nord (données d'après Angelone, 2013); *Oryctolagus cuniculus* de Lunel-Viel, Lazaret, caune de l'Arago, Terra-Amata et Orgnac 3 (données d'après Desclaux, 1992; Donard, 1982; El Guennouni, 2001). Les barres représentent l'écart-types pour chaque série, avec le nombre de spécimens entre parenthèses.

3.2.1.2. Additional elements. The mandibles from Bois-de-Riquet have relatively large, round mental foramina, which are located within 3 mm of the p3. A similar pattern was noted (Table 2) with the Cueva Victoria individuals (see De Marfà, 2008). The majority of the upper incisors (11) have a rounded mesial lobe, and the ellipsoidal P2 have three inflexions (Fig. 4H–J). The lagicone has surface area equal to or greater than that of the mesial hypercone. The paraflexus penetrates obliquely and more deeply than the mesoflexus and the hypoflexus, reaching the middle of the tooth's length with a slight irregularity on the anterior edge. Generally, the mesoflexus is less pronounced than the hypoflexus, as is the case in *O. giberti* from Cueva Victoria, but differs substantially from larger species such as *O. lacosti*, *O. valdarnensis* and *O. burgi* (Fig. 5B–d). This tooth varies significantly between rabbit species and, although not currently a key element in the characterization of Pleistocene populations, nevertheless provides useful information. Regarding the rest of the upper dentition, the hypoflexus is undulating on the mesial edge (between five

and seven undulations) and penetrates a little more than half the width of the crown.

While the highly fragmented scapulae have not been described in detail, the glenoid cavity (Table 2) is significantly smaller than in hares (see Donard, 1982), allowing three fragments to be assigned to the genus *Oryctolagus*. The tibial intercondylar eminence is formed by two small but prominent tubercles. The tibial crest is clearly discontinuous and oriented laterally. In cranial view, the distal epiphysis has a slight depression on the shaft, and the distal edge of the articular surface shows a regular rounded notch in caudal view. While these characteristics are typical of rabbits, they are not species specific. The dimensions of the tibia (Table 2) also argue in favor of the specimens representing *Oryctolagus* (see De Marfà, 2009; Donard, 1982). Similarly, although there is no particular anatomical aspect of the calcaneum that separates different leporid species, its size is nevertheless diagnostic and places this element within the variability of *O. giberti* (see De Marfà, 2008). Finally, the rectangular trochlea of the talus again indicates an attribution to the genus *Oryctolagus*. The size (Table 2) of the talus also falls within the variability of rabbits and clearly differs from *Lepus* (see Donard, 1982).

3.2.2. *Lepus* sp.

Genus *Lepus* Linnaeus, 1758

Six teeth can unquestionably be attributed to *Lepus* sp. Although the upper incisor has a rounded mesial lobe, a trait more characteristic of *Oryctolagus*, its size (2 mm long and 3.1 mm wide) ranks it amongst the hares (see Donard, 1982). The P2 are ellipsoidal and have three inflexions (Fig. 4K–L). The surface of the lagicone is similar to the mesial hypercone, and the paraflexus penetrates deeper than both the weakly developed mesoflexus and hypoflexus. These traits are shared by the individuals from Bois-de-Riquet and the *Lepus* sp. from Sima del Elefante (Fig. 5B–g), but are in stark contrast with larger forms such as *O. lacosti*, *O. valdarnensis* and *O. burgi* (Fig. 5Bb–c and e).

The p3 come from a mature and juvenile individual. The p3 of the mature individual is broken along the lingual edge (Fig. 4F) and has a highly developed vestibular anteroconid. Although the lingual anteroconid is fragmented, it appears small and tapered. The protoflexid is weakly expressed, unlike what is observed in hares, for example those from Sima del Elefante (Fig. 5A–g). The heavily-damaged hypoflexid is deep and occupies almost the entire width of the tooth. The paraflexid and entoconid are not well-developed and rather small (Table 4). The anteroconids of the juvenile p3 are well-developed but asymmetric, characterized by a rather elongated vestibular anteroconid. The protoflexid forms an acute angle, and the hypoflexid is smooth and runs across almost the entire width of the tooth. Finally, the paraflexid is absent on the juvenile p3.

