THE FOSSIL RABBIT FROM VALDEMINO CAVE (BORGIO VEREZZI, SAVONA) IN THE CONTEXT OF WESTERN EUROPE ORYCTOLAGINI OF QUATERNARY

by

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CONTENTS

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ABSTRACT

The present research deals with the remains of a lagomorph found at Valdemino cave and comes to the conclusion that it is a rabbit with peculiar characteristics in comparison with the other known species *Oryctolagus laynensis*, *O. lacosti* and *O. cuniculus*.

We studied other fossil remains of rabbit populations from Villafranchian and middle Pleistocene deposits and compared them with data from the literature and with recent material.

The analysis leads us to maintain two phylogenetic hypotheses about the history of Oryctolagini. The first one, already formulated by Lopez Martinez, suggests that *O. cuniculus* derives from *O. laynensis*, while the origin of *O. lacosti* is unknown; according to the second hypothesis *O. laynensis* would be the common ancestor of two phyletic lineages, *O. lacosti* and *O. cuniculus*. In both cases the lagomorph from Valdemino would be the form derived from *O. lacosti*, from which however it differs in peculiar characteristics.

Since the rabbit from Valdemino survives until the beginning of Postgalerian, its disappearance may coincide with the retreat of *O. cuniculus* from western Europe in Spain and, perhaps, in south-western France, before the last glaciation. *O. cuniculus* survived in Spain, from where it spread once again over western Europe as a result of man.

RESUME

Des restes d'un lagomorphe, appartenant à une faune du Galerien moyen, ont été retrouvés dans le gisement de la grotte Valdemino (Borgio Verezzi, Savona). Leur étude a mis en évidence des caractères particuliers qui diversifient cette espèce des trois espèce de *Oryctolagus*, connues jusqu'à présent: *Oryctolagus laynensis*, *O. lacosti*, *O. cuniculus*.

L'analyse d'autres restes fossiles de lapins, provenants des gisements Villafranchien et du Pléistocène moyen, et leur comparaison avec les données en literature et le matériel actuel de référence a permis de formuler deux hypothèses phylogénetiques sur l'évolution des Oryctolagines. D'après la prémière hypothèse, déjà soutenue par Lopez Martinez, *O. cuniculus* serait issu de *O. laynensis*, tandis que les origines de *O. lacosti* seraient encore inconnues; la déuxième hypothèse prévoit la dérivation des deux lignes phyletiques de *O. cuniculus* et de *O. lacosti* à partir de *O. laynensis*. En tout cas le lagomorphe de la grotte Valdemino est interprété comme une forme issue de *O. lacosti*, mais qui diffère pour des caractères particuliers.

Du fait que le lapin de Valdemino survit jusqu'au debut du Postgalerien, sa disparition, avant la dernière glaciation, pourrait correspondre avec le retrait de *O. cuniculus* de l'Ouest de l'Europe, qui reste seulement en Espagne et peut être dans le Sud-ouest de la France.

INTRODUCTION

This note regards the morphological and dimensional study of a lagomorph found in middle Pleistocene levels of the Valdemino cave near Borgio Verezzi, Savona. This site was the object of excavations and studies carried out both in the early seventies (Tozzi, 1969) and more recently (Fornasiero, 1989; Sala *et al.*, 1992; Nocchi, 1993; Davì, 1994).

The lagomorph in question was found in two distinct faunal assemblages, one

attributable to the Galerian and the other to a later association precedent to the last glacial. The oldest assemblage included the remains of tortoise, *testudo hermanni*, elephant, *Mammuthus armeniacus* (= *trogontherii*), Merk rhinoceros, *Stephanorhinus* cf. *kirchbergensis*, some cervids, wild boar, *Sus scrofa*, aurochs, *Bos primigenius*, Barbary ape, *Macaca sylvana* and various carnivores such as *Ursus* sp., *Canis mosbachensis*, *Panthera pardus*, *Felis (Lynx)* gr. *spelaea* and a sabre-toothed tiger, *Homotherium* sp. As regards the micromammals, in this association *Microtus (Iberomys) brecciensis* is dominant over *Apodemus* sp., *Allocricetus bursae*, *Clethrionomys* sp., *Pliomys episcopalis*, *Microtus (Terricola)* sp. and a small mole. The more recent faunal assemblage was composed of *Canis lupus*, *Vulpes vulpes*, *Sus scrofa*, *Mustela putorius*, *Panthera pardus*, *Cervus* sp., *Cervus elaphus*, *Bos primigenius* and *Crocuta crocuta spelaea*. The micromammals included *Erinaceus europaeus*, *Myoxus glis*, *Arvicola terrestris*, *Microtus arvalis-agrestis*, *Microtus* (*Terricola*) sp. and *Apodemus* sp.

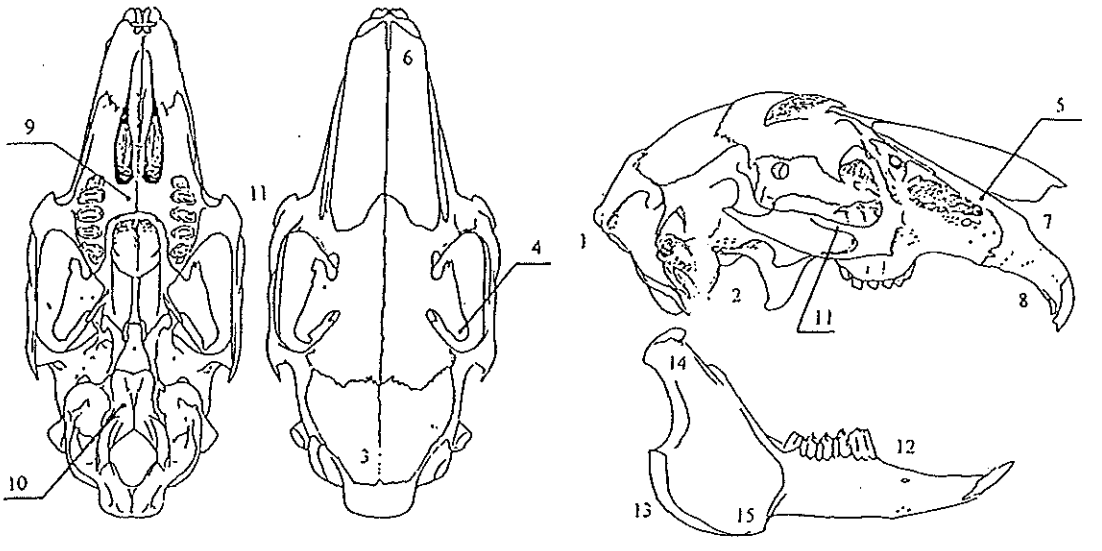
DESCRIPTION OF THE MATERIAL

The dimensions of the postcranial skeleton and the proportion between the size of the skull and that of the body in the leporid from Valdemino cave are intermediate between those of modern rabbits and modern hares. Furthermore, as Tozzi (1969) already noted, the tibia is proportionately more elongated with respect to the femur compared with modern rabbits; consequently the main problem which was posed at the beginning of the research was the attribution of this lagomorph to the genus of *Oryctolagus* or *Lepus*. Therefore modern comparative material was studied, consisting of both wild (from Tuscany and Sicily) and domestic (from Venetia) rabbits and white and common hares (from Venetia, Emilia Romagna); with the help of the literature (Corbet, 1978 and 1984; Dechaseaux, 1958; Ellerman & Morrison-Scott, 1966; Koby, 1960; Kurtén, 1968; and in particular Miller, 1912) we tried to individualize the diagnostic characteristics of the Oryctolagini and Leporini tribes by studying material of secure determination. This resulted in the identification of some cranial, mandibular (Fig. 1) and postcranial characteristics.

