MORPHOLOGICAL DIVERSITY, EVOLUTION AND BIOGEOGRAPHY OF EARLY PLEISTOCENE RABBITS (GENUS ORYCTOLAGUS)

by MAXIME PELLETIER

Archaeology, History, Culture and Communication Studies, Faculty of Humanities, University of Oulu, Oulu, Finland; maxime.pelletier@oulu.fi

Abstract: The early Pleistocene is the key period for understanding the evolutionary history and palaeobiogeography of rabbits (Genus Oryctolagus). In western Europe, many species were endemic, making them a reliable indicator of the evolution of the terrestrial ecosystems in which many species have evolved. However, the morphological variability of rabbit species is still poorly understood and their phylogeny remains a subject of debate. Through both qualitative (morphological description) and quantitative (linear measurements and two-dimensional geometric morphometrics) approaches, we address here the morphometric diversity of the third lower premolar (p3), a tooth commonly used to distinguish leporid species, in order to assess intra- and inter-regional morphological variations in several early Pleistocene rabbit populations. Our results suggest that the different approaches are complementary and allow, on different levels, a full characterization of the p3 variability of early Pleistocene rabbits and to imply relations between populations. The size and shape variations of this tooth reflect the taxonomic and phylogenetic signals of the different species but were probably also significantly impacted by geographical position and local climatic conditions. In view of the great morphometric variability highlighted in this work, we suggest a careful reconsideration of certain dental criteria previously considered ‘diagnostic’ in the characterization of these species. However, the overall results allowed us to discuss the phylogeny of the genus Oryctolagus and to hypothesize the ecological requirements and different phases of the dispersal of taxa in western Europe, probably associated with global climate changes.

Key words: Oryctolagus, geometric morphometrics, early Pleistocene, morphological diversity, palaeoclimate, palaeobiogeography.

The quantification of morphological diversity is essential for achieving a better understanding of the evolutionary processes of species in time and space (e.g. Foote 1997; Hopkins & Gerber 2017). Studies of fossil specimens generally attempt to apprehend the factors responsible for morphometric and phenotypic variations (e.g. environmental and/or evolutionary event), their hypothetical phylogenetic links and the ecological characteristics that would make them valid and distinct species (Mayr 1963). This would prevent the amplification of specific differentiations (i.e. when anatomical characters differ between individuals) and the over complication of taxonomy. In absolute terms, these studies should be considered in the same comparative framework. However, the characterization of morphological diversity in a taxonomic group is often based on the use of distinct methods by the different authors, such as the description of morphological characters, traditional (i.e. using linear measurements) or geometric (i.e. landmarks and/or semi-landmarks) morphometrics. This has often hampered attempts to explore the interrelationships of different taxa, as well as their respective morphometric variability.

Descriptive approaches to morphology tend to focus on cladistic data sets in broad taxonomic scope studies (Lloyd 2016; Gerber 2019). They also allow us to grasp unique morphological characters. However, these approaches are less effective in addressing more tenuous changes in size, shape and/or proportion among individuals of the same genus or species. Conversely, traditional (i.e. linear measurements) or geometric (i.e. landmarks and/or semi-landmarks) morphometrics can quantitatively characterize this kind of variation between specimens in a single study (Bookstein 1991; Zelditch et al. 2012). One of the strengths of these quantitative methods, and in particular the geometric morphometrics (GMM) now widely used in palaeontology, is identifying the processes that are at the core of these variations. Thus, none of these methods can necessarily be considered more effective since they are used...
in different circumstances. However, when we are interested in a particular taxon, it is often difficult to combine all of these different data from the scientific literature to assess and refine general macroevolutionary patterns. To solve these various issues, recent studies have compared these different qualitative and quantitative approaches to highlight whether patterns of morphological variation are congruent or contrasting (Hetherington et al. 2015; Hopkins 2017; Mongiardo Koch et al. 2017; Ferrón et al. 2020; Schaeffer et al. 2020). To this end, we explore the evolution of morphological diversity in rabbits of the genus _Oryctolagus_, the most abundant leporids in the Quaternary paleontological and archaeological records from southwestern Europe. Over the past two decades, numerous old collection revisions and new material descriptions have allowed the taxonomy of Pleistocene taxa and their biochronological and palaeogeographical frameworks to be significantly improved. Despite this, the taxonomy and phylogeny of Pleistocene species still remain in flux and the subject of debate (Nocchi & Sala 1997; De Marfà & Mein 2007; López-Martínez 2008; De Marfà 2008, 2009; Angelone & Rook 2012; Angelone 2013; Pelletier et al. 2015a; Pelletier 2018; Angelone et al. 2019, 2020). Consequently, six fossil species of _Oryctolagus_ are now known in Europe (Fig. 1). However, three of these species were only present during the early Pleistocene, while only one species, the extant European rabbit, is now known in Europe (e.g. De Marfà 2008, 2009, and references therein; López Jiménez et al. 2020), _O. giberti_ spread in south-eastern France at the end of this period (around 1.1–0.9 Ma), with notable occurrences in the Bois-de-Riquet (Hérault) and Vallonnet (Alpes-Maritimes) deposits (Pelletier et al. 2015a; Pelletier 2018). _Oryctolagus giberti_ and _O. valdarnensis_ disappeared from the fossil record at the end of the early Pleistocene (i.e. 0.8 and 1.2 Ma, respectively) and two other taxa emerged from the beginning of the middle Pleistocene in the Iberian and Italian peninsulas: _O. cicindelus_ and _O. burgi_. The first species represents the extant European rabbit, known from the beginning of the middle Pleistocene (around 0.7–0.6 Ma) in south-western Spain in the Cúllar de Baza (Andalusia) and Benisants (Valencia) deposits (López-Martínez 1989; Pelletier 2018), as well as in south-eastern France at Balaruc 1 (Hérault) and the Escale cave (Bouches-du-Rhône) (Pelletier 2018). The second species was present at Valdemino (Liguria) (Nocchi & Sala 1997a, b; Sala & Masini 2007) and potentially at Ponte Galeria 3 (Lazio) (Kotsakis & Barisone 2008), only around 0.6 Ma (Sala & Masini 2007; López-Martínez 2008; Angelone et al. 2020). It had previously been proposed that _O. burgi_ could have been phylogenetically associated with _O. lacosti_ and _O. valdarnensis_ (Nocchi & Sala 1997b; De Marfà 2009; Pelletier et al. 2015a). However, in the present state of research, the phylogenetic relationships of this form with the congeneric species are not clear (Nocchi & Sala 1997a, b; Pelletier 2018; Angelone et al. 2020). Furthermore, the status of this species has recently been questioned and it could be a synonym of _O. cicindelus_, notably due to the great morphological similarities and the geographical proximity of the individuals of Valdemino to those of Balaruc 1 and the Escale cave (Pelletier 2018).

Ultimately, it would appear that all forms of the early Pleistocene coincide with specific periods and/or geographical areas (Fig. 1). For example, _O. laynensis_ seems to be mainly present in the Piacenzian of Spain. As specimens from Fonelas P-1 could belong to _O. laynensis_ (but thus far have been assigned to _Oryctolagus_ sp.; Laplana &
Blain 2008), this leaves the upper boundary of the chronological distribution still open to discussion, possibly up to 2.5 Ma (López-Martínez 1989, 2008); 4, Maluenda 3 (van Dam & Sanz-Rubio 2003); 5, El Rincón 1 (Alberdi et al. 1997); 6, Fonelas P-1* (Lapiana & Blain 2008); 7, Perrier (De Marfà & Mein 2007); 8, Montoussé 5 (Chaline et al. 2000); 9, Saint-Vallier (Martín-Suárez & Mein 2004); 10, Montagnola Senese, 11, Torre di Picchio, 12, Casa Sgherri, Valdarno, Casa Frata, 13, Fontana Acetosa, 14, Pietrafitta, 15, Monte Argentario, 16, Pirro Nord, 17, Monte Peglia* (Angelone et al. 2020 and references therein); 18, Casablanca 1 (De Marfà 2009); 19, Xàbia II (Sarroín 2012); 20, Illes Medes, 21, Venta Micena, Barranco León 5, Fuente Nueva 3, 22, Quibas, 23, Sima del Elefante (De Marfà 2009 and references therein); 24, Incarcal I and V (Galobart et al. 2003); 25, Vallonnet cave, 26, Bois-de-Riquet (Pelletier et al. 2015a); 27, Cueva Victoria (De Marfà 2008); 28, Huéscar I (Mazo et al. 1985); 29, Cueva Negra (López-Jiménez et al. 2020); 30, Pontón de la Oliva* (Sesé & Ruiz Bustos 1992); 31, Cúllar de Baza (López-Martínez 1989); 32, Benisants, 33, Balaruc 1, 34, Escale cave (Pelletier 2018); 35, Valdemino (Nocchi & Sala 1997a); 36, Ponte Galeria 3 (Kotsakis & Barisone 2008). *In the current state of knowledge although it could be affiliated with this taxon, it has been left in the open nomenclature (Oryctolagus sp.) Benthic δ18O curve (per mil) from Lisiecki & Raymo (2005). Rabbit silhouette © 1996 ArcheoZoo.org / Michel Coutureau (Inrap), Vianney Forest (Inrap).