The scapular fragment exhibits significant differences in terms of size and morphology. In ventral view, the glenoid cavity, supraglenoid tubercle and coracoid process of the articular surface meet in a relatively flat, non-articular surface (Fig. 8D–c), a trait unique to hares (Callou, 1997). Additionally, the dimensions of the glenoid cavity

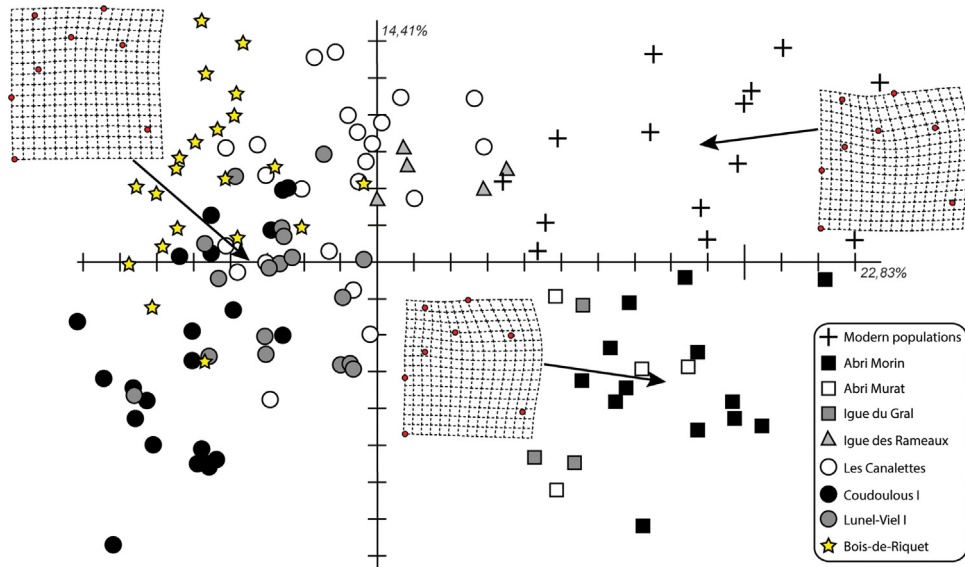


Fig. 7. (Color online.) Principal Component Analysis (PCA) and deformation grids obtained from eight landmarks. The axes 1 and 2 represent 37.24% of the total variance.

Fig. 7. (Couleur en ligne.) Analyse en composantes principales (ACP) et grilles de déformation obtenues à partir des huit points repères. Les axes 1 et 2 représentent 37,24% de la variance totale.

(Table 4) fall within the variability of both Pleistocene and present-day hares (see Donard, 1982).

The humerus has a thick trochlea and a relatively blunt medial epicondyle. These dimensions are clearly more similar to *Lepus* from Spanish sites (Table 5). The humerus is slightly larger than hares from same period at Sima del Elefante and smaller than the Pleistocene hares known from France. The most complicated element of the hind

limb is the limited number of distinctive morphological traits between the two genera, especially in terms of the tarsals. On the other hand, hares, which are better suited to running, have much longer and more robust legs than do wild rabbits, meaning that size criteria alone are sufficient for distinguishing between genera. Two of the largest calcaneums were found at Bois-de-Riquet (23.06 mm for the only complete specimen) feature immature characters

Table 3

Comparison of measurements for *Oryctolagus cf. giberti* from **Bois-de-Riquet** with other Pleistocene populations.

Tableau 3

Mesures comparatives des *Oryctolagus cf. giberti* du **Bois-de-Riquet** avec d'autres populations pléistocènes.