Cranial characteristics:

1 - Viewed laterally the profile of the occipital forms a right angle with the axis of the brain case in rabbits and an acute angle in hares. In *L. timidus* it forms a right angle, as in rabbits.

2 - The plane containing the major axes of the tympanic bullae is nearly parallel to the posterior surface of the occipital in *Oryctolagus*, and these axes are slightly oriented towards the outside; in hares this plane forms a more inclined angle with the posterior surface of the occipital.



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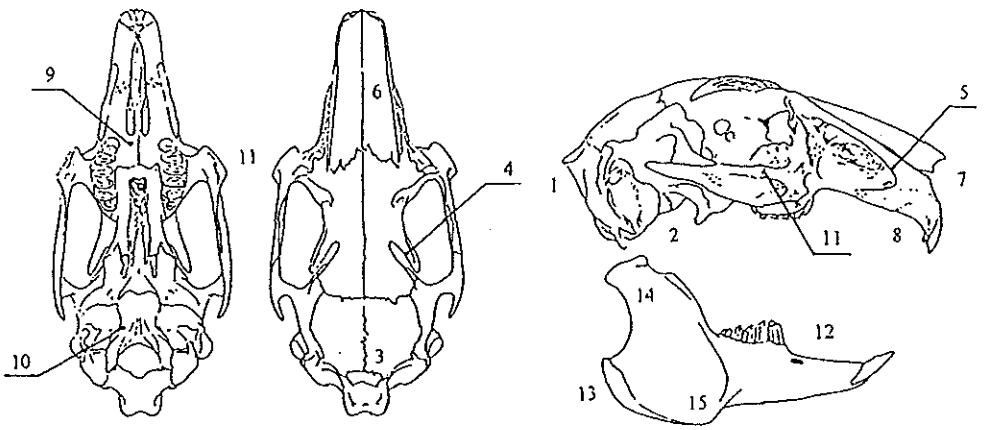


b)

Fig. 1.— Dorsal and lateral view of skull and mandibula of *Lepus europaeus* and *Oryctolagus cuniculus* (from Miller, 1954, redrawn). Numbers: cranial and mandibular diagnostic characteristics in text.

3 - In rabbits the interparietal, which has a rhomboidal shape, sutures with the parietals and, posteriorly, with the supraoccipitals; in hares the interparietal is absent; in some cases there may be small portions of parietals which are not fused with the rest of the bone, but these are however of small dimensions and do not have the rhomboidal form of the interparietal.

4 - The distal portion of the postorbital processes is long and narrow in rabbits, whileit is triangular in hares. It is necessary to point out that in large sized domestic

rabbits the distal portion of the processes may become thicker and assume a triangular form.

5 - The nasals are in continuous contact with the premaxillae almost up to their proximal termination in rabbits, while in hares the nasals are detached from the premaxillae in the anterior portion.

6 - In rabbits the whole of the rostral part is tapering; this characteristic is evident in the nasals which are elongated and dorsally obscure the incisive forame. In hares the rostral part is only slightly tapering, while the nasals are wider and shorter than in *Oryctolagus* and dorsally the incisive forame is visible.

7 - The dorsal margin of the premaxilla at the height of the detachment of the nasals forms an obtuse angle of about 150° with the terminal part which descends abruptly in rabbits; in hares this angle is closer to 170°. Since, in hares, the nasals detach from the premaxilla in a more backward position than in rabbits, this angle is also located further back and therefore the terminal part of the premaxilla descends less abruptly than in *Oryctolagus*.

8 - In rabbits the first upper anterior incisor (I^1) is not visible on the surface of the premaxilla, while in hares it is clearly visible.

9 - In rabbits the minimum diameter of the palatal bridge is greater than the width of the coanae (measured immediately behind the palatine), which is the opposite in hares. However, it should be pointed out that in one specimen of *Oryctolagus* (Table 3 - O.c. 564) a leporine palate was found, although this is an insular form.

10 - In rabbits, behind the suture between the basisphenoid and the basioccipital the latter widens and then narrows abruptly almost at the level of the condyles, often forming a circle. In hares the lateral edges of the basioccipital are nearly parallel, and the narrowing near the condyles is not marked. This morphology does however show individual variations and in some cases resembles that of rabbits.

11 - In rabbits the upper margin of the zygomata is narrow; proximally the ventral one is flattened and protrudes laterally in a very marked manner. This protrusion is also clear when viewed dorsally. In hares the upper margin of the zygomata is flattened or overturned in the proximal half; proximally the ventral edge is flattened and protrudes laterally, but not in a very marked way. This protrusion is not visible when viewed dorsally.

Mandibular characteristics:

12 - In rabbits the mental foramen is large and lies close to the first lower premolar (P_3), while in hares it is very small and lies in a very forward position on the diastema.

13 - The posterior portion of the gonial region is very developed with respect to the ascending branch of the mandible in rabbits, while in hares it is less developed.

14 - In rabbits the mandibular condyle is deeper mesio-distally than in hares.

15 - The lower angle of the angular process is rounded in rabbits, and more angular in

hares.

Dental characteristics (first lower premolar P_3):

16 - The profile of the tooth is subquadrangular in *Oryctolagus*, while in *Lepus* it forms a semicircle.

17 - In rabbits the anteroflexid is deep, sometimes wide, and always parallel to the mesio-distal axis of the tooth; in hares it may be quite deep and is generally inclined with respect to the mesio-distal axis of the tooth.

18 - In *Oryctolagus* the anteroconids are subequal, and have a regular rounded form; in *Lepus* the buccal anteroconid folds mesio-buccaly and it is generally narrower than the lingual one.

19 - The paraflexid is either absent or only marked by a slight concavity in the profile of the tooth in rabbits; when it is present in hares, it forms a notch in the profile of the tooth.

20 - In *Oryctolagus* the protoflexid forms an acute angle; in *Lepus* it is often wide and rounded, although in some cases it forms an angle which recedes into the profile of the tooth.

21 - The protoconid is smaller than or the same size as the labial anteroconid in *Oryctolagus*, while in *Lepus* it is larger than the anteroconid.

22 - In rabbits the mesial edge of the hypoflexid is generally crenulated, with introflexions which may penetrate deeply into the trigonig of the tooth, although sometimes it is smooth and similar to that found in fossil forms. In hares the mesial edge of the hypoflexid is slightly undulated. In *L. timidus* this undulation is more marked, although the folds are shallower than in *Oryctolagus*.

Postcranial skeleton:

23 - The humerus is longer than the radius in rabbits, while in hares it is shorter than the radius (Table 1 and Fig. 5).

24 - With respect to the dimensions of the postcranial skeleton, in rabbits the skull and the mandible are larger than in hares (Table 2 and Fig. 6).