**FIG. 1.** Palaeobiogeographic and temporal distribution of the genus Oryctolagus data in the late Pliocene and early-middle Pleistocene, based on published data. Squares represent the sites analysed in this study. Sites: 1, Layna, 2, Gorafe 2, 3, Córdoba (López-Martínez 1989, 2008); 4, Maluenda 3 (van Dam & Sanz-Rubio 2003); 5, El Rincón 1 (Alberdi et al. 1997); 6, Fonelas P-1* (Lapiana & Blain 2008); 7, Perrier (De Marfà & Mein 2007); 8, Montoussé 5 (Chaline et al. 2000); 9, Saint-Vallier (Martín-Suárez & Mein 2004); 10, Montagnola Senese, 11, Torre di Picchio, 12, Casa Sgherri, Valdarno, Casa Frata, 13, Fontana Acetosa, 14, Pietrafitta, 15, Monte Argentario, 16, Pirro Nord, 17, Monte Peglia* (Angelone et al. 2020 and references therein); 18, Casablanca 1 (De Marfà 2009); 19, Xàbia II (Sarroín 2012); 20, Illes Medes, 21, Venta Micena, Barranco León 5, Fuente Nueva 3, 22, Quibas, 23, Sima del Elefante (De Marfà 2009 and references therein); 24, Incarcal I and V (Galobart et al. 2003); 25, Vallonnet cave, 26, Bois-de-Riquet (Pelletier et al. 2015a); 27, Cueva Victoria (De Marfà 2008); 28, Huéscar I (Mazo et al. 1985); 29, Cueva Negra (López-Jiménez et al. 2020); 30, Pontón de la Oliva* (Sesé & Ruiz Bustos 1992); 31, Cúllar de Baza (López-Martínez 1989); 32, Benisants, 33, Balaruc 1, 34, Escale cave (Pelletier 2018); 35, Valdemino (Nocchi & Sala 1997a); 36, Ponte Galeria 3 (Kotsakis & Barisone 2008). *In the current state of knowledge although it could be affiliated with this taxon, it has been left in the open nomenclature (Oryctolagus sp.) Benthic δ18O curve (per mil) from Lisiecki & Raymo (2005). Rabbit silhouette © 1996 ArcheoZoo.org / Michel Coutureau (Inrap), Vianney Forest (Inrap).
morphological characters in early Pleistocene rabbit species. Thus, it is quite conceivable that the differences observed between the fossil populations may be the result of chronological and/or geographical variations linked to environmental conditions, omitting the notion of intra- and inter-specific variability. In addition, early Pleistocene rabbit fossils remain relatively rare, often fragmented and with a wide spatiotemporal distribution. Traditionally for the genus Oryctolagus, apart from studies on the quantification of variations in body size (e.g. Donard 1982; Sharples et al. 1996; Callou 2003; Davis & Moreno-García 2007; Pelletier et al. 2015a, b; Pelletier 2018, 2019; Davis 2019), the vast majority of palaeontological works is based on the study of shape variations of the third lower premolar (p3). This tooth is widely used to distinguish leporid species and to reveal their phylogenetic relationships (Petter 1959, 1961; Hibbard 1963; López-Martínez et al. 1976; Palacios 1976, 1996; Palacios & López-Martínez 1980; López-Martínez 1980, 1989; Donard 1982; Suchentrunk et al. 1994; Nocchi & Sala 1997a; Suchentrunk et al. 2000; De Marfà & Mein 2007; De Marfà 2008, 2009; Angelone & Rook 2012; Angelone 2013; Pelletier et al. 2015a, b; Pelletier 2018, 2019). However, the relevance of these dental criteria could be revised in relation to the data acquired on modern individuals. Indeed, it has been shown that some of these variations could be caused by selective processes such as adaptation to environmental conditions or regional gene flows (Suchentrunk et al. 2000). Moreover, it has also been demonstrated that latitude, temperature and precipitation (among other environmental parameters) are the main factors that drive the shape variation of p3 in the various modern populations of O. cuniculus (Pelletier 2019). This suggests the existence of a significant polymorphism and would call into question certain criteria that are generally used to identify rabbit species. In addition, the specific characterizations of fossil individuals using a description of these morphological characters could vary across authors, be subject to biases resulting from inpopulation variations and potentially result in lack of consensus regarding the subjectivity of the criteria used to define a species.

Since it has been demonstrated that genetic divergence significantly impacts tooth morphology (e.g. Polly 2001; Caumul & Polly 2005; Ledevin et al. 2016; Cucchi et al. 2017, 2019), a more detailed analysis of dental shape using GMM could allow a distinction to be made between species or an assessment of taxonomic and phylogenetic signals. These approaches, now increasingly used in leporids (Patnaik 2002; De Marfà 2009; Pelletier et al. 2015a, b; Sawaura et al. 2018; Pelletier 2018, 2019), could then enable the quantification of the variability of rabbit populations from the early Pleistocene and the recognition of how these could be related instead to intrinsic or extrinsic factors. Thus, in this work, we use three distinct approaches to characterize the morphological variability of the p3: (1) the description of dental characters; (2) the analysis of linear measurements; and (3) a two-dimensional (2D) GMM analysis of seven early Pleistocene populations, representing the three species described for this period (i.e. O. lacosti, O. valdarnensis and O. giberti). Thus, geometric morphometric characterization of the p3 will provide a fair and effective comparison with the two other methods more commonly used in studies of fossil leporids. It will also provide an opportunity to assess and discuss the relative effects of different factors (e.g. size, phylogeny, geographical position and climate) on morphological differentiation, in order to interpret the temporal, phylogenetic and ecological context of the evolution of early rabbits.

**MATERIAL AND METHOD**

**Sample**

The analysed fossil sample includes 76 individuals from seven early Pleistocene populations representing the three species described for this period: O. lacosti, O. valdarnensis and O. giberti (Table 1). This includes rabbits from the deposits of: (1) Perrier (Puy-de-Dôme, France) positioned c. 2.5–2.4 Ma (Chaline 1986) and including the lectotype for O. lacosti (De Marfà & Mein 2007); (2) Saint-Vallier (Drôme, France), where the same species has been identified in levels dated to c. 2.1–2.0 Ma (Guérin et al. 2004; Martín-Suárez & Mein 2004); (3) Pirro Nord 13 (Foggia, Italy), possibly related to O. valdarnensis (Angelone 2013; Angelone et al. 2020), between 1.6 and 1.3 Ma (López-García et al. 2015), and which could represent one of the most abundant palaeontological collections (in terms of number of specimens) for this species; (4) Cueva Victoria (Murcia, Spain) providing the holotype for O. giberti, initially estimated at 1.4 Ma (De Marfà 2008), but whose chronology was refined to the end of the early Pleistocene, c. 0.9–0.8 Ma (Gibert et al. 2016); (5) Xàbia II (Valencia, Spain), positioned c. 1.8–1.6 Ma (Sarrión 2012) and which could represent one of the earliest records of O. giberti in Spain (Pelletier 2018); (6) the Vallonnet cave (Alpes-Maritimes, France); and (7) Boisse de Riquet (Hérault, France). The latter two are currently the only known deposits in France where O. giberti has been identified (Pelletier et al. 2015a; Pelletier 2018), dated to c. 1.2–1.1 Ma (Michel et al. 2017) and 1.0–0.9 Ma (Lozano-Fernández et al. 2019), respectively. The GMM study also incorporates 117 individuals from four modern populations from western Europe (Table 1) that
TABLE 1. Fossil sites and modern populations used in this study, according to locality, species, chronological range and number of individuals studied (N).

| Site (location)        | Species | Chronology | N  |
|-----------------------|---------|------------|----|
| **Lower Pleistocene**  |         |            |    |
| Bois-de-Riquet (Héraul, France) | O. giberti | 1.0–0.9 Ma | 15 |
| Cueva Victoria (Murcia, Spain) | O. giberti | 0.9–0.8 Ma | 5  |
| Perrier (Puy-de-Dôme, France) | O. lacosti | 2.5–2.4 Ma | 1  |
| Pirro Nord 13 (Foggia, Italy) | O. valdarnensis | 1.6–1.3 Ma | 43 |
| Saint-Vallier (Drôme, France) | O. lacosti | 2.1–2.0 Ma | 2  |
| Vallonnet cave (Alpes-Maritimes, France) | O. giberti | 1.2–1.1 Ma | 8  |
| Xàbia II (Valencia, Spain) | O. giberti | 1.8–1.6 Ma | 2  |
| **Modern populations** |         |            |    |
| Las Lomas (Andalusia, Spain) | O. cuniculus | Present  | 31 |
| Navarre (Navarre, Spain) | O. cuniculus | Present  | 30 |
| Santarém (Alentejo, Portugal) | O. cuniculus | Present  | 36 |
| Tour du Valat (Bouches-du-Rhône, France) | O. cuniculus | Present  | 20 |

Details of each specimen including catalogue numbers and repositories are provided in Appendix S1.

have already been the subject of a specific study of the morphological variability of the extant European rabbit (Pelletier 2019). The details for each specimen including catalogue numbers and repositories are provided in Appendix S1.

Institutional abbreviations. FSL, Collections de Paléontologie du Laboratoire de Géologie de Lyon, Terre, Planètes, Environnement (LGL-TPE), Université Claude Bernard-Lyon 1, Villeurbanne, France; IGF, Sezione di Geologia e Paleontologia, Museo di Storia Naturale di Firenze, Florence, Italy; NMB, Natural History Museum of Basel, Switzerland; MENTON, Musée de Préhistoire Régionale de Menton, Menton, France; VIGAL, Villa Gallego, Pézenas, France; MCBN, Museu de Ciências Naturais de Barcelona, Spain; MNP, Musée National de Préhistoire, Les Eyzies-de-Tayac-Sireuil, France; MRSN, Dipartimento di Scienze della Terra, Università di Torino, Italy; MUPREVA, Museu de Prehistória de Valencia, Servei d’Investigació Prehistòrica, Diputació de València, Valencia, Spain; UNIFE, Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, Italy.

Description and tooth measurements

The description of dental characters and the measurements of the p3 are based on the work of Donard (1982) (Fig. 2). Metric data were collected using a Dino-Lite Digital Microscope (AM7013MT). Our sample is described, compared and discussed with previously published data, including the type-species and affiliate specimens described for the early Pleistocene. The individuals of O. lacosti from Perrier and Saint-Vallier were compared with those from Montoussé 5 (Chaline et al. 2000) and the population of Pirro Nord 13 with individuals from Valdarno and Pirro Nord 10 (Angelone & Rook 2012, Angelone 2013). The individuals from Bois-de-Riquet, Cueva Victoria, the Vallonnet cave and Xàbia II were compared with those from Barranco León 5, Casablanca 1, Fuente Nueva 3, Quibas, Sima del Elefante (De Marfà 2009), Huéscar I (Mazo & al. 1985) and Cueva Negra (López Jiménez et al. 2020). Finally, a few individuals from the Balaruc I and Escale cave deposits that belong to the first representatives of O. cuniculus from western Europe were also included (Pelletier 2018).

Geometric morphometric analysis

Data were collected from 2D digital photographs of the occlusal surface of each p3 using a standardized protocol (Pelletier 2019): teeth were positioned in a direction perpendicular to the focal plane, with parallax controlled for by symmetrically adjusting the lingual anteroconid and entoconid to limit biases resulting from the vestibulo-lingual obliquity of the tooth. Pictures were taken using the same Dino-Lite Digital Microscope. This 2D protocol involves six landmarks positioned on the inner edge of the enamel and corresponds to the points of maximum curvature (Fig. 2). Between landmarks 1 and 2, and 6 and 1, two curves, each composing 30 equidistant semilandmarks, were used to characterize the contours of the anteroflexid and the vestibular (or labial) and lingual anteroconids. As it has recently been shown that the morphological variations on the mesial portion of the tooth are directly impacted by different geographical and climatic factors, this protocol is relevant to identify what comes under taxonomic or extrinsic factors (Pelletier 2019). The hypoflexid was excluded from the analysis because although many authors report it as a trait of great phylogenetic importance, it does not appear to be related to taxonomy. For example, it has been shown that the number of crenulations increases with age and that the shape of these crenulations is correlated with their number, which is very variable within and among individuals (Bertonnier-Brouty 2019).
The landmark and semi-landmark coordinates were derived from digital photographs using tpsDig2 v.2.16 (Rohlf 2010a). All specimen coordinates were aligned using the generalized Procrustes superimposition to remove the position, scale and orientation parameters from the initial point configurations (Bookstein 1991). Unlike landmarks, semi-landmarks do not have an exact correspondence on the curvature of the enamel, and instead ‘slide’ along the line between adjacent points to minimize the sum of the Procrustes distances between each individual and the average shape (Perez et al. 2006; Gunz & Mitteroecker 2013). The generalized Procrustes superimposition of landmark and semi-landmark coordinates was conducted using tpsRelw v.1.49 (Rohlf 2010b).