Measurements	Site	Species	Min	Max	n	Mean	σ	References
DT distal humerus	Valdarno, Tuscany (I)	<i>O. valdarnensis</i>	11.08	11.86	2	–	–	De Marfà, 2009
	Caune de l'Arago, Pyrénées-Orientales (F)	<i>O. cuniculus</i>	8.30	10.18	129	9.22	0.47	Desclaux, 1992
	Valdemino, Savona (I)	<i>O. burgi</i>	9.20	12.90	31	10.31	0.90	Nocchi and Sala, 1997a
	Cova del Bolomor IV, Valencia (S)	<i>O. cuniculus</i>	8.06	10.04	10	8.92	0.62	Sanchis-Serra, 2010
	Lunel-Viel, Hérault (F)	<i>O. cuniculus</i>	7.90	9.40	30	8.48	0.40	Donard, 1982
	Lazaret, Alpes-Maritime (F)	<i>O. cuniculus</i>	8.00	10.82	159	9.30	0.52	El Guennoui, 2001
	Bois-de-Riquet, Hérault (F)	<i>O. cf. giberti</i>	8.86	9.79	7	9.27	0.36	This paper
DAP coxal	Perrier, Auvergne (F)	<i>O. lacosti</i>	–	–	1	8.87	–	De Marfà, 2009
	Cueva Victoria, Murcia (S)	<i>O. giberti</i>	7.11	7.50	2	–	–	De Marfà, 2009
	Valdemino, Savona (I)	<i>O. burgi</i>	8.01	8.54	2	–	–	De Marfà, 2009
	Cova del Bolomor IV, Valencia (S)	<i>O. cuniculus</i>	8.87	9.65	4	9.20	0.37	Sanchis-Serra, 2010
	Lunel-Viel, Hérault (F)	<i>O. cuniculus</i>	7.80	9.20	32	8.31	0.31	Donard, 1982
	Lazaret, Alpes-Maritime (F)	<i>O. cuniculus</i>	7.02	9.20	56	8.31	0.43	El Guennoui, 2001
Bois-de-Riquet, Hérault (F)	<i>O. cf. giberti</i>	7.85	9.05	5	8.30	0.46	This paper	
DT distal femur	Valdarno, Tuscany (I)	<i>O. valdarnensis</i>	–	–	1	16.60	–	De Marfà, 2009
	Cueva Victoria, Murcia (S)	<i>O. giberti</i>	13.94	15.82	3	14.59	1.07	De Marfà, 2009
	Caune de l'Arago, Pyrénées-Orientales (F)	<i>O. cuniculus</i>	12.85	16.63	16	14.03	0.69	Desclaux, 1992
	Valdemino, Savona (I)	<i>O. burgi</i>	15.00	17.80	24	16.35	0.72	Nocchi and Sala, 1997a
	Cova del Bolomor IV, Valencia (S)	<i>O. cuniculus</i>	14.08	14.77	3	14.46	0.35	Sanchis-Serra, 2010
	Lazaret, Alpes-Maritime (F)	<i>O. cuniculus</i>	14.04	16.20	31	15.20	0.56	El Guennoui, 2001
	Bois-de-Riquet, Hérault (F)	<i>O. cf. giberti</i>	14.11	14.15	2	–	–	This paper

F: France; I: Italy; S: Spain.