The leporidae from Valdemino cave belongs to the genus *Oryctolagus* on the basis of cranial characteristics 1,2, 4, 6, 7, 8, 9, 10, 11; mandibular characteristics 12 and15; dental characteristics 16, 17, 18, 19, 20, 21. Due to the state of preservation of the bones it was not possible to observe characteristics 3, 5, 13 and 14.

From this study of the cranial, mandibular and dental characteristics it emerged however that, with respect to the modern rabbit, the rabbit from Valdemino cave differed in the following characteristics:

– the first upper premolar (P^2) is less crushed mesio-distally and the three mesial flexes

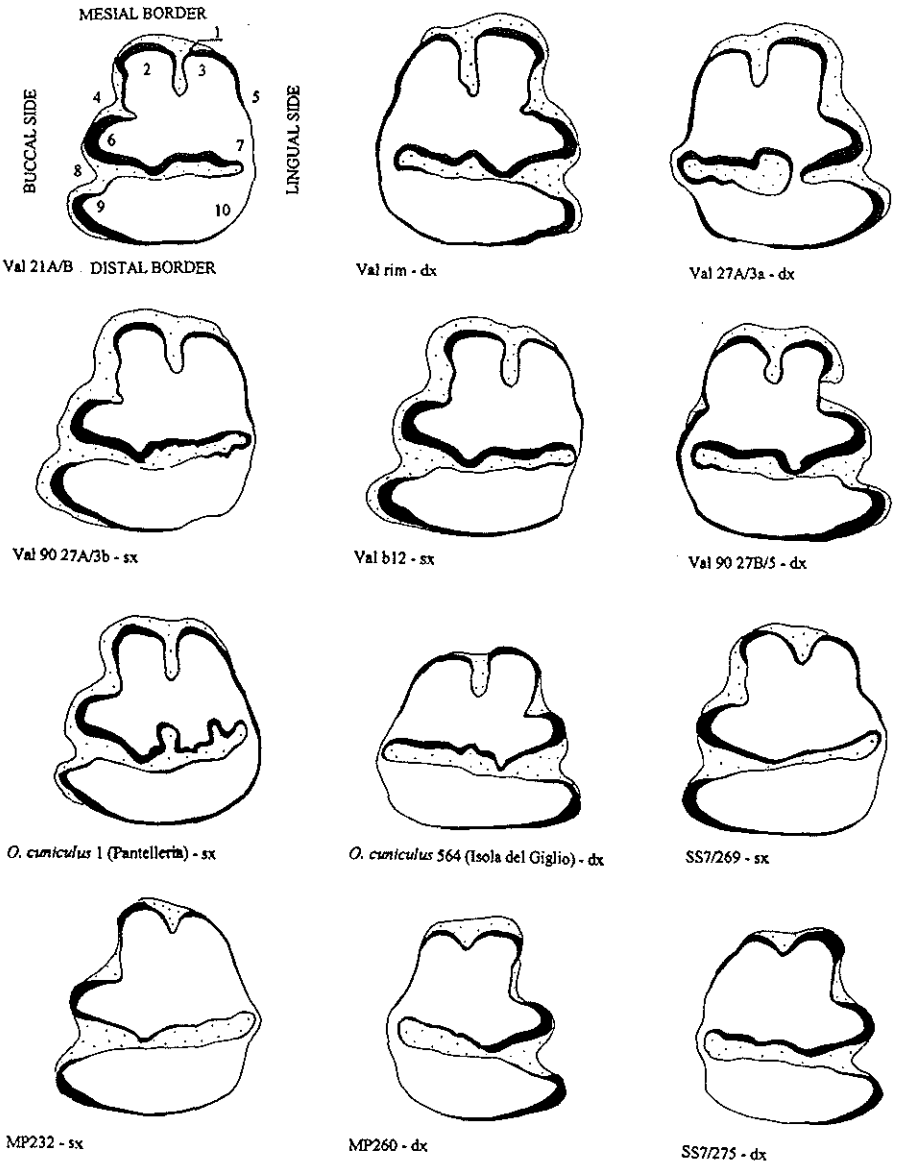


Fig. 2.— First lower premolar (P_3) of fossil rabbits from Valdemino (Val), San Sidero (SS7), Melpignano (MP) and of modern *O. cuniculus* from Sicily (Pantelleria) and Tuscany (Isola del Giglio). Black: enamel; white: dentine; dotted: cement. 1) anteroflexid, 2) check anteroconid, 3) lingual anteroconid, 4) protoflexid, 5) paraflexid, 6) protoconid, 7) metaconid, 8) hypoflexid, 9) hypoconid, 10) endoconid. (From Donard, 1982). (x8)

are always very deep. The walls of enamel which delimit each flex are parallel and smooth (Fig. 3),

- as is common in fossil forms, the hypoflexid of the first lower premolar (P_3) is nearly always smooth or slightly undulating; this undulation, if present, is less evident than in modern *O. cuniculus*,
- the dimensions of the postcranial skeleton are much larger (Table 1),

- in relation to a mandibular length (the distance between the aboral edge of the M_3 alveolus and the Infradentale) the bones of the postcranial skeleton are longer with respect to those of modern rabbits (Table 2 and Fig. 6),
- the tibia is particularly long, and the calcaneum and the 3rd metatarsal are proportionately short.

Because of the long tibia and relatively short calcaneum, the proportions of the rabbit from Valdemino cave are similar to those of a white hare.

Research on this particular rabbit was widened to include a study of other fossil populations of *Oryctolagus*, referable to the three known species *O. laynensis*, *O. lacosti* and *O. cuniculus*, in order to identify the possible characteristics in common as well as the differences. The elements retrieved in this second phase of the research derive from observations carried out in the laboratory on some of the populations (San Sidero, Melpignano, Lazaret, Vallonnet, Valdarno, Saint Vallier) and from the collection of bibliographic data on others.

The sites of San Sidero (Foggia) (De Giuli, 1983) and Melpignano (Lecce) (Bologna *et al.*, 1994) contain post-Galerian fauna of a temperate-warm phase preceding the last glaciation. The rabbits from these sites are very similar to modern rabbits, both in their dimensions and in their cranial and skeletal morphology, yet they differ from these and other fossils in the following characteristics:

- the first lower premolar (P_3) has a shallow anteroflexid which diverges mesially and a more open protoflexid which in some cases is wide and rounded (Fig. 2),
- the humerus is proportionately slightly longer with respect to the radius and femur (Table 1),
- the calcaneum is very elongated with the respect to the 3rd metatarsal,
- the 3rd metatarsal is proportionately short with respect to the femur and tibia.

Apart from these differences, all the other characteristics of the rabbits from these two sites fall within the range of the modern species *O. cuniculus* and therefore they are referred to that species.

The population from Lazaret (Serre, 1993) is post-Galerian in age and referable to a cold episode during the penultimate glacial. The few whole long bones indicate a slightly larger rabbit than modern ones and those of the fossils from San Sidero and Melpignano, but clearly smaller than that from Valdemino. Despite the absence of some long bones such as the radius and tibia, the morphological study demonstrated that this lagomorph shows the following cranial, dental and postcranial variations with respect to *O. cuniculus*:

- the row of cheek teeth tends to be proportionately longer with respect to the least longitudinal diameter of palate and the width of the coanae (Table 3),
- the first lower premolar (P_3) has a wide and rounded protoflexid (Fig. 4),
- the calcaneum is elongated with respect to the femur, while the 3rd metatarsal is very elongated with respect to the femur and the calcaneum (Table 2).