To assess the order of magnitude of the morphological variation, as well as to identify whether the main source of this variation corresponds to chronology or taxonomy, we first compared the p3 morphology of early Pleistocene rabbits with that of modern populations (O. cuniculus). To do this, the shape differences between groups were estimated using a multivariate analysis of variance (MANOVA), with significant interaction ($\alpha = 5\%$) assumed to reflect the population and/or taxonomic differences. We then assessed the specific and/or population assignment accuracy by calculating the cross-validated correct classification percentages on the fossil sample, using a canonical analysis of variance (CVA). So as not affect the cross-validation results, we reduced the dimensionality of our data set by keeping the values of the main components expressing 95% of the total variance before each canonical analysis (Kovarovic et al. 2011). However, given the limited number of p3 specimens in some deposits, we were forced to only keep the groups that had a sufficiently large number of individuals to perform this analysis (n > 5). We then focused the study on fossil populations in order to morphologically compare only early Pleistocene taxa with each other. Size differences were evaluated from log-transformed centroid sizes, using Kruskal–Wallis tests with an error threshold set at $\alpha = 5\%$. Pairwise comparisons of the populations were performed using multiple Wilcoxon rank tests according to these different categories. To control the false discovery rate, a multi-comparison correction was applied to the p-values using the ‘Benjamini–Hochberg’ method (Benjamini & Hochberg 1995). The shape differences between these different groups were also estimated using a MANOVA, and the shape variation was visualized using principal component analysis (PCA) based on Procrustes coordinates. The phenotypic similarities between groups were calculated from Mahalanobis distances derived from canonical variates and visualized with a neighbour-joining network (Mahalanobis 1936). Finally, allometry was assessed using multivariate regressions of shape variables on the log-transformed centroid sizes. All morphometric statistics were performed with Rstudio v.1.1.383 (R Core Team 2018), using the ‘ade4’ (Dray & Dufour 2007) and ‘geomorph’ (Adams & Otárola-Castillo 2013) libraries.

**RESULTS**

**Description**

*Oryctolagus lacosti*: The single p3 from Perrier (FSL-211647) has two large anteroconids separated by a shallow anteroflexid (Fig. 3A). The vestibular anteroconid is ellipsoidal, smaller and more elongated than the lingual anteroconid. The protoflexid has an angle of approximately 90° with small undulations on the vestibular edge. The lingual edge of the tooth has a paraflexid with a slight sinusosity. The two p3 specimens from Saint-Vallier (FSL-211901 and FSL-495764) also have two large anteroconids whose size and shape are quite close to the Perrier individual. The V-shaped protoflexid marks an angle of
90° with some small undulations also present in specimen FSL-211901 (Fig. 3A). However, the anteroflexid is deeper for both Saint-Vallier individuals than for Perrier one. Finally, the paraflexid is well marked, with cement visible on the occlusal surface.

**Oryctolagus valdarnensis**: The population of Pirro Nord 13 (n = 43) includes p3 specimens with relatively variable morphological characters (Fig. 3B). With the exception of one individual whose vestibular anteroconid is larger than the lingual one, and five individuals for whom both anteroconids have a relatively similar size and shape, most p3 specimens have a larger lingual anteroconid than the vestibular one (n = 37). The vestibular anteroconid is generally ellipsoidal for most the individuals and longer than the lingual one (n = 30) but may also be rather rounded (n = 13). However, the lingual anteroconid is generally globular (n = 19) or even rounded (n = 13), though rarely subsquare (n = 6) or subtriangular (n = 5). The depth of the anteroflexid greatly varies in this population since it can be from very deep (n = 25; e.g. Fig. 3B, UNIFE P13-USC3-QB2_44) to moderately deep (n = 12), as observed in the *O. lacosti* specimens from Saint-Vallier or generally in the extant rabbit *O. cuniculus* (Fig. 3D). Some specimens show a relatively short anteroflexid (n = 6; e.g. Fig. 3B, UNIFE P13-USD16-QB3_7) as observed in *O. lacosti* from Perrier or in *O. giberti* (Fig. 3C). The depth of the paraflexid, although always present, also varies significantly among individuals. It is often deep (n = 25) with cement observable on the occlusal surface in most cases (e.g. Fig. 3B, UNIFE P13-USD16-QB3_7, P13-USD15-QB4_15) for *O. lacosti* or generally in the extant rabbit *O. cuniculus* (Fig. 3D). Some specimens show a relatively short paraflexid (n = 6; e.g. Fig. 3B, UNIFE P13-USD16-QB3_7, P13-USD15-QB4_15), but it can also only be marked by a slight sinuosity on the lingual edge of the tooth (n = 12; e.g. Fig. 3B, UNIFE P13-USC3-QB2_44, P13-USC8-QB3_11), or even be virtually absent (n = 6). The protoflexid is generally V-shaped with an angle of 90° or less (n = 38). Only five individuals present an obtusely angled protoflexid. Finally, the protoflexid has small undulations on the vestibular edge in one third of cases (n = 14), as observed in *O. lacosti* (Fig. 3A).

**Oryctolagus giberti**: The p3 of Xabia II (n = 2) have an ellipsoidal vestibular anteroconid and a wider and subtriangular lingual anteroconid (Fig. 3C). The anteroflexid is...
In terms of size, we note a clear difference between O. lacosti from Perrier (n = 1) and Saint-Vallier (n = 2) in central-eastern France, with a larger p3, and p3 from Montoussé 5 (n = 2) in south-western France (Fig. 4). A significant size difference is also present in Italy between O. valdarnensis from Pirro Nord 13 (n = 43) in the province of Foggia, with a smaller p3, and those from Upper Valdarno (n = 2) in Tuscany. Although there are some overlaps between the rabbits of Pirro Nord 13, Montoussé 5, Vallonnet, Bois-de-Riquet, Cueva Victoria and Xàbia II, it seems that in general O. lacosti and O. valdarnensis are the taxa with the largest p3. Conversely, the populations of south-eastern Spain affiliated to O. giberti (Baranco León 5, Cueva Victoria, Fuente Nueva 3, Huéscar I, Quibas, Xàbia II) have the smallest teeth. In general, these rabbits have a smaller p3 than those of the same species in south-eastern France (Vallonnet cave, Bois-de-Riquet). In addition, the members of the population from Sima del Elefante (Castile and León, north-western Spain) have a larger p3. Finally, we note that whatever species considered, there is a relatively large range of values in the dimensions of the p3, with significant overlaps. However, although some samples are relatively small, it seems that there are significant size differences in the same species depending on their geographical location.

Two-dimensional tooth morphology

For each p3, the factorial MANOVA found significant differences in shape among the different groups (all p << 0.05; Table 2). The discriminant model found correct chronological (i.e. early Pleistocene vs modern populations) and specific identification for 91% and 95% of the classifications after cross-validation, respectively (Table 2). This shows that this model can accurately distinguish an isolated p3 from the archaeological record in an early Pleistocene context. However for each site, the discriminating model only classified 69% of the p3 specimens. On the other hand, a clear taxonomic signal segregated the populations into three groups (Fig. 5): (1) the four modern populations belonging to O. cuniculus (i.e. Las Lomas, Navarre, Santarém and Tour du Valat); (2) the Bois-de-Riquet, Cueva Victoria and Vallonnet populations related to O. giberti; and (3) the population of Pirro Nord 13 affiliated to O. valdarnensis. Although the differences are tenuous, the visualization of the shape changes along canonical axes 1 and 2 showed that in modern populations, the anteroflexid is deeper, vestibular and lingual anterocnids are symmetrical and the parafoxid is very weak compared to the early Pleistocene species. For the p3 specimens from Pirro Nord 13, the anteroflexid is shallower and the anteroconids are asymmetrical: the vestibular anterocnid is rectangular and more elongated mesially, while the lingual anteroconid is rounded. This asymmetry is explained by the presence of a very marked
FIG. 4. Biometric relationship between mesio-distal diameter (MDD) and vestibulo-lingual diameter (VLD) of p3 (in mm) in early Pleistocene rabbits: Barranco León 5, Casablanca 1, Fuete Nueva 3, Quibas, Sima del Elefante (data from De Marfà 2009); Huéscar I (data from Mazo et al. 1985); Montoussé 5 (data from Chaline et al. 2000); Valdarno (data from Angelone & Rook 2012); Bois-de-Riquet, Cueva Victoria, Perrier, Pirro Nord 13, Saint-Vallier, Vallonnet cave, Xàbia II (this study).

TABLE 2. Results using MANOVA of the differences between the chronology (early Pleistocene vs modern populations), populations by sites, as well as species, and the percentage of correct cross-validated classification (CCV).

|                          | d.f. | Pillai | F     | num d.f. | den d.f. | p-value      | CCV   |
|--------------------------|------|--------|-------|----------|----------|--------------|-------|
| Lower Pleistocene: modern| 1    | 0.956  | 9.516 | 132      | 58       | <2 × 10⁻¹⁶   | 91.10 |
| Sites                    | 7    | 5.704  | 1.933 | 924      | 406      | 4.965 × 10⁻¹⁴ | 69.63 |
| Species                  | 2    | 1.805  | 4.056 | 264      | 116      | 1.259 × 10⁻¹⁵ | 95.81 |

num d.f., number of degrees of freedom in the model; den d.f., number of degrees of freedom associated with the model errors.

FIG. 5. Canonical analysis of variance (CVA) comparing the p3 shape in each rabbit population with the visualization of shape differences along axes 1 (CV1) and 2 (CV2) at the extreme values of each axis.
Finally, the p3 of *O. giberti* from Bois-de-Riquet, Cueva Victoria and Vallonnet are closer to those from Pirro Nord 13, particularly concerning the shape of the mesial part of the tooth (CV1). However, the paraflexid remains present but less marked (CV2).

In the fossil populations investigated, a Kruskal–Wallis test produced significant differences in the centroid size of the p3 between the different rabbit species \( (p = 1.72 \times 10^{-6}; \text{Fig. 6A}) \) as well as the different fossil populations \( (p = 5.14 \times 10^{-5}; \text{Fig. 6B}) \). Although the Perrier, Saint-Vallier and Xàbia II deposits only yielded a relatively small number of individuals (all \( n < 3 \)), the centroid size of the p3 of *O. lacosti* was the largest, while the centroid size of Xàbia II rabbits (*O. giberti*) was the smallest (Fig. 6). The populations of *O. giberti* did not differ significantly from one another (Table 3) but their p3 were always smaller than the rabbits of Pirro Nord 13, assigned to *O. valdarnensis*. In addition, MANOVA (with \( p = 7.79 \times 10^{-4} \)) showed a clear structuring of p3 shape variation (Fig. 7). Individuals from Perrier and Saint-Vallier had a similar shape and showed greater affinity with the population from Pirro Nord 13. The populations of south-eastern France (Bois-de-Riquet and Vallonnet) and Spain (Cueva Victoria and Xàbia) showed a close dental shape. Variations in p3 shape in early Pleistocene rabbits correspond to a deepening/shallowing of the anteroflexid (PC1) associated with the enlargement/narrowing of the lingual and vestibular anteroconids (PC2; Fig. 8). The population of Pirro Nord 13 had a relatively deeper anteroflexid, a marked paraflexid, as well as a large lingual anteroconid, rounded and projecting towards the inside of the mandible. In the *O. giberti* populations, the anteroflexid and the paraflexid were more reduced and the anteroconids are proportionally smaller and less rounded. Finally, *O. lacosti* from Perrier and Saint-Vallier had a shape that was closer to the average shape of the sample analysed, with a paraflexid of intermediate size, as well as two large anteroconids of the same size. However, despite the large size differences previously observed in the centroid size of p3 (Fig. 6), the allometric component indicated no relationship between size and shape \( (p = 0.06) \).