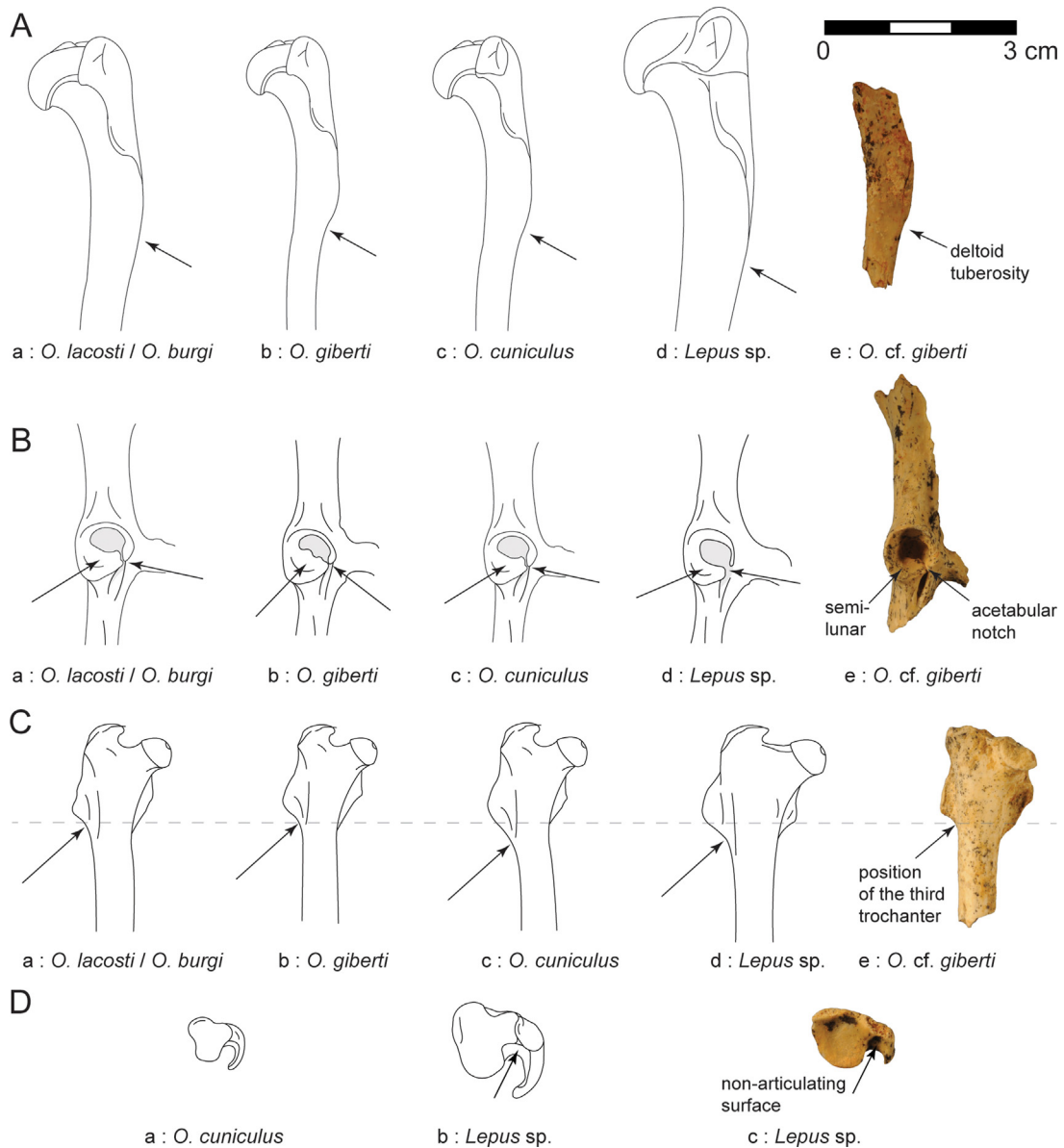


Fig. 8. (Color online.) Distinctive characteristics of the different leporid species from Pleistocene Western Europe. Right humerus (A) in lateral view (A–a from Nocchi and Sala, 1997a; A–b from De Marfà, 2008; A–c and A–d from Callou, 1997; A–e BDR12 X37A – MP0014), on right coxal (B) in ventral view (B–b from De Marfà, 2008; B–e BDR08 L2 – MP0123), on right femur (C) in cranial view (C–a from Nocchi and Sala, 1997a; C–b from De Marfà, 2008; C–c and C–d from Callou, 1997; C–e BDR08 K2 – MP0259) and on right scapula (D) in ventral view (D–a and D–b from Callou, 1997; D–c BDR10 W33 – MP0083). The arrows indicate the differences for a diagnosis.