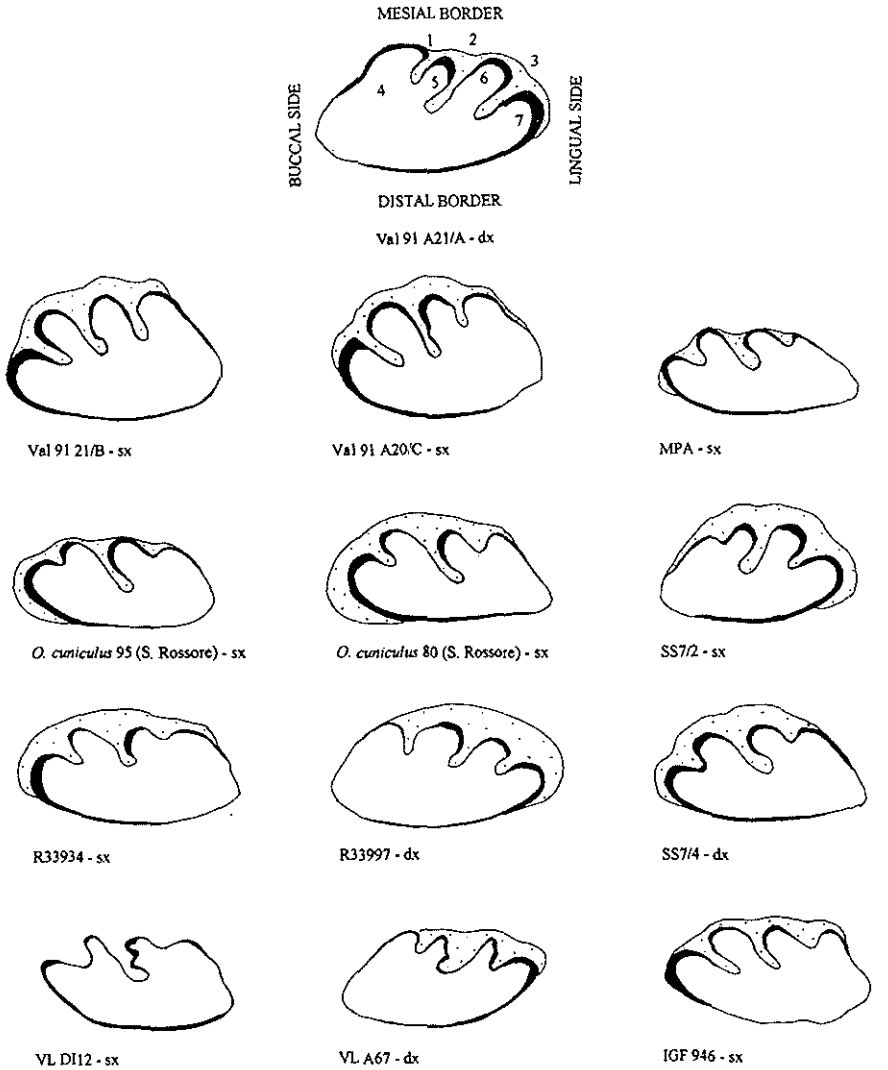


Fig. 3.— First upper premolar (P^2) of fossil rabbits from Valdemino (Val), San Sidero (SS7), Melpignano (MP), Lazaret (R), Vallonnet (VL), Valdarno (IGF) and of modern *O. cuniculus* from Tuscany (San Rossore). Black: enamel; white: dentine; dotted: cement. 1) mesoflex, 2) paraflex, 3) hypoflex, 4) postcone, 5) lagicone, 6) mesial hypercone, 7) distal hypercone. (From Donard, 1982). (x8)

However, these differences are not sufficient for the rabbit from Lazaret to be considered distinct from *O. cuniculus*.

Other fossil species preceding *O. cuniculus* have been taken into consideration. The oldest is *Oryctolagus laynensis* LOPEZ MARTINEZ, 1977, characteristic of the Spanish site of Layna which dates to the lower Villafranchian, and to which Lopez Martinez (1977) also dubitatively attributed the Leporidae from sites of Cordoba and the Medas islands.

The few finds of this species indicate a rabbit of slightly larger dimensions than modern rabbits and the fossil rabbits from Melpignano and San Sidero, but smaller dimensions than those observed in the population from Valdemino.

The characteristics which most distinguish this species are dental ones: the first upper premolar (P^2) has the three flexes typical of the rabbits, of which the central one (paraflex) is the deepest, while the two lateral ones (buccal mesoflex and lingual hypoflex) are shallow but evident. More particular are the other premolars (P^3 and P^4) and the upper molars which are characterised by an hypoflex which reaches up to half the width of the tooth and not up to two thirds as in all the other known Leporidae. The first lower premolar does not in fact show any particularities and morphologically it is similar to that of the modern rabbits.

The other known species is *Oryctolagus lacosti* (POMEL, 1853) which is present in middle and upper Villafranchian faunal associations.

Diverse forms have been referred to these species, some of them with leporine characteristics. For this reason researchers in the past have attributed some finds to the genus *Lepus*: *L. lacosti* POMEL, 1853; *L. valdarnensis* WEITHOFER, 1889; and *L. etruscus* BOSCO, 1899.

Finds were studied from the populations from Saint Vallier (Viret, 1954) (middle Villafranchian) and Valdarno (late Villafranchian) (Bosco, 1899; Forteleoni, 1968) and data was collected from the literature on the middle Villafranchian populations from Senèze (Schaub, 1943), Pardines (Koby, 1960) and other Spanish sites (Lopez Martinez, 1977) and the late Villafranchian of Montagnola Senese (Fondi, 1972).

The finds were always very scarce and included some cranial fragments with teeth, very few long bones and some calcanea and astragali.

The diagnostic characteristics of the species are difficult to individualise since different forms have been included; for example, in the populations from El Carmel and Saint Vallier the least longitudinal diameter of palate is smaller than the width of the coanae, while in other populations such as the one from Valdarno the width relationship of the coanae/least longitudinal diameter of palate is like that of a rabbit, in other words less than one (Table 3).

As regards the teeth, the first upper premolar (P^2) of the population from Saint Vallier has three mesial flexes which are always deep and very clear and, despite the walls of enamel which delimit the paraflex sometimes being crenulated, they are similar to those from Valdemino. The only specimen studied from the Valdarno population also has three very clear flexes (Fig. 3). In the first upper premolar of the population from El Carmel (Lopez Martinez, 1977) on the other hand, the central flex (paraflex) is well developed and deep, while the labial mesoflex is very slight or in some cases even absent, and the lingual hypoflex is also very slight. The P_3 of the population from Saint Vallier (Viret, 1954) is sometimes leporine, as the profile of the tooth is more rounded lingually and approximatively forms a semicircle, while in others it is typically rabbit-like with a squared profile and the two anteroconids subequal. The anteroflexid has a variable morphology: in some cases it is deep, wide and delimited by parallel walls of