**FIG. 6.** Box plots of the p3 centroid sizes (log) of rabbit species (A), as well as the different populations from early Pleistocene (B). Numbers in square brackets indicate the number of individuals.

**TABLE 3.** Multi-test comparisons (p-values) of log-transformed centroid sizes of the p3 between the different early Pleistocene populations.

|                  | Bois-de-Riquet | Cueva Victoria | Perrier | Pirro Nord 13 | Saint-Vallier | Vallonnet |
|------------------|----------------|----------------|---------|---------------|---------------|-----------|
| Cueva Victoria   | 0.706          | –              | –       | –             | –             | –         |
| Perrier          | 0.202          | 0.437          | –       | –             | –             | –         |
| Pirro Nord 13    | **0.001**      | 0.106          | 0.106   | –             | –             | –         |
| Saint-Vallier    | 0.062          | 0.167          | 1.000   | **0.014**     | –             | –         |
| Vallonnet        | 0.576          | 0.706          | 0.333   | 0.117         | 0.106         | –         |
| Xàbia II         | 0.062          | 0.167          | 0.706   | **0.014**     | 0.437         | 0.106     |

Pairwise Wilcoxon rank tests after the Benjamini–Hochberg correction. A significant contribution was considered for \( p < 0.05 \) (in bold).
DISCUSSION

Evolution and morphological variability of early Pleistocene rabbits

Overall, the morphometric descriptions and GMM analyses presented here have allowed, on different levels, a more optimal characterization of the morphological variability of fossil rabbit p3 in various early Pleistocene populations. Firstly, the p3 of *O. lacosti* has been described as presenting two large anteroconids with a more elongated and ellipsoidal vestibular anteroconid than the lingual anteroconid, which is wider. However, the depth of the anteroflexid seems to vary more than previously described by De Marfà & Mein (2007) (Fig. 3); it is relatively shallow in specimens from Perrier (FSL-211647; this work) and Montoussé 5 (F-120 and F171; Chaline et al. 2000, p. 101), while it is deeper in Saint-Vallier (FSL-211901 and FSL-495764, this work). In this species, the paraflexid is always present, although it is significantly more marked in Saint-Vallier than in the two other above-mentioned Gelasian deposits. Thus, the overall p3 conformation of Perrier is clearly closer to the individuals from Montoussé 5 than Saint-Vallier. In the Pirro Nord 13 deposit, despite significant inter-individual morphological variability, the p3 morphology coincides more with those of the few individuals of *O. valdarnensis* described in Valdarno and Pirro Nord 10 (Angelone & Rook 2012; Angelone 2013). The vestibular anteroconid is generally more elongated than the lingual anteroconid, which instead has a more globular shape. This is notably due to the presence of a very marked paraflexid in the majority of individuals, although it is shallower in a few individuals at Pirro Nord 10 (Angelone 2013). However, these authors report a deep and wide anteroflexid, whereas it clearly has quite a variable depth, relatively shallow (e.g. in NMB VA1798, IGF 10129 and MRSN PU126998) or very deep (e.g. in IGF 12741 and MRSN PU126995) (Angelone & Rook 2012, p. 136; Angelone 2013, p. 97). At Pirro Nord 13, the depth of the anteroflexid also varies considerably, which allows us to refute the argument that *O. valdarnensis* is characterized, among other things, by the exclusive presence of a deep anteroflexid. In addition, some *O. valdarnensis* p3 specimens from Valdarno (e.g. IGF 10129 and IGF 12741, Angelone & Rook 2012, p. 136) evoke the general morphology of the individual FSL-211901 from Saint-Vallier (*O. lacosti*), particularly the shape of the lingual anteroconid, the presence of a well-marked paraflexid and the depth of the anteroflexid. Thus, on the

**FIG. 7.** Neighbour-joining tree using Mahalanobis distances based on p3 shape data from early Pleistocene populations.

**FIG. 8.** p3 differentiation in the morphospace based on 2D GMM. Shape changes along the major axes of variations (PC1 and PC2) are shown for the extreme values of each axis.
sole basis of this morphological description, and the limited dental material available for *O. lacosti*, there are no grounds for clearly separating *O. lacosti* and *O. valdarnensis* into two distinct species. On the contrary, they would appear to quite similar morphologically. However, *O. lacosti* and *O. valdarnensis* were quite distinct from *O. giberti*, particularly on the mesial part of the tooth. Indeed, although there may be some individual variations, the anteroflexid is generally shallow in all *O. giberti* populations. In this species, the p3 appears to have two anteroconids with similar size and shape, particularly in the French specimens from Bois-de-Riquet and Vallonnet, while the lingual anteroconid tends to be wider in the Spanish deposits. In Bois-de-Riquet and Vallonnet, the protoflexid is U-shaped and has an angle of 90° or less, while it is V-shaped at Cueva Victoria and Xàbia II. The paraflexid almost always has a slight sinuosity. Generally, the p3 also appears to be less elongated mesiodistally than in other species. These observations slightly differ from the description proposed by De Marfà (2008), which indicated in particular the presence of a deep anteroflexid in the holotype of *O. giberti*. Thus, the observations made in our sample are closer to the description proposed by López Jiménez et al. (2020) for the Cueva Negra rabbits (i.e. two large anteroconids with a similar shape and size, separated by a shallow anteroflexid and a well-marked paraflexid), with the exception of the protoflexid shape, which has obtuse angle. However, we agree with De Marfà (2008) that *O. giberti* can be distinguished from modern *O. cuniculus*, which generally has large symmetrical anteroconids, a deep anteroflexid and a more attenuated paraflexid. Thus, when we compare the different populations and species with each other, the descriptions of dental characters allow us to mainly identify the general tendencies within a population or group, rather than the characters that are strictly exclusive to each group. Indeed, although our observations are quite consistent at the species level with the descriptions of their respective lectotypes and holotypes (e.g. the depth of the anteroflexid and paraflexid or the general shape of the anteroconids), we also noted the presence of a relatively significant intra- and inter-population polymorphism which induces variations in the descriptions of the different authors. For example, De Marfà & Mein (2007) and Angelone & Rook (2012) described a p3 with a deep anteroflexid in *O. giberti* and *O. valdarnensis* respectively, but this depth is actually very variable, not only at the species level, but also within a given population. This could unfortunately result in the misidentification of an isolated tooth or a small sample.

However, despite the reduced number of specimens for these periods, it is possible to identify trends in metric variations in p3 size related to the geographical position of the populations (Fig. 4). Indeed, *O. lacosti* has significantly larger dental dimensions in Perrier and Saint-Vallier, located in central-eastern France, than in Montoussé 5, located at a lower latitude in south-western France. The same observation was made in *O. valdarnensis* specimens, in which individuals from Valdarno in northern Italy also had a larger p3 than those individuals from Pirro Nord 13 in the south-eastern part of the country. Finally, the *O. giberti* from southern France are generally larger than those from south-eastern Spain. This can be explained by the fact that in western Europe, there is a strong correlation between the body size of rabbits (i.e. the size of dental and bone elements) and both geographical location and local environmental conditions (Sharples et al. 1996; Callou 2003; Davis & Moreno-García 2007; Davis 2019; Pelletier 2019). Populations are distributed according to several known factors, including latitude and temperature (which are often directly related), according to Bergmann’s rule (Bergmann 1847), which states that the largest body sizes are distributed in the north and the smallest sizes in the south. However, the very large size of the dental and bone elements of *O. lacosti* and *O. valdarnensis* has been proposed as one of the distinguishing criteria of both these species (De Marfà & Mein 2007; Angelone & Rook 2012), compared to *O. laynensis*, *O. giberti* and *O. cuniculus*, which are mainly present in the Iberian Peninsula and southern France. Therefore, the size of dental and bone elements cannot be considered to be a reliable criterion for specific identification, since it can vary considerably and be directly related to local conditions. We also noted significant variability in the measurements taken by the different authors of the p3 of the same individuals, up to 0.3 mm of difference in the mesio-distal diameter (MDD) and vestibulo-lingual diameter (VLD). We noted, for example, a significant difference in the dental measurements of the two individuals from Upper Valdarno between the works of De Marfà (2009) (i.e. IGF 10129: MDD = 3.81 mm, VLD = 3.82 mm; IGF 12741: MDD = 3.90 mm, VLD = 3.85 mm) and Angelone & Rook (2012) (i.e. IGF 10129: MDD = 4.10 mm, VLD = 4.07 mm; IGF 12741: MDD = 4.00 mm, VLD = 4.10 mm). However, these differences seem less important in the measurements of the p3 from Cueva Victoria between the works of De Marfà (2009) (i.e. MCBN v6189-4: MDD = 3.18 mm, VLD = 2.90 mm; v6188-2: MDD = 2.97 mm, VLD = 2.90 mm, v6200-7: MDD = 2.85 mm, VLD = 2.90 mm; v6233: MDD = 3.20 mm, VLD = 2.98 mm) and the present study (i.e. MCBN v6189-4: MDD = 3.14 mm, VLD = 3.00 mm; v6188-2: MDD = 2.91 mm, VLD = 3.00 mm, v6200-7: MDD = 2.87 mm, VLD = 2.69 mm; v6233: MDD = 3.27 mm, VLD = 3.00 mm). These differences can, to a different degree, also induce a bias in the body size interpretations of fossil rabbits.
Our 2D GMM study also provides additional information on morphological descriptions and variations in dental measurements, which revealed numerous overlaps between the different populations. First, it allows us to support the validity of the two species present during the Calabrian: *O. giberti* and *O. valdarnensis*. As had been previously hypothesized, our results confirm that all the rabbits that occupied the Iberian Peninsula (De Marfà 2008, 2009) and south-eastern France (Pelletier et al. 2015a; Pelletier 2018) during this period belonged to the same species: *O. giberti*. Our results also support the presence of a distinct species in the Pirro Nord 13 deposit in Italy during the same period. In the Pirro Nord locality, rabbit remains had already been affiliated to *O. valdarnensis* (Angelone 2013, Angelone et al. 2020), but in other fossiliferous karst fissures (i.e. Pirro Nord 10A and 10F). Although no comparative morphometric study has yet been conducted on other Italian populations, our results are consistent with the hypothesis of Angelone & Rook (2012) who considered that all the early Pleistocene *Oryctolagus* remains collected thus far in Italy belong to *O. valdarnensis*. Morphologically, the analysis supports the hypothesis that the two Calabrian species are mainly distinguished by the depths of the anteroflexid and paraflexid, significantly deeper and more marked in *O. valdarnensis* than in *O. giberti*, leading to a notable asymmetry of the two anteroconids. However, most of the variance is observed on axis 1 (26%) and is expressed on the intra-specific scale, thereby proving the great morphological variability in the different fossil populations in time and space (Fig. 8). This particularly suggests that there is a greater variation in the depth of the anteroflexid in each species, as well as a mesiodistal narrowing or enlargement of the occlusal surface, effectively impacting the size and shape of the anteroconids. As such, the recent study on different modern *O. cuniculus* populations from western Europe showed, for example, that the anteroflexid was shorter in south-western populations on the Iberian Peninsula (evolving in an environment in which the average annual temperatures are higher, average annual precipitation is lower and with a Mediterranean scrub-type vegetation) than in the populations of northern Spain or southern France (evolving in a more oceanic climate and with more precipitation and lower temperature, under a 'temperate forest' type vegetation) (Pelletier 2019). Thus, when we take into account the notion of intra-specific or intra-population variability, as well as the likely global/local environmental impact on this variation, our results show a degree of subjectivity in some of the qualitative morphological criteria for the description or redefinition of a species, particularly on the mesial part of the p3 (i.e. anteroflexid, paraflexid, anteroconids).