Fig. 8. (Couleur en ligne.) Caractères distinctifs des différentes espèces de léporidés du Pléistocène d'Europe occidentale. Humérus droit (A) en vue latérale (A–a d'après Nocchi et Sala, 1997a; A–b d'après De Marfà, 2008; A–c et A–d d'après Callou, 1997; A–e BDR12 X37A – MP0014); coxal droit (B) en vue ventrale (B–b d'après De Marfà, 2008; B–e BDR08 L2 – MP0123); fémur droit (C) en vue crâniale (C–a, d'après Nocchi et Sala, 1997a; C–b d'après De Marfà, 2008; C–c et C–d, d'après Callou, 1997; C–e BDR08 K2 – MP0259); scapula droite (D) en vue ventrale (D–a et D–b d'après Callou, 1997; D–c BDR10 W33 – MP0083). Les flèches indiquent les différences pour une diagnose.

(porous bone and unfused ends). Comparison with *Oryctolagus cf. giberti* juveniles from the deposits indicates an attribution to *Lepus*. In proximal view, the talus has a relatively square trochlea. In addition to this characteristic feature of hares (Callou, 1997), the dimensions (Table 4) are also closer to those of *Lepus* based on measurements available in Donard (1982).

4. Discussion

The Bois-de-Riquet leporid assemblage contains two taxa previously documented from Lower Pleistocene deposits on the Iberian Peninsula: *Oryctolagus cf. giberti* and *Lepus sp.* The dental and skeletal morphology of the *Oryctolagus* remains are similar to those described for *O. giberti* at

Table 4

Measurements for *Lepus* from Bois-de-Riquet. Number of elements (*n*), minimum and maximum values for each measurement, and mean and standard deviations (σ).

Tableau 4

Mesures réalisées sur les différentes parties anatomiques des *Lepus* du Bois-de-Riquet. Sont figurés le nombre de mesures (*n*), les valeurs minimums et maximums pour chaque mesure, la moyenne, ainsi que l'écart-type associé.

Measurements (mm)	<i>n</i>	Min	Max	Mean	σ
VLD p3 juv	1	2.95	–	–	–
MDD p3 juv	1	3.30	–	–	–
VLD p3	1	3.00	–	–	–
MDD p3	1	3.30	–	–	–
VLD P2	3	3.35	4.00	3.68	0.3253
MDD P2	3	1.85	2.20	2.02	0.1756
DAP scapula neck	1	7.06	–	–	–
DCG scapula	1	10.17	–	–	–
DT distal humerus	1	11.24	–	–	–
DAP distal humerus	1	8.31	–	–	–
Talus length	1	14.54	–	–	–
DT talus trochlea	3	6.16	6.64	6.42	0.2417

Cueva Victoria (De Marfà, 2008). The p3 have fairly deep anteroflexid with converging edges, an ellipsoidal vestibular anteroconid and an extended lingual anteroconid that is relatively rectangular. Conversely, the morphology of the Bois-de-Riquet individuals approaches that of the so-called “modern” *O. cuniculus* given their similar anteroconids and deeper anteroflexid (Figs. 4 and 5). Moreover, the morphological and metric traits of the p3 from Bois-de-Riquet individuals appear significantly different from those of *O. valdarnensis*, which is found in Italy during the same period (Fig. 5A–c and Fig. 6).

In addition, while De Marfà (2008) has stated that dental configuration alone is insufficient to distinguish *O. giberti* and *O. cuniculus*, our geometric morphometrics succeeded in differentiating middle and late Upper Pleistocene population from extant groups despite the relatively low variance. Furthermore, although distinguishing the Bois-de-Riquet population and the Middle Pleistocene samples was not clear, our preliminary analysis suggests that a larger comparative sample ought to provide more reliable results. In terms of the post-cranial skeleton,

the deltoid tuberosity is relatively well-developed, the auricular surface of the coxal bone is wide and V-shaped, and the third trochanter is in a high position. The available morphological data for the different species of Pleistocene rabbits (Fig. 1) indicates the principle diagnostic criteria to relate to the humerus, pelvis and femur (Fig. 8).