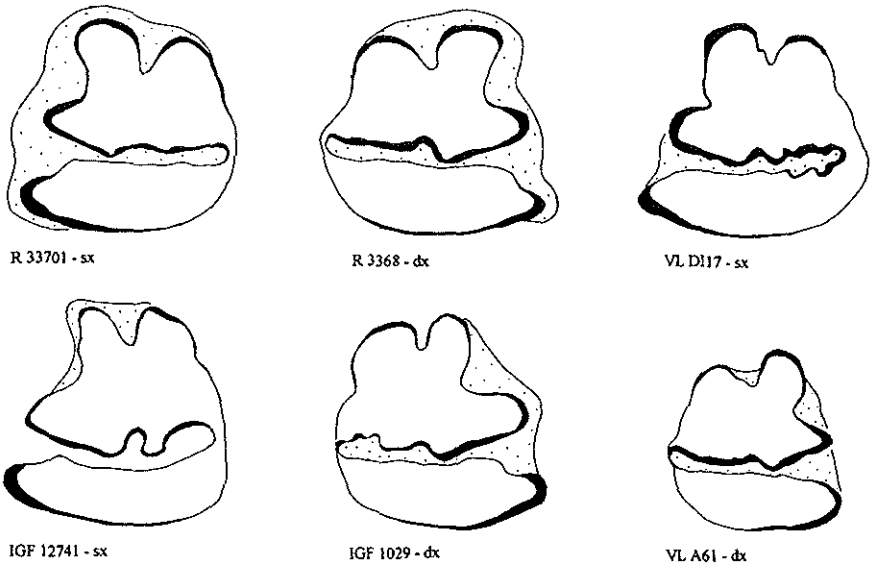


Fig. 4.— First lower premolar (P_3) of fossil rabbits from Lazaret (R), Vallonnet (VL), Valdarno (IGF). (x8)

enamel, while in others it is shallower and the walls diverge mesially. The hypoflexid is often very crenulated, as in the modern rabbit. In the population from El Carmel the anteroflexid is shallow and the protoconid larger than the labial anteroconid, the latter being a leporine characteristic.

The populations of *O. lacosti* always have larger dimensions than all the others studied (Table 1). From the few data collected it seems that the dimensions tend to diminish passing from the oldest finds to the more recent ones. In fact the greatest dimensions are found in the population from Saint Vallier, closely followed by those of Senèze and Pardines, and than Valdarno. According to Lopez Martinez (1977), *O. lacosti* from El Carmel resembles the rabbit from Valdarno in its dimensions and morphology.

At the site of Bagur 2 (Lopez Martinez *et al.*, 1976; Lopez Martinez, 1977), remains of lagomorphs were found which were dubitatively attributed to *O. lacosti* since the dental characteristics did not fall with certitude within the range of the species in question. The same conclusion was reached after having examined the data reported by Fondi (1972) on the rabbit from Montagnola Senese.

We also had occasion to study part of the material from the site of Vallonnet (Moullé, 1992), which should appertain to the lower Galerian and therefore would be older than that from Valdemino. The poor state of preservation did not consent an evaluation of the precise dimensions and relative ratios between the long bones of this rabbit, although their proximal and distal epiphyses, the calcanea (Table 1) and the astragali are similar to those of the modern rabbit. The dental characteristics of the first upper premolar (Fig. 3) and of the first lower premolar (Fig. 4) are similar to those found in the population from Lazaret, but they are not dissimilar to those of *O. laynensis* either. Furthermore, lacking comparisons with the other teeth and given the

very recent age with respect to *O. laynensis* and relatively old age with respect to *O. cuniculus*, it seems prudent to indicate this rabbit as *Oryctolagus* gr. *laynensis-cuniculus*.

ANALYSIS OF THE DATA

For the populations of modern and fossil rabbits on which the measurements were taken personally, the hypothesis of the equivalence of the variations was tested and demonstrated. We therefore calculated the Student's t-test with a level of significance of 1%. This test showed that the average values for the lengths of the bones of the population from Valdemino are different to those of the other populations studied. An indirect check of the validity of the test was carried out by comparing the average values of the lengths of the bones of the populations from San Sidero and Melpignano, for which the hypothesis of equivalence was demonstrated, as was expected.

The average lengths of the long bones of all the populations studied have been compared and reproduced in ratio diagrams in the form of absolute length, length compared to mandibular length and ratios between the bones. The resulting graphics have allowed us to identify affinities and differences between the various populations.

The most significant diagrams are those of the absolute lengths of the long bones and calcanea and those compared to a mandibular length of modern and fossil rabbits and modern hares.

In the first diagram (Fig. 5) the ratios are shown of the absolute lengths of the bones of each sample and the corresponding ratio in wild reference rabbit. In the diagram and in table 1 the differences in size of the populations examined are clear; Melpignano, San Sidero and Lazaret have values similar to those of modern rabbits while the rabbit from Valdemino is similar to those of *O. lacosti* from the French sites (Saint Vallier, Senèze, Pardines). All the rabbits show an overall similarity in the proportions of the long bones.

Lepus timidus and *L. europaeus* differ from rabbits in their clearly larger dimensions and the graph highlights the different proportions between the bones (the radius is longer than the humerus and the tibia is proportionately more elongated than the femur).

Observing in detail the graph of the Leporidae from Valdemino one notes in the femur-tibia tract a different inclination with respect to the other rabbits; this indicates that in this lagomorph the tibia is proportionately more elongated with respect to the femur, as in hares; the tibia/femur ratio is in fact greater than that of other rabbits and intermediate between that of the common hare and the white hare.

As regards the rabbits from San Sidero and Melpignano, the 3rd metatarsal is proportionately shorter with respect to the tibia and calcaneum.