As expected, our discriminating analysis reveals that early Pleistocene species can be considered to be distinct from the extant species *O. cuniculus*. It is very important to take into account that this model can accurately distinguish an isolated p3 from the archaeological record in an early Pleistocene context, given both the great morphological variability and eco-ethology of the modern rabbit. Indeed, this species is a burrowing animal capable of producing complex and substantial underground warrens (Biadi & Le Gall 1993) and entering an archaeological or a palaeontological site naturally and/or accidentally (Pelletier et al. 2016, 2020). This particularity increases the possibility of discovering its remains in the fossil record and poses questions about the contemporaneity of these remains with other assemblage components (Pelletier et al. 2015b, 2016, 2017, 2020). Thus, in the case of old excavations and a lack of taphonomic context, our results show that the dental morphology of extinct species can be useful and complementary to taphonomic analyses in order to ensure the integrity of the archaeostratigraphy and the reliability of the studied material, as well as for biostatigraphic purposes.

Nevertheless, the major concern of our study is to highlight the validity of the *O. lacosti* species. In this respect, Angelone & Rook (2012) have already made the point that it was not a well-characterized species. Many collections from the early Pleistocene originally attributed to *O. lacosti* or *O. aff. lacosti* (e.g. López-Martínez 1989, 2008; Argenti & Kotsakis 2009; Angelone 2013) have been reassigned to *O. giberti* in Spain (De Marfà 2008, 2009) or to *O. valdarnensis* in Italy (Angelone & Rook 2012; Angelone et al. 2020). Thus, only a few isolated remains have been distributed between the Perrier, Saint-Vallier or Montousse 5 deposits, making it difficult to establish distinctive criteria for this species. In light of our results and both the qualitative and quantitative data from the literature, we are currently unable to make a clear distinction between *O. valdarnensis* and *O. lacosti*. However, we have noted that a few isolated individuals such as the individuals in Perrier and Valdarno were quite similar, whereas the morphometric characteristics of the Perrier and Saint-Vallier rabbits highlighted in the GMM study are relatively close to those observed at Pirro Nord 13 (Fig. 7). In any event, the individuals from Perrier and Saint-Vallier share significantly and statistically more morphological similarities with *O. valdarnensis* than with other species of rabbits. Consequently, it is entirely reasonable to envisage: (1) a phylogenetic succession between *O. lacosti* and *O. valdarnensis*, in which the latter would then have become the endemic form on the Italian Peninsula in the second half of the early Pleistocene, as already hypothesized (Angelone 2013); or (2) a synonymy between the two forms in which *O. valdarnensis* could be a more recent form than *O. lacosti* and these two forms should be considered to be geo-chronospecies, as previously proposed (Pelletier 2018). Moreover, due to the limited amount of data (individuals, deposits) widely
dispersed across western Europe during this period, we do not have a sufficient number of elements to suggest any scenario. More *O. lacosti* material from Gelasian contexts would be needed to extend this debate. This would allow us to better evaluate the chronology of the *Oryctolagus* from this period to establish whether or not the French and Italian deposits were coeval. Indeed, the last *O. lacosti* from France are reported from around 2.1–2.0 Ma in Saint-Vallier while the first *O. valdarnensis* from Italy have been placed around 2.1 Ma in Montagnola Senese. However, these relative datings (i.e. not radiometric) are not accurate enough to establish whether or not they really overlap. However, despite the obvious phylogenetic proximity between the analysed individuals of *O. lacosti* and *O. valdarnensis*, we propose at this stage that these two taxa should be retained, representing only geo-chronologically these two rabbit forms in southern France and Italy, respectively.

*Palaeoecology and palaeobiogeography of rabbits during the early Pleistocene*

As well as understanding more about the phylogenetic relationships between the different rabbit species from the early Pleistocene, our study also makes it possible to discuss their diffusion dynamics in western Europe. Indeed, the expansion or isolation events of rabbit populations could have been conditioned by various ecological factors. Although the palaeoecology of the different early Pleistocene rabbit species has not been clearly established, their ranges were very close to that of the Pleistocene *O. cuniculus* (Pelletier 2018). Thus they could have been conditioned by the same biotic and abiotic factors. This would tend to assume that the *Oryctolagus* species shared, at least partially, similar ecological requirements to the extant European rabbit. These requirements could also explain why the genus *Oryctolagus* naturally spread only between the Iberian Peninsula, southern France and the Italian Peninsula during the Pleistocene, and not to northern France, central Europe or the Balkan Peninsula. Environmental components such as aridity, altitude and soil conditions are fundamental for the development of the extant European rabbit, mainly for the establishment of their burrows and for the maintenance of populations. Consequently, the European rabbit prefers loose and well-drained soils on flat or sloped terrain, such as sand dunes or grasslands, with low vegetation comprising bushes and shrubs at altitudes of up to 1000 m (Biadi & Le Gall 1993). It therefore does not colonize arid, overly dry or frozen (i.e. permafrost), mountainous, wetland or large forest areas. Thus, both topography and fluvial geodynamics are factors that have clearly conditioned the population migrations in western Europe (Fig. 9). In the south of the Iberian Peninsula, the three main rivers, the Tagus, the Guadiana and the Guadalquivir, have probably conditioned rabbit populations along the Mediterranean coast. Moreover, the mountains of the Iberian System in the centre of the Peninsula and the Sierra Nevada in the south, could have been an obstacle to an east–west circulation and, towards the north, the Ebro and the Pyrenees mountains would also have limited the dispersal of these species. Thus, the palaeontological data available for this period are in agreement with the genetic data, which have identified a refuge area in southern Spain and along the Mediterranean coast (Branco et al. 2002). The current lack of rabbit remains from the early Pleistocene in south-western France allows us to consider a single route of migration to the west of the Pyrenees, via Catalonia, between France and Iberia. The Garonne, the Tarn, the Loire and the Massif Central then preferentially orientated migrations towards the south-east. In south-eastern France, rabbits appear to have prospered on a narrow region between the Rhône delta, the Rhône Valley and the Southern Alps. Thus, the narrow passage between the Alpine chain and the Mediterranean Sea was the only possible route taken by *Oryctolagus* to reach Italy. Rabbits were then able to extend their distribution towards the south of the Italian Peninsula. The lack of palaeontological data thus far beyond the Northern Apennines chain suggests that these mountains have limited the diffusion of populations to the north and instead favoured a diffusion corridor along the west coast.

Although these geographical constraints may initially have guided the preferential migration routes of early Pleistocene rabbits, it is also likely that local and/or global environmental variations, such as temperature or precipitation, may have affected these dispersions. It has already been assumed that the climatic oscillations of the middle and late Pleistocene considerably influenced the geographical distribution of the extant rabbit in western Europe (Pelletier 2018). Indeed, although *O. cuniculus* is a species that is more adapted to a Mediterranean-type climate, it has adapted relatively well to brief or slight Pleistocene climatic variations. However, during sudden or extremely unfavourable climatic events, the rabbit occasionally disappeared from certain regions during the middle and late Pleistocene. Generally, it is during these critical climatic events that the fragmentation or isolation of continental biotopes can occur (Blondel 1986). These environment segmentations have regularly been observed during the Pleistocene glacial periods, generating veritable ‘refuge areas’ for different animal species (e.g. Hewitt 1996, 2004; Sommer & Nadachowski 2006; Valensi 2009). The isolation of populations in these refuge areas often leads to founder events responsible for speciation processes. It has also been shown that the rates of speciation and extinction significantly increase during these critical phases,
highlighting a close link between ecological and evolutionary changes (Gómez Cano *et al.* 2013). During climatic favourable phases, these processes can be followed by expansion(s) and/or recolonization(s) that have a significant impact at the genetic and phenotypic level (e.g. Mayr 1942; Hewitt 2000).

According to Nocchi & Sala (1997b, p. 183), all Oryctolagus had a common western European origin, which can be recognized either in *O. laynensis* or in an unknown progenitor form. As previously mentioned (see Fig. 1), *O. laynensis* seems to have been confined to the Iberian Peninsula until the end of the Piacenzian or perhaps even until the beginning of the Gelasian, and was known to be generally associated with an arid, warm subtropical savannah-type fauna (López-Martínez 2008). In southern France, *O. lacosti* were only present in the region from the Gelasian and evolved under a relatively humid but not particularly cold climate in a mosaic landscape comprising a mixture of steppe and open wooded areas (Guérin *et al.* 2004). Thus, an allopatric speciation seems possible between these two *Oryctolagus* lineages, which are quite distinct ecologically and morphologically (López-Martínez 2008) and could have occurred following their geographical segregation by the Pyrenean chain. These speciations, not necessarily synchronous, could be consistent with the sudden increases in aridity during the Pliocene (around 4.0, 3.6, 3.2 or 2.8 Ma), which led to significant changes in the small mammal communities of western Europe (Agustí *et al.* 2001). The Gelasian is then characterized by a long period of climatic stability, favouring the dispersion of many mammals in southern Europe (Azzaroli *et al.* 1988; O’Regan *et al.* 2011; Bellucci *et al.* 2014). Although the lack of data in the Iberian Peninsula does not allow us to understand the evolution of *O. laynensis* during this period (i.e. maintenance, new speciation or disappearance), it was probably favourable for the maintenance and dispersal of *O. lacosti*. It was also during this period that the first *Oryctolagus* reached Italy (around 2.1 Ma). Whether *O. lacosti* and *O. valdarnensis* are synonymous or two distinct species, the endemic nature of *O. valdarnensis*, due to an isolation phase, could have resulted from the cold climatic event clearly marked at marine isotope stage (MIS) 82 (Popescu *et al.* 2010). It is also probable that after this climatic event *Oryctolagus* disappeared from southern France and was isolated in the peninsulas.