From an osteometric perspective, the leporids from Bois-de-Riquet are slightly smaller than those assigned to *Oryctolagus* sp. from Sima del Elefante (Burgos, Spain), which are dated to around 1.2 Ma (Cuenca-Bescós and Rofes, 2004; Rosas et al., 2006) but are slightly larger than *O. giberti* from Cueva Victoria (Murcia, Spain), dated to 1.4 Ma (Gibert et al., 1999). It is important to note that the remains from the Lower Pleistocene deposits of Sima del Elefante probably belong to *O. giberti* (De Marfà, 2009).

The remains attributable to *O. giberti* from Bois-de-Riquet, dated to between 1.2 and 1 Ma, indicate that this species developed in areas outside the Iberian Peninsula. Previously, this possibility was hinted at only by the presence of *O. gr. laynensis-cuniculus* at about 1 Ma from Vallonnet (Nocchi and Sala, 1997b). The limited number of remains and the lack of species specific attribution precluded identifying *O. giberti* at this site. Its extension beyond the Pyrenees certainly marks the beginning of the expansion of this lineage from the Lower Pleistocene onwards. On the other hand, larger rabbits from central Mediterranean (*O. lacosti* – *O. valdarnensis* – *O. burgi*) became isolated in Tuscany before disappearing during the late Middle Pleistocene (cf. Fig. 1). The rabbits from Bois-de-Riquet suggest a gradual evolution of the genus *Oryctolagus* that began in the Lower Pleistocene and was spread across a more substantial area than previously thought (cf. Fig. 1).

The second group of leporids from Bois-de-Riquet has been assigned to the genus *Lepus* based on the characters proposed by Callou (1997). The scapula presents a non-articular surface (ventral view) between the glenoid cavity, supraglenoid tubercle and coracoid process. The humerus has a relatively thick trochlea and a blunt medial epicondyle, while the talus has a square trochlear morphology in proximal view. Unfortunately, the limited number of remains made identifying the exact species impossible.

Table 5

Comparison of measurements for *Lepus* sp. of Bois-de-Riquet with other Pleistocene populations.

Tableau 5

Mesures comparatives du *Lepus* sp. du Bois-de-Riquet avec d'autres populations pléistocènes.

Measurements	Site	Species	Min	Max	<i>n</i>	Mean	σ	References
DT distal humerus	Sima del Elefante, Burgos (S)	<i>L. sp.</i>	9.50	10.71	8	10.07	0.39	De Marfà, 2009
	Cova del Bolomor Ie, Valencia (S)	<i>L. sp.</i>	–	–	1	11.11	–	Sanchis-Serra and Fernández-Peris, 2011
	Camp de Peyre, Lot-et-Garonne (F)	<i>L. timidus</i>	11.00	12.70	8	11.78	0.62	Donard, 1982
	Le Regourdou, Dordogne (F)	<i>L. timidus</i>	11.50	12.20	7	11.90	0.22	Donard, 1982
	Moros Gabasa, Huesca (S)	<i>L. sp.</i>	–	–	1	11.80	–	Sanchis-Serra, 2010
	Aitzbitarte IV, Cantabria (S)	<i>L. sp.</i>	–	–	1	12.20	–	Altuna, 1972
	Urriaga D, Cantabria (S)	<i>L. sp.</i>	–	–	1	11.50	–	Altuna, 1972
	Urriaga F, Cantabria (S)	<i>L. sp.</i>	–	–	1	12.10	–	Altuna, 1972
	La Madeleine, Dordogne (F)	<i>L. timidus</i>	11.40	13.30	45	12.47	0.45	Donard, 1982
	Bois-Ragot, Vienne (F)	<i>L. timidus</i>	11.70	13.80	51	12.70	0.58	Donard, 1982
	Le Quéroy, Charente (F)	<i>L. europaeus</i>	11.50	12.90	10	11.89	0.40	Donard, 1982
	Bois-de-Riquet, Hérault (F)	<i>L. sp.</i>	–	–	1	11.24	–	This paper

F: France; S: Spain.