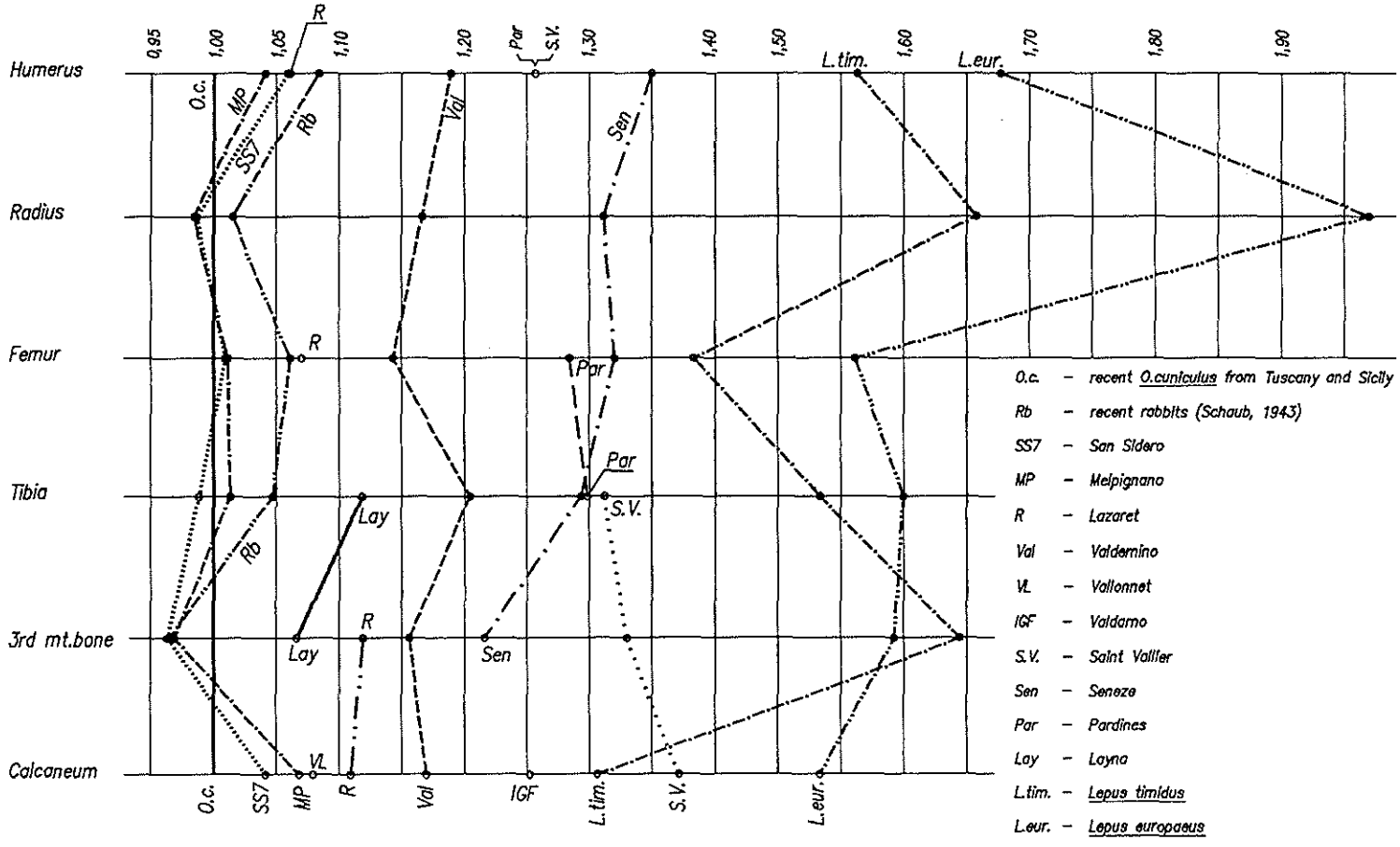


Figure 5.— Ratio-diagram of the lengths of the humerus, radius, femur, tibia, 3rd metatrsal and calcaneum of each population studied with respect to those of *O. cuniculus* (O.c.) (from Tuscany and Sicily) in relation to 1. In the graph of the Leporidae from Valdemino the femur-tibia tract has a different inclination with respect to the other rabbits, because the tibia is proportionately more elongated with respect to the femur, as in hares. *O. cuniculus* (O.c.) (from Tuscany and Sicily), *L. timidus* and *L. europaeus*, the fossil populations from San Sidero, Melpignano, Lazaret, Vallonnet, Valdemino, Valdarno and Saint Vallier were measured personally; the data of the other samples were derived from literature: recent rabbits (Rb) and Senèze (Schaub, 1943), *O. laynensis* (Lopez Martinez, 1977); Pardines (Koby, 1960).

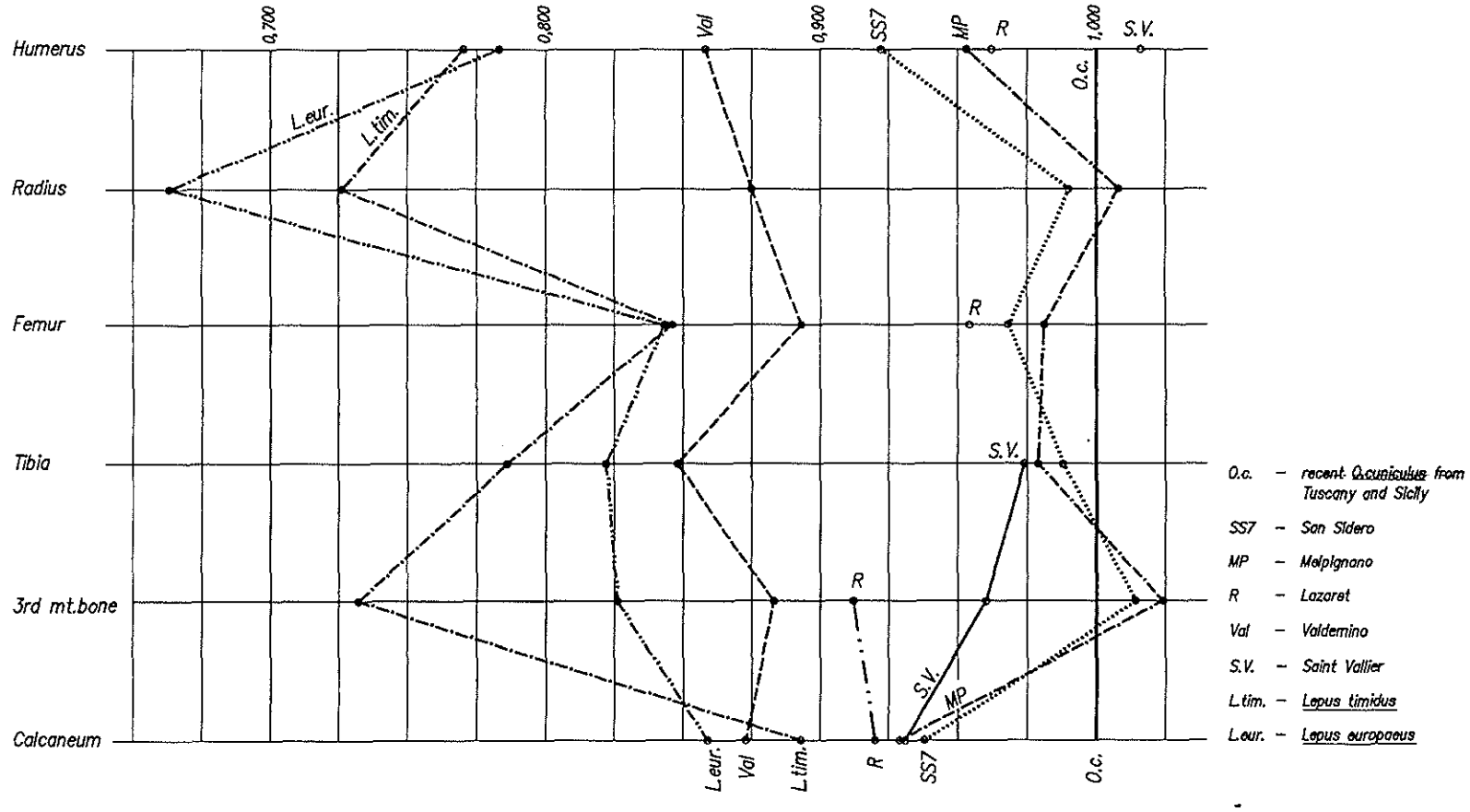


Figure 6.— Ratio-diagram of the lengths rationalised with respect to a mandibular length (distance between the aboral edge of the M_3 alveolus and the Infradentale), the humerus, radius, femur, tibia, 3rd metatarsal and calcaneum of each population studied with respect to those of *O. cuniculus* (from Tuscany and Sicily) in relation to 1. The graphic for the rabbit from Valdemino is isolated with respect to that of the rabbits and hares; its position indicates that the proportion between the size of the skull and the postcranial skeleton is intermediate between that in rabbits and hares (in the former the skull is large with respect to the rest of the body, while in the latter it is smaller). The data are based on own measurements.