The Calabrian subsequently shows several major climatic changes (Agustí *et al.* 2010). Thus, it is probably

![Figure 9](image-url)  
*Fig. 9.* Main topographic and fluvial constraints that conditioned the dispersal routes of the early Pleistocene *Oryctolagus* in western Europe. Arrows represent the preferred migration routes; dots represent the same sites and species as in Figure 1.
one of these major changes, marked by a general drop in temperature and an increase in aridity around 1.9–1.7 Ma (Agustí et al. 2009; Bertini 2013), which, in turn, impacted the evolutionary and biogeographic dynamics of rabbits, isolated in the Iberian and Italian peninsulas during this period. In fact, it seems that it was after this climatic event that the first O. giberti appeared in Spain. This species was abundant in the south-east of the Iberian Peninsula, where the Xàbia II population could represent the oldest evidence of this species in Europe. The palaeontological occurrences would indicate a diffusion of the species which would mainly have occurred towards the north, along the Mediterranean coast. Around 1.4–1.2 Ma, this phase is characterized by a sharp increase in temperature and precipitation (Agustí et al. 2009) followed by relative climatic stability with warm conditions (between 1.2 and 0.9 Ma; Altolaguirre et al. 2019). This could explain the rapid expansion of rabbits towards the north of the Iberian Peninsula and the south-east of France. In addition, we found that the O. giberti populations of south-eastern Spain had a smaller p3 size than those of south-eastern France (Figs 4 and 6), which could indicate that the size of rabbits during this period was influenced by the same latitudinal variations as modern populations (see above). However, locations with relatively similar latitudes can also have quite different climates (Peel et al. 2007), and thus present contrasting results. In modern populations, a peculiarity has been reported concerning the populations of Navarre (northern Spain), latitudinally lower than the populations of southern France but with equivalent or even slightly higher average size values (Callou 2003; Pelletier 2018, 2019). In this case, the influence of the local environment overrides the effect of latitude. In fact, the populations of Navarre evolved under a climate subject to oceanic and mountainous influences, unlike the populations of southern France that live in a Mediterranean climate, where the annual average temperatures are relatively higher with lower pluviometry. Thus, climatic factors could have strongly influenced the population of Sima del Elefante in northern Spain, currently undergoing the same environmental conditions as in Navarre and with dental dimensions larger than those of the populations of southern France in the Vallonnet cave and Bois-de-Riquet, yet located at higher latitudes. It is also important to weigh these results against the micromammal associations of these deposits, which are not strictly coeval. For example, the micromammals reflect a generally temperate climate in Sima del Elefante (Rodríguez et al. 2011; Bennásar et al. 2016), while a cooler and drier climate is recorded in the Vallonnet cave (Montuire & Desclaux 1997; Moullé 2012), or a relatively more humid climate in Bois-de-Riquet (Lozano-Fernández et al. 2019). Thus, it is crucial that geographical data are taken into account in the palaeontological studies of rabbits because this can provide additional elements of discussion that could enable a better reconstitution of the microclimate variations and local environments.

As we have noted, the period between 1.2 and 0.9 Ma was favourable to the expansion of the Spanish O. giberti populations towards south-eastern France. However, another major event that led to the disappearance of O. valdarnensis from the Italian fossil record around 1.2 Ma may correspond to the maximum cold peak of MIS 36 (Joannin 2007, Altolaguirre et al. 2019). This event was marked by a general change in the composition of forests and a major renewal of the mammal community in Europe (Head & Gibbard 2005; Magri & Palombo 2013). However, it would be important to include more material from O. valdarnensis in our study to gain a better insight into the impact of climatic conditions on migration and evolution dynamics across the entire Italian Peninsula, as is the case in Spain and France for O. giberti. Nevertheless, although body size gradually increases with latitude, a different impact has been noted between O. giberti and O. valdarnensis. Indeed, for similar latitudes, we have found that Italian rabbits are comparatively larger than individuals from south-eastern Spain and south-eastern France. This could be partially explained by the rather temperate and dry environments (Pavia et al. 2012; Combourieu-Nebout et al. 2015). However, the differential body size variations between the two peninsulas could also be an argument to suggest that these rabbits belong to two distinct phyletic groups. As such, despite the impact of environmental conditions on the body size of individuals, the allometric component was not significant in our GMM analysis. This suggests that the morphological differences between these two species are not only related to the variation in the body size of individuals, but could also reflect a taxonomic and phylogenetic signal. Finally, the transition between the early and middle Pleistocene is also marked by significant global cooling, causing deep mutations, particularly in the biomes of the northern hemisphere (Head & Gibbard, 2005; Joannin 2007). This cooling led to the fragmentation of landscapes and the isolation of various Villafranchian species in more favourable areas (Bennet et al. 1991; Bonifay & Brugal 1996). The different regions of Europe then underwent deep faunal renewal (Magri & Palombo 2013) which, in rabbits, corresponds to the extinction of O. giberti and the appearance of the extant rabbit O. cuniculus.

CONCLUSION

Most palaeontological studies have used p3 morphology to explore taxonomic and phylogenetic relationships in different Oryctolagus species. Unfortunately, most early Pleistocene species have been described or redefined from a small sample of individuals (i.e. n < 5), which is
unlikely to accurately reflect the morphological variability of a particular population or species. Intra- and inter-populational studies appeared to be an important and unprecedented attempt to identify these variations, which are essential to more accurately specifying the phylogeny and biogeography of the genus. Overall, the different methods of analysis used in this study (i.e. morphological description, linear measurements and 2D GMM) have proven to be relatively complementary and enabled, on different levels, a characterization of the morphological diversity of early Pleistocene rabbits and to make connections among populations.

By means of a precise dental nomenclature widely used in palaeontology, morphological description seems to be adequate for describing an isolated individual or a small group of individuals, and to make small-scale comparisons. However, when the samples are larger, the descriptions are often limited to an average shape or the recurrence of main criteria. This method does not adequately capture the overall intra- and inter-populational or intra-specific variations, which, given the large morphometric variability of rabbits, could be problematic for identifying the species from an isolated p3. From one or two direct measurements of the tooth, linear measurement analyses enables the p3 size of an individual or group of individuals to be quickly captured and compared with other populations. However, as the body size of rabbits is directly related to their geographical position and local environmental conditions, this does not allow the identification of a given species. Nevertheless, to a certain extent, it could provide some clues about environmental variations in the immediate vicinity of a deposit. Lastly, GMM allows a comparison to be made of all individuals in a sample in the same morphological space and to directly visualize the results of statistical analysis in terms of conformation difference. This makes it possible to more easily recognize character variations that might be linked to intrinsic (i.e. phylogenetic) or extrinsic (i.e. ecological) processes. However, this method requires a relatively large data set and the establishment of a precise protocol, which takes longer to implement. Thus, GMM appears to be more adequate in a multi-regional study and over a long chronology, as was the case in this work. In this sense, neither of these approaches is necessarily more effective, and their use should depend on the research question under consideration.

Firstly, this work allowed us to confirm the specific status of two of the species previously defined in early Pleistocene, namely, *O. giberti* in the Iberian Peninsula and south-eastern France (probably throughout the Calabrian; i.e. 1.8–0.8 Ma) and *O. valdarnensis* in the Italian Peninsula (between 2.1 and 1.2 Ma). This also allowed us to phylogenically relate the Gelasian species *O. lacosti* and *O. valdarnensis*. Due to the limited material available for *O. lacosti*, as well as an imprecise chronological position (i.e. relative, not radiometric), it is currently impossible for us to state whether these two species coexisted in western Europe or whether *O. valdarnensis* immediately succeeded *O. lacosti* in time and space. Further research, including more Gelasian populations, should allow us to refine our palaeobiogeographical knowledge and our hypotheses on the phylectic relationships that unite these two species. However, our study highlights the great morphological variability of rabbits from this period, at both the inter-specific and intra-populational level. Thus, although these species had previously been adequately recognized and defined from morphological descriptions and linear measurements, our results suggest that local environmental conditions are the main factors behind the variation in p3 shape. In fact, in this relatively important geographical and chronological context, this leads us to temper certain so-called ‘diagnostic’ criteria traditionally used to identify species, such as anteroexid depths or even the shape of the anteroconids, because they might reflect ecological parameters rather than taxonomical variations. In this sense, these results strongly suggest that GMM analysis of dental traits are relevant markers that could be used to document the diversity and distribution of fossil rabbit species. Finally, geographical and chronological distributions and their associations with other mammals indicate that the ecological requirements of early Pleistocene species should partially correspond to those of the extant European rabbit. Thus, we can discuss population dynamics in Europe that were conditioned by topography, fluvial geodynamics and climatic and environmental variations. New palaeontological discoveries and the extension of studies to other dental and skeletal remains should ultimately allow even better clarification of the phylogeny, palaeoecology and palaeobiogeography of early Pleistocene rabbits in western Europe.

Acknowledgements. I would like to thank Jean-Philip Brugal and Arturo Morales-Muñiz for their help and support throughout my research. I would also like to thank Cécile Callou, curator of the National Museum of Natural History (MNHN, Paris), who granted me access to modern rabbit collections from Santarém, Las Lomas, Navarre and Tour du Valat. In addition, I would like to thank Laurence Bourguignon (INRAP, ARSCAN) and Jean-Yves Crochet (ASPROGEO) for entrusting me with the study of rabbits from Bois-de-Riquet; Emmanuel Robert (Claude Bernard University Lyon 1) for rabbits from Perrier and Saint-Vallier; Pierre-Elie Moullet (Regional Prehistory Museum of Menton) for rabbits from Vallonnet; Vincent Vicedo and Jaume Galleli (Museum of Natural Sciences of Barcelona) for rabbits from Cueva Victoria; Alfred Sanchis and Helena Bonet Rosado (Prehistory Museum of Valencia) for rabbits from Xabía; Marta Arzarello and Claudio Berto (University of Ferrara) for rabbits...
from Pirro Nord. I am very grateful to Marie Matu, the reviewers, editors and publications officer for their constructive comments that greatly improved the quality of the manuscript. Finally, this work was financed by an A*MIDEX grant (No. ANR-11-IDEX-0001-02) from the French Government programme ‘Investissements d’avenir’, and I would like to warmly thank the University of Oulu’s archaeology lab for its support.

Editor. Lionel Hautier

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12575):

Appendix S1. List of specimens studied including their catalogue number and repository, as well as the raw linear measurement of the p3 used in this study. Abbreviations: MDD, mesiodistal diameter; VLD, vestibulo-lingual diameter.

REFERENCES

ADAMS, D. C. and OTÁROLA-CASTILLO, E. 2013. Geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology & Evolution, 4, 393–399.

AGÜSTÍ, J., OMS, O. and REMACHA, E. 2001. Long Pliocene-Pleistocene terrestrial record of climate change and mammal turnover in Southern Spain. Quaternary Research, 56, 411–418.

