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General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

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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ARTICLE INFO

Article history:

Received 4 November 2014

Accepted after revision 20 March 2015

Available online 13 June 2015

Handled by Lars van den Hoek Ostende

Keywords:

Evolution

Biochronology

Systematic

Oryctolagus cf. *giberti**Lepus* sp.

2D geometric morphometry

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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R É S U M É

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

Mots clés :

Évolution

Biochronologie

Systématique

Oryctolagus cf. *giberti**Lepus* sp.

Morphométrie géométrique 2D

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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.

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