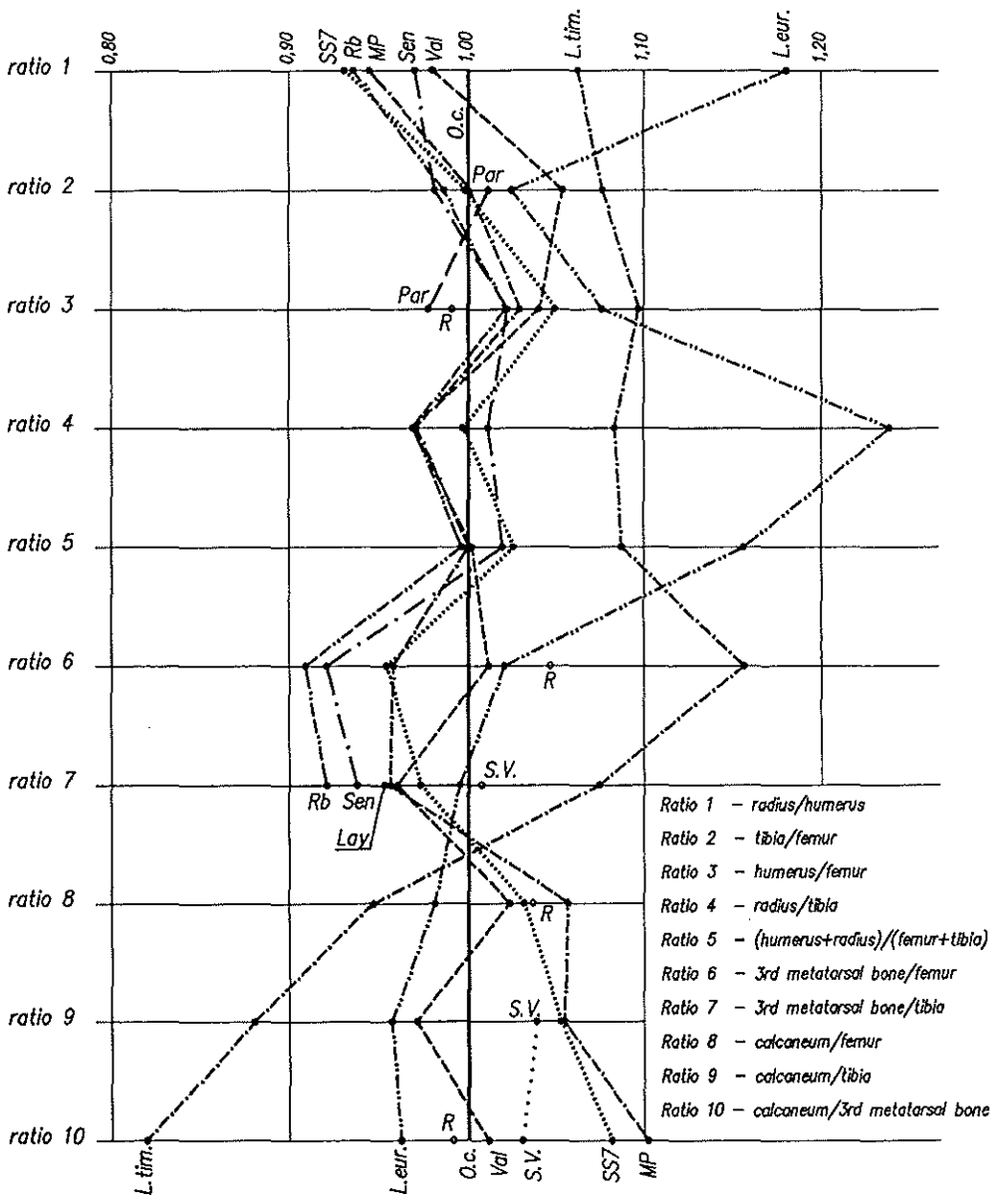


Fig. 7.— Ratio-diagram of the ratios between the limb bones of each population studied with respect to those of *O. cuniculus* from Tuscany and Sicily in relation to 1. In correspondence with ratio 2 (tibia/femur) the value corresponding to the rabbit from Valdemino differs from that of other rabbits (it is greater) and falls between those of the two hares (from Venetia and Emilia Romagna). Data were derived from the values previously considered.

To resolve the size differences one generally uses a cranial length as a parameter; in this case, given the difficulty of finding well preserved skulls, we chose a mandibular measurement: the distance between the aboral edge of the M_3 alveolus and the Infradentale (von den Driesch, 1976). Limited to those species for which such a parameter was available, we constructed a second diagram (Fig. 6) analogous to the first

but substituting absolute length with the parameter/absolute length ratios. In the diagram in figure 6 and in table 2 one observes that the rabbit from Saint Vallier, which is of a large size, lies close to the references axis thus uniting it with the rabbit group, while the Valdemino rabbit remains in an intermediate position between the hares and the rabbits. From this one can deduce that in the rabbit from Valdemino the skull is smaller with respect to the dimensions of the postcranial skeleton compared with recent and fossil rabbits, and larger compared with recent hares.

The particular elongation of the tibia with respect to the femur in the rabbit from Valdemino is highlighted in the last ratio-diagram (Fig. 7), in which the ratios between the limb bones are shown.

The values relating to *Oryctolagus* fall within a restricted range of variability with respect to corresponding values for wild reference rabbits, which indicates that the proportions between the limb bones are more or less equal indipendently of the size of the samples examined.

The graphs relative to *L. timidus* and *L. europaeus* differ from one another and from that of the rabbits, which indicates that they have different proportions among the bones. It should be noted that in correspondence with ratio 2 (tibia/femur) the value corresponding to the rabbit from Valdemino differs from that of other rabbits (it is greater) and falls between those of the two hares.

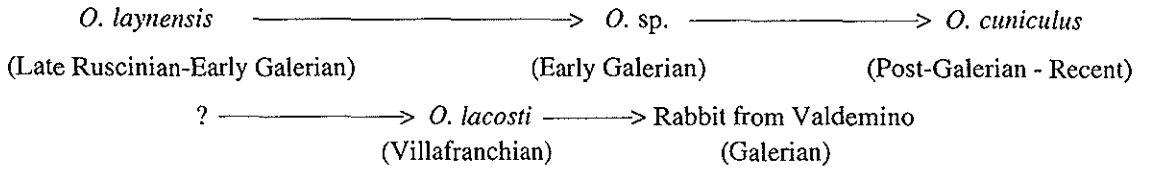
CONSIDERATIONS

From what has been demonstrated above and from the schematic diagrams of the postcranial skeleton one ascertains that the rabbit from Valdemino differentiates itself from the three known species of *Oryctolagus* as a result of dental characteristics, the long tibia and proportionately short calcaneum, the dimensions and proportions between the size of the head and the dimensions of the postcranial skeleton, which are intermediated between those of *Oryctolagus* and *Lepus*.

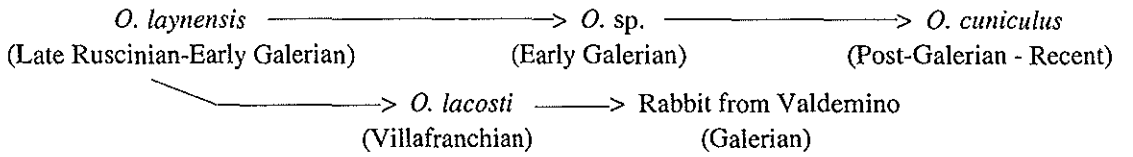
This Leporidae can therefore be considered to be different from those known in the literature and in a future publication a new species will be instituted for it.