—. BLAIN, H.-A., CUENCA-BESCÓS, G. and BAILLON, S. 2009. Climate forcing of first hominid dispersal in Western Europe. Journal of Human Evolution, 57, 815–821.

—. FURIÓ, M., DE MARFA, R. and SANTOS-CUBEDO, A. 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. Quaternary International, 223–224, 162–169.

ALBERDI, M. T., CERDEÑO, E., LÓPEZ-MARTÍNEZ, N., MORALES, J. and SORIA, M. D. 1997. La fauna vil-lafraquienne de El Rincón-1 (Albacete, Castilla-La Mancha). Estudios Geológicos, 53, 69–93.

ALTOLAGUIRE, Y., POSTIGO-MIJARRA, J. M., BARRÓN, E., CARRIÓN, J. S., LEROY, S. A. G. and BRUCH, A. A. 2019. An environmental scenario for the earliest hominins in the Iberian Peninsula: Early Pleistocene palaeovegetation and palaeoclimat. Review of Palaeobotany & Palynology, 260, 51–64.

ANGELONE, C. 2013. Fossil lagomorpha from Pirro Nord (Apulia, southern Italy). Palaeontographica Abteilung A, 298, 95–105.

— and ROOK, L. 2012. Late Neogene and Quaternary lagomorphs from Tuscany: a revision based on specimens in Basel Naturhistorisches Museum and Florence University collections. Swiss Journal of Palaeontology, 131, 127–145.

ANGELONE, C., MONCUNILL-SOLÉ, B. and KOTSAKIS, T. 2019. Contribution of fossil Lagomorpha (Mammalia) to the refinement of the late Miocene-quaternary palaeobiogeographical setting of Italy. Comptes Rendus Palevol, 18, 1025–1040.

— — 2020. Fossil Lagomorpha (Mammalia) of Italy: systematics and biochronology. Rivista Italiana di Paleontologia e Stratigrafia, 126, 157–187.

ARGENTI, P. and KOTSAKIS, T. 2009. The fossil remains of Soricidae and Leporidae (Mammalia) in the Lower Pleistocene of Pietrafitta (Perugia, Central Italy). Bollettino della Società Paleontologica Italiana, 48, 59–62.

AZZAROLI, A., DE GIULI, C., FICcarelli, G. and TORRE, D. 1988. Late Pliocene to Early Mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events. Palaeogeography Palaeoclimatology Palaeoecology, 66, 77–100.

BELLUCCI, L., BONA, F., CORRADO, P., MAGRI, D., MAZZINI, I., PARENTI, F., SCARDIA, G. and SARDELLA, R. 2014. Evidence of late Gelasian dispersal of African fauna at Coste San Giacomo (Anagni Basin, central Italy): Early Pleistocene environments and the background of early human occupation in Europe. Quaternary Science Reviews, 96, 72–85.

BENJAMINI, Y. and HOCHBERG, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society Series B, 57, 289–300.

BENNASAR, M., CÁCERES, I. and CUENCA-BESCÓS, G. 2016. Palaeoecological and microenvironmental aspects of the first European hominids inferred from the taphonomy of small mammals (Stima del Elefante, Sierra de Atapuerca, Spain). Comptes Rendus Palevol, 15, 635–646.

BENNETT, K. D., TZEDAKIS, P. C. and WILLIS, K. J. 1991. Quaternary refugia of North European trees. Journal of Biogeography, 18, 103–115.

BERGMANN, C. 1847. Über die verhältnisse der wärmeökono-mie der thiere zu ihrer größe. Göttinger Studien, 3, 595–708.

BERTINI, A. 2013. Climate and vegetation in the Upper Valdarno Basin (central Italy) as a response to Northern Hemisphere insolation forcing and regional tectonics in the late Pliocene-early Pleistocene. Italian Journal of Geosciences, 132, 157–148.

BERTONNIER-BROUTY, L. 2019. Dental development and replacement in Lagomorpha. Unpublished PhD thesis, University of Lyon, 264 pp.

BIADI, F. and LE GALL, A. 1993. Le lapin de garenne: Vie gestion et chasse d’un gibier authentique. Office national de la chasse Hatier, Paris, 160pp.

BLONDEL, J. 1986. Biogéographie évolutive. Masson, 221 pp.

BONIFAY, M.-F. and BRUGAL, J.-P. 1996. Biogéographie et biostratigraphie des grandes faunes du Pléistocè dén inférieur et moyen en Europe du sud: apport des gisements français. Paléoé, 8, 19–29.

BOOKSTEIN, F. L. 1991. Morphometric tools for landmark data: Geometry and biology. Cambridge University Press, 435 pp.

BRANCO, M., MONNEROT, M., FERRAND, N. and TEMPLETON, A. R. 2002. Postglacial dispersal of the European rabbit (Oryctolagus cuniculus) on the Iberian Peninsula reconstructed from nested clade and mismatch analyses of mitochondrial DNA genetic variation. Evolution, 56, 792–803.
References:

Callou, C. 2003. De la garenne au clapier: étude archéozoologique du lapin en Europe occidentale. Mémoires du Muséum national d’Histoire naturelle, 189, 358 pp.

Caumul, R. and Polley, P. D. 2005. Phylogenetic and environmental components of morphological variation: skull, mandible and molar shape in marmots (Marmota, Rodentia). Evolution, 59, 2460–2472.

Chaline, J. 1986. Continental faunal units of the Plio-Pleistocene of France. Memorie Della Società Geologica Italiana, 31, 175–183.

— Erbajeva, M. A. and Montuire, S. 2000. Upper Pliocene leporids (Mammalia, Lagomorpha) from Montoussé-5 (Hautes-Pyrénées, France). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 2, 93–106.

Combourieu-Nebout, N., Bertini, A., Russos-Ermolli, E., Peyron, O., Klotz, S., Montade, V., Faquettu, S., Allen, J., Fusco, F., Goring, S., Huntley, B., Joannin, S., Lepreton, V., Magri, D., Martinetto, E., Orain, R. and Sadori, L. 2015. Climate changes in the central Mediterranean and Italian vegetation dynamics since the Pliocene. Review of Palaeobotany & Palynology, 218, 127–147.

Cucchi, T., Mohaseb, A., Peigné, S., Debue, K., Orlando, L. and Mashkour, M. 2017. Detecting taxonomic and phylogenetic signals in equid cheek teeth: towards new palaeontological and archaeological proxies. Royal Society Open Science, 4, 160997.

— Stopf, B., Schafberg, R., Lesur, I., Hassanin, A. and Schibler, J. 2019. Taxonomic and phylogenetic signals in bovid cheek teeth: towards new biosystematic markers to explore the history of wild and domestic cattle. Journal of Archæological Science, 109, 104993.

Davis, S. J. M. 2019. Rabbits and Bergmann’s rule: how cold was Portugal during the last glaciation? Biological Journal of the Linnean Society, 128, 526–549.

— and Moreno-García, M. 2007. Of metapodials, mandible and molar shape in marmots (Mammalia, Lagomorpha) from Montoussé-5 (Hautes-Pyrénées, France). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 2, 93–106.

Cucchi, T., Mohaseb, A., Peigné, S., Debue, K., Orlando, L. and Mashkour, M. 2017. Detecting taxonomic and phylogenetic signals in equid cheek teeth: towards new palaeontological and archaeological proxies. Royal Society Open Science, 4, 160997.

— Stopf, B., Schafberg, R., Lesur, I., Hassanin, A. and Schibler, J. 2019. Taxonomic and phylogenetic signals in bovid cheek teeth: towards new biosystematic markers to explore the history of wild and domestic cattle. Journal of Archaeological Science, 109, 104993.

Davis, S. J. M. 2019. Rabbits and Bergmann's rule: how cold was Portugal during the last glaciation? Biological Journal of the Linnean Society, 128, 526–549.

— and Moreno-García, M. 2007. Of metapodials, measurements and music — eight years of miscellaneous zooarchaeological discoveries at the IPA, Lisbon. O Arqueólogo Português, 25, 9–165.

De Marfa, R. 2008. Oryctolagus giberti n. sp. (Lagomorpha, Mammalia) du Pléistocène inférieur de Cueva Victoria (Murcie, Espagne). Comptes Rendus Palevol, 7, 305–313.

— 2009. Els lagomorfs (O. Lagomorpha; Cl. Mammalia) del Pliocè i Pleistòcè europeus. Unpublished PhD thesis, University of Barcelona, 206 pp.

— and Mein, P. 2007. Revision d’Oryctolagus lacosti (Lagomorpha, Mammalia) du pliocène supérieur de Perrier (Auvergne, France). Comptes Rendus Palevol, 6, 327–334.

Donard, E. 1982. Recherches sur les Léporins quaternaires (Pliocénien moyen et supérieur, Holocène). Unpublished PhD thesis, University of Bordeaux I, Talence, 161 pp.

Dray, S. and Dufour, A.-B. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software, 22, 1–20.

Ferron, H. G., Greenwood, J. M., Deline, B., Martínez-Pérez, C., Botella, H., Sansom, R. S., Ruta, M. and Donoghue, P. C. J. 2020. Categorical versus geometric morphometric approaches to characterizing the evolution of morphological disparity in Osteostraci (Vertebrata, stem Gnathostomata). Palaeontology, 63, 717–732.

Fondi, R. 1972. Fauna cromeriana della Montagnola senese. Palaeontographia Italica, 38, 1–27.

Foote, M. 1997. Evolution of morphological diversity. Annual Review of Ecology & Systematics, 28, 129–152.

Galobart, A., Quintana, J. and Maroto, I. 2003. Los lagomorfas del Pleistoceno inferior de Incarcal (Girona, NE de la Península Ibérica). Palaeontologia i Evolució, 34, 69–77.

Gerber, S. 2019. Use and misuse of discrete character data for morphospace and disparity analyses. Palaeontology, 62, 305–319.

Gibert, L., Scott, G. R., Scholz, D., Budskey, A., Ferrández, C., Ribot, F., Martin, R. A. and Lería, M. 2016. Chronology for the Cueva Victoria fossil site (SE Spain): evidence for Early Pleistocene Afro-Ibrian dispersals. Journal of Human Evolution, 90, 183–197.

Girotti, O., Capasso Barbato, L., Esu, D., Glizzi, E., Kotsakis, T., Martinetto, E., Petronio, C., SardeIa, R. and Squazzini, E. 2003. The section of Torre Picchio (Terni, Umbria, Central Italy): a Villarfranchian site rich in vertebrates, molluscs, ostracods and plants. Rivista Italiana di Paleontologia e Stratigrafia, 109, 77–98.

Guérin, C., Faure, M., Argant, A., Argant, J., Crégut-Bonnoure, É., Debard, É., Delson, E., Eisenmann, V., Hugueney, M., Limondin-Lozouet, N., Martín-Suárez, E., Mein, P., Mourer-Chauviré, C., Parenti, F., Pastre, J.-F., Sen, S. and Valli, A. 2004. Le Gigament pliocène supérieur de Saint-Vallier (Drôme, France): synthèse biostratigraphique et paléoclimatique. Géobios, 37, S349–S360.