Lepus sp. from Bois-de-Riquet seems to be smaller than both Middle and Upper Pleistocene hares from Western Europe as well as modern European hares. The reduced body size of *Lepus* sp. in the Lower Pleistocene sample could be explained by the possibility that:

- hares were not yet clearly differentiated (López-Martínez, 1980);
- environmental conditions controlled body size;
- hares experienced substantial interspecific competition with rabbit (Flux, 2008; Frugulione, 1960).

The identification of *Lepus* sp. at Bois-de-Riquet is the first time this genus has been recorded outside Central Europe (Fladerer, 1987; Kretzoi, 1956; Paunović and Jambrešić, 1997), Germany (Maul, 2001), Italy (Van der Meulen, 1973) or Spain (De Marfà, 2009; Galobart et al., 2003; Mazo et al., 1985), suggesting the previously suggested palaeobiogeographic hiatus is an artifact of research intensity. The morphological and hence taxonomic similarities between the Bois-de-Riquet and Sima del Elefante leporids, as well as the simultaneous presence of *Lepus* sp. and *Oryctolagus* cf. *giberti* in both deposits, suggest the two sites occupy a similar chronological position. However, the two taxa of Bois-de-Riquet are comparatively larger than the Spanish population.

There is a clinal variation in the size of wild rabbits (Callou, 2003), with the largest populations occupying higher latitudes (northern France) and smaller populations found in more southerly regions (Spain and Maghreb). Moreover, a mathematical relationship has been demonstrated between the size of extant rabbits and temperature (Davis and Moreno-García, 2007) that is in line with Bergmann's rule. Leporid body size is highly dependent on geography and climate. For example, El Guennouni (2001) has shown substantial differences in body size for *O. cuniculus* from southern France and northern Spain, explaining biometric variations of Middle and Upper Pleistocene rabbits with reference to different climatic conditions.

The Bois-de-Riquet leporids are larger than those from the more southern Cueva Victoria, which is consistent with the clinal variation observed by Callou (2003). On the other hand, they are smaller than examples from Sima del Elefante, which also lies at a lower latitude. This pattern is likely explained by local climatic influences. Both Bois-de-Riquet and Cueva Victoria are located on the Mediterranean coast (cf. Fig. 1), while Burgos is exposed to the more oceanic conditions of northern Spain (Peel et al., 2007). Although difficult to demonstrate conclusively, similar climatic differences between these regions may have existed during the Lower Pleistocene. For example, it is reasonable to assume that the Mediterranean coast presented more favorable climatic conditions during this period, leading to a reduction in the size of rabbits (Davis and Moreno-García, 2007) according to Bergman's rule.

In the light of what little data is currently available from sites across Western Europe and the considerable period of time involved, size criteria alone are sufficient only to differentiate Lower Pleistocene leporids by genus (i.e., *Oryctolagus* and *Lepus*). The identification of different

species requires detailed morphological and morphometric traits of both dental remains and post-cranial skeletons bearing in mind both chronological and geographical factors.

5. Conclusion

The Bois-de-Riquet assemblage sheds new light on the evolutionary history of extant rabbits and the Lower Pleistocene geography of leporids, including evidence for a wider geographical range of *Oryctolagus* cf. *giberti* and the presence of *Lepus* sp., linking the Iberian Peninsula and Central Europe. Furthermore, the absence of leporids in certain regions of Western Europe most likely reflects research intensity rather than a genuine biochronological hiatus.

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