In her doctoral thesis, Lopez Martinez (1977) hypothesised that the oldest form of rabbit, *O. laynensis*, could have been the progenitor of *O. cuniculus*, while *O. lacosti* appertained to a distinct lineage which had no descendants. As a result of the research carried out here, we propose two phyletic hypotheses, which can be schematically summarised as follows:

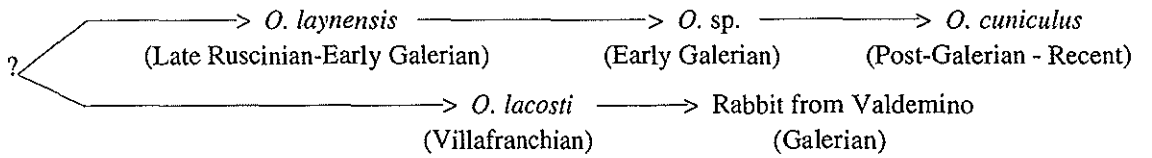
first hypothesis



Second hypothesis (a)



Second hypothesis (b)



The first hypothesis is in agreement with Lopez Martinez (1977), according to which *O. laynensis* would have given origin to *O. cuniculus* across intermediate forms such as the rabbit from Vallonnet.

According to the second hypothesis, which we sustain, all the rabbits (small and large size) had a common western origin, which can be recognised either in *O. laynensis* (a) or in an unknown progenitor form (b).

In both contexts the rabbit from Valdemino could be seen as the most recent species originating from *O. lacosti*, with reduced dimensions with respect to the progenitor form but larger dimensions than those of *O. cuniculus*, and with some rabbit-like characteristics and one more like a hare (tibia).

During the late Pleistocene rabbits were absent in western Europe except in Spain and perhaps in south-western France. The rabbit in the Mediterranean area would have had moments of explosion and radiation alternating with moments in which it would have retreated to survival niches in the south-west.

In the middle and late Villafranchian *O. lacosti* could have occupied the niche of the hare, not yet known in western Europe, and later given origin to the Valdemino rabbit as an endemic form in Liguria. This relict form would have lived during the middle Pleistocene and disappeared before the last glacial.

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Bone	O.c.			Rb			SS7			MP			R			Val			VL		
	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s
humerus	5	62,06	1,44	*	67,30	–	10	65,72	1,53	14	64,58	1,61	5	67,78	1,81	8	73,82	1,51	–	–	–
radius	4	59,80	3,88	*	60,70	–	7	58,97	0,78	3	58,83	1,36	–	–	–	11	69,76	1,20	–	–	–
femur	6	82,80	2,22	*	87,90	–	14	83,53	2,20	12	83,70	1,66	2	88,60	–	8	94,65	1,99	–	–	–
tibia	6	92,05	3,07	*	96,40	–	1	91,00	–	20	93,21	3,45	–	–	–	6	110,80	2,68	–	–	–
3rd mt.bone	5	34,70	1,72	*	33,50	–	6	33,41	1,15	8	33,61	1,22	20	38,84	1,00	25	40,12	1,36	–	–	–
calcaneum	5	22,25	1,31	*	–	–	6	23,16	0,43	5	23,76	0,99	16	24,68	0,18	14	26,02	0,98	3	24,00	0,43

%

Bone	IGF			S.V.			Sen			Par			Lay			L.tim.			L.eur.		
	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s	n	Lm	s
humerus	–	–	–	1	78,00	–	*	83,80	–	2	78,00	–	–	–	–	2	93,90	–	3	107,50	11,48
radius	–	–	–	–	–	–	*	78,40	–	–	–	–	–	–	–	2	96,10	–	2	114,80	–
femur	–	–	–	–	–	–	*	109,30	–	1	106,30	–	–	–	–	3	114,10	2,95	3	125,13	2,43
tibia	–	–	–	2	120,75	–	*	119,00	–	1	119,50	–	1	102,90	–	3	136,50	0,98	4	142,57	2,35
3rd mt.bone	–	–	–	2	46,15	–	*	42,20	–	–	–	–	1	37,00	–	3	55,30	2,80	2	53,50	–
calcaneum	4	27,82	0,71	1	30,50	–	–	–	–	–	–	–	–	–	–	1	28,70	–	1	33,60	–

O.c. – recent O.cuniculus from Tuscany and Sicily
Rb – recent rabbits (Schaub, 1943)
SS7 – San Sidero
MP – Melpignano
R – Lazaret
Val – Valdemino
VL – Vallonnet
IGF – Valdarno
S.V. – Saint Vallier
Sen – Seneze
Par – Pardines
Lay – Layna
L.tim. – Lepus timidus
L.eur. – Lepus europaeus

Table 1.— Absolute lengths. n: number of samples examined; L_m: mean length; s: standard deviation. O.c., SS7, MP, R, VL, IGF, S.V., L. tim and L. eur were personally measured; Rb and Sen from Schaub (1943); Par from Koby (1960); Lay from Lopez Martinez (1977).

Bone	O.c.	SS7	MP	R	Val	S.V.	L.tim.	L.eur.
humerus	53,14	49,02	50,66	51,14	45,62	54,01	40,99	41,62
radius	55,15	54,63	55,61	–	48,27	–	40,05	36,60
femur	39,83	38,57	39,09	38,01	35,58	–	33,73	33,58
tibia	35,82	35,40	35,10	–	30,39	34,89	28,19	29,47
3rd mt.bone	95,04	96,43	97,35	86,71	83,94	91,28	69,60	76,54
calcaneum	148,22	139,11	137,71	136,46	129,43	138,13	132,45	127,33
Parameter	32,98	32,22	32,72	33,68	33,68	42,13	38,49	42,02

Table 2.— Parametric lengths. L_p: parameter/absolute length. Data in table were obtained from our measurements. For sample abbreviation see table 1.

Sample	SS7/241	SS7/261	SS7/262	MPA 249	MPE 264	Val 457	Val 459	R 30229	R 33753	R 33769
m.11/m.9	43,50	42,28	44,44	43,04	45,39	54,60	57,04	42,00	38,65	43,33
m.20/m.11	94,02	93,65	86,76	93,84	84,37	71,08	69,13	80,95	93,65	80,00
m.20/m.9	39,59	38,56	40,62	40,79	38,52	38,81	39,43	34,00	36,19	34,66

Sample	R 33773	S.V.161959	IGF 946	O.c. 80	O.c. 95	O.c. 498	O.c. 564	O.c. 13153	O.c.103/M	O.c. 2119/93
m.11/m.9	40,64	(32,60)	–	44,03	47,61	42,45	36,27	46,66	52,30	55,59
m.20/m.11	85,71	151,66	(83,75)	89,49	70,00	83,88	114,06	72,85	63,72	68,90
m.20/m.9	34,83	(49,78)	–	39,41	33,33	35,61	41,37	34,00	59,92	38,30

Table 3.— Ratios of cranial measurements. Measurement 9: length of check tooth row; measurement 11: least longitudinal diameter of palate; measurement 20: width of choanae. The data in the table were obtained from our measurements. For sample abbreviation see table 1.