Gómez Caño, A. R., Cantalapiedra, J. L., Mesa, A., Moreno Boharull, A. and Hernández Fernández, M. 2013. Global climate changes drive ecological specialization of mammal faunas: trends in rodent assemblages from the Iberian Pleistocene. BMC Evolutionary Biology, 13, 94.

Gunz, P. and Mitteroecker, P. 2013. Semilandmarks: a method for quantifying curves and surfaces. Hystrix, 24, 103–109.

Head, M. J. and Gibbard, P. L. 2005. Early-Middle Pleistocene transitions: an overview and recommendation for the defining boundary. Geological Society, London, Special Publications, 247, 1–18.

Hetherington, A. J., Sherratt, E., Ruta, M., Wilkinson, M., Deline, B. and Donoghue, P. C. J. 2015. Do cladistic and morphometric data capture common patterns of morphological disparity? Palaeontology, 58, 393–399.

Hewitt, G. M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society, 58, 247–276.

— 2000. The genetic legacy of the Quaternary ice ages. Nature, 405, 907–913.
2004. Genetic consequences of climatic oscillations in the Quaternary. Philosophical Transactions of the Royal Society B, 359, 183–195.

HIBBARD, C. W. 1963. The origin of the p3 pattern of Sybilagus, Caprolagus, Oryctolagus and Lepus. Journal of Mammalogy, 44, 1–15.

HOFFMAN, R. S. and SMITH, A. T. 2005. Order Lagomorpha. 185–211. In WILSON, D. E. and REEDER, D. M. (eds). Mammal species of the world. Third edition. Johns Hopkins University Press, 2142 pp.

HOPKINS, M. J. 2017. How well does a part represent the whole? A comparison of cranialid shape evolution with exoskeletal character evolution in the trilobite family Pteroccephaliidae. Palaeontology, 60, 309–318.

and GERBER, S. 2017. Morphological disparity. 1–12. In NUNO DE LA ROSA, L. and MÜLLER, G. B. (eds). Evolutionary developmental biology. Springer.

IUCN. 2020. IUCN red list of threatened species. v. 2020-1. http://www.iucnredlist.org

JOANNIN, S. 2007. Changements climatiques en Méditerranée à la transition Pléistocène inférieur-moyen: pollens, isotopes stables et cyclostratigraphie. Unpublished PhD thesis, Claude Bernard Lyon I University, 249 pp.

KOTSAKIS, T. and BARISONE, G. 2008. Cenni sui vertebrati fossili di Roma. Memorie descrittive della Carta Geologica d’Italia, 80, 115–143.

KOVAROVIC, K., AIELLO, L. C., CARDINI, A. and LOCKWOOD, C. A. 2011. Discriminant function analyses in archaeology: are classification rates too good to be true? Journal of Archaeological Science, 38, 3006–3018.

LAPLANA, C. and BLAIN, H.-A. 2008. Microvertebrados (Squamata, Lagomorpha, Erinaceomorpha y Rodentia) de Fonelas P-1 (Cuenca de Guadix, Granada). 65–83. In ARRIENTES, A. (ed.) Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero, 10, 607 pp.

LEDEVIN, C., CHEVRAT, P., GANEM, G., BRITTON-DAVIDIAN, J., HARDOUIN, E. A., CHAPUIS, J.-L., PISANU, B., DA LUZ MATHIAS, M., SCHLAGER, S., AUFFRAY, J.-C. and RENAUD, S. 2016. Phylogeny and adaptation shape the teeth of insular mice. Proceedings of the Royal Society B, 283, 20152820.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Tenth edition (revised). Laurentii Salvii, Holmiae, 824 pp.

LISIECKI, L. E. and RAYMO, M. E. 2005. A Pliocene–Pleistocene stack of 57 globally distributed benthic δ¹⁸O records. Paleoceanography, 20, PA1003.

LLOYD, G. T. 2016. Estimating morphological diversity and tempo with discrete character–taxon matrices: implementation, challenges, progress, and future directions. Biological Journal of the Linnean Society, 118, 131–151.

LÓPEZ-GARCÍA, J. M., LUZI, E., BERTO, C., PERETTO, C. and ARZARELLO, M. 2015. Chronological context of the first hominin occurrence in southern Europe: the Allocapraeomys raffoi (Arvicolinae, Rodentia, Mammalia) from Pirro 13 (Pirro Nord, Apulia, southwestern Italy). Quaternary Science Reviews, 107, 260–266.

LÓPEZ JIMÉNEZ, A., HABER URIARTE, M., LÓPEZ MARTÍNEZ, M. and WALKER, M. J. 2020. Small-mammal indicators of biochronology at Cueva Negra del Estrecho del Río Quipar (Caravaca de la Cruz, Murcia, SE Spain). Historical Biology, 32, 18–33.

LÓPEZ-MARTÍNEZ, N. 1977. Revisión sistemática y bioestratigráfica de los lagomorfos (Mammalia) del Terciario y Cuaternario de España. Unpublished PhD Thesis, University of Madrid, 470 pp.

— 1980. Los lagomorfos (Mammalia) del Pléistoceno superior de Jaurens. Nuevos Archivos del Museo d’Histoire naturelle de Lyon, 18, 1–16.

— 1989. Revisión sistemática y bioestratigráfica de los lagomorfos (Mammalia) del Terciario y Cuaternario de España. Memorias del Museo Paleontológico de la Universidad de Zaragoza, 3, 343 pp.

— 2008. The lagomorph fossil record and the origin of the European rabbit. 27–46. In ALVES, P. C., FERRAND, N. and HACKLÄNDER, K. (eds). Lagomorph biology. Springer, 414 pp.

— MICHUX, J. and VILLALT A, J. F. 1976. Rongeurs et Lagomorphes de Bagar-2 (Province de Gérome, Espagne), Nouveau remp lissage de fissure du début du Pléistocène Moyen. Acta Geológica Hispánica, 11, 46–54.

LOZANO-FERNÁNDEZ, I., BLAIN, H.-A., AGUSTÍ, J., PIÑERO, P., BARSKY, D., IVORRA, J. and BOURGUIGNON, L. 2019. New clues about the late Early Pleistocene peopling of Western Europe: small vertebrates from The Bois-de-Riquet archeo-paleontological site (Lézignan-La Cèbe, southern France). Quaternary Science Reviews, 219, 187–203.

MAGRI, D. and PALOMBO, M. R. 2013. Early to Middle Pleistocene dynamics of plant and mammal communities in South West Europe. Quaternary International, 288, 63–72.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. Proceedings of the National Institute of Science of India, 2, 49–55.

MARTÍN-SUÁREZ, E. and MEIN, P. 2004. The late Pleistocene locality of Saint-Vallier (Drôme, France). Eleven micro-mammals. Geobios, 37, SI15–SI25.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, 334 pp.

— 1963. Animal species and evolution. Harvard University Press, 797 pp.

MAZO, A. V., SESÉ, C., RUIZ BUSTOS, A. and PEÑA, J. A. 1985. Geología y paleontología de los yacimientos Pleistocenos de Huéscar (Depresión de Guadix-Baza, Granada). Estudios Geológicos, 41, 467–493.

MICHEL, V., SHEN, C.-C., WOODHEAD, J., HU, H.-M., WU, C.-C., MOULLE, P.-É., KHATIB, S., CAUCHE, D., MONCEI, M.-H., VALENSI, P., CHOU, Y.-M., GALLIER, S., ECHASSOUX, A., ORANGE, F. and DE LUMLEY, H. 2017. New dating evidence of the early presence of hominins in Southern Europe. Scientific Reports, 7, 10074.
VALLVERDÚ, J., BENNASAR, M. L., BLASCO, R., BERMUDEZ DE CASTRO, J. M. and CARBONELL, E. 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). Quaternary Science Reviews, 30, 1396–1412.

ROHLF, F. J. 2010a. tpsDig. Stony Brook, New York.
— 2010b. RelativeWarp. Stony Brook, New York.

SALA, B. and MASINI, F. 2007. Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. Quaternary International, 160, 4–16.

SARRIÓN, I. 2012. Restos paleontológicos del Pleistoceno inferior en la sima del Pla de les Llomes (Serra, Valencia). Archivo de Prehistoria Levantina, 29, 9–51.

SAWAURA, R., SAWADA, J., SATO, T., SUZUKI, T. and SASAKI, K. 2018. Late Pleistocene hares of the Japanese archipelago: paleobiogeographic implication at the Last Glacial Maximum. International Journal of Osteoarchaeology, 28, 179–187.

SCHAeffER, J., BENTON, M. J., RAYFIELD, E. J. and STUBBS, T. L. 2020. Morphological disparity in theropod jaws: comparing discrete characters and geometric morphometrics. Palaeontology, 63, 283–299.

Sesé, C. and Ruiz Bustos, A. 1992. Nuevas faunas de micromamíferos del Pleistoceno del Norte de la Provincia de Madrid (España). Boletín de la Real Sociedad Española de Historia Natural. Sección Geológica, 87, 115–139.

Sharples, C. M., Fa, J. E. and Bell, D. J. 1996. Geographical variation in size in the European rabbit Oryctolagus cuniculus (Lagomorpha: Leporidae) in Western Europe and North Africa. Zoological Journal of the Linnean Society, 117, 141–158.

SomméR, R. S. and NadachowsKı, A. 2006. Glacial refugia of mammals in Europe: evidence from fossil records. Mammal Review, 36, 251–265.

Suchentrunk, F., Willing, R. and Hartl, G. B. 1994. Non-metrical polymorphism of the first lower premolar (P3) in Austrian brown hares (Lepus Europaeus): a study on regional differentiation. Journal of Zoology, 232, 79–91.
— Alkon, P. U., Willing, R. and Yom-Tov, Y. 2000. Epigenetic dental variability of Israeli hares (Lepus sp.): ecogenetic or phylogenetic causation? Journal of Zoology, 252, 503–515.

Valensí, P. 2009. Évolution des peuplements mammaliens en Europe méditerranéenne occidentale durant le Pléistocène moyen et supérieur. Un exemple régional: les Alpes du Sud françaises et italiennes. Quaternaire, 20, 551–567.

Van Dam, J. A. and Sanz-Rubio, E. 2003. Late Miocene and Pliocene small mammals from the Calatayud Basin (Central Spain). Coloquios de Paleontología, Extra 1, 115–126.

Van Der Meulen, A. J. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of Microtus (Rodentia). Quaternaria, 17, 1–144.

Viret, J. 1954. Le less à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères villafranchiens. Nouvelles archives du Musée d’Histoire naturelle de Lyon, 4, 1–200.

Weithofer, K. A. 1889. Ueber die tertiären Landsäugethiere Italiens. Jahrbuch der kaisertlichen k Oniglichen Geologischen Reichsanstalt, 39, 80–81.

Zelditch, M. L., Swiderski, D. L. and Sheets, H. D. 2012. Geometric morphometrics for biologists: A primer. Academic Press, 488 pp.