Perseverance of pikas in the Miocene

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Perseverance of pikas in the Miocene

Interplay of climate and competition in the evolution of Spanish Ochotonidae (Lagomorpha, Mammalia)

Overleving van fluithazen in het Mioceen
De rol van klimaat en competitie in de evolutie van Spaanse Ochotonidae
(Lagomorpha, Mammalia)

(met een samenvatting in het Nederlands)

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Contents

CHAPTER 1

Introduction, summary and background

1.1 Introduction

Pikas represent a family of small-sized herbivores that is closely related to the family of rabbits and hares. Although they are currently extinct in Europe, pikas are a common component in small-mammal fossil assemblages of Miocene age in which they are often abundantly present. In spite of their regular occurrence, they are a relatively sparsely studied mammal group, in particular in comparison to rodents. Teeth represent the most important fossils of small mammals, because of their excellent preservation potential in the geologic record and their high diagnostic potential in taxonomy, which is often distinctive at the species level. In addition to its phylogenetic value, tooth shape is strongly related to diet and may provide information on past environmental conditions.

The sedimentary succession near the village of Villafeliche in the Calatayud-Montalbán Basin (Figure 1.1) is well known for its exceptionally rich fossil mammal record spanning the Early and Middle Miocene interval and has been magnetostratigraphically dated (Krijgsman *et al.*, 1994, 1996; Daams *et al.*, 1999a). Extensive research has been focused on Neogene mammal paleontology in the Daroca-Villafeliche area for the last five decades, which has resulted in a database consisting of several tens of thousands of small-mammal teeth collected from over 100 mammal localities spanning the interval between ~17 and 10 Ma. The time interval covered by the mammal succession is characterized by major shifts and distinctive episodes in global climate, such as the Miocene Climate Optimum, which represents the warmest phase of the Neogene, and the Middle Miocene Climate Transition, which encompasses one of the major cooling phases in the Cenozoic (Flower & Kennett, 1994; Zachos *et al.*, 2001).

The combination of a rich and dense fossil record with good time control provide ideal conditions for studying the biostratigraphy, evolutionary trends and changes in the community structure of small mammals under the influence of major changes in climate. In recent years, studies focusing on the rodents have yielded significant new insights in small-mammal community dynamics (van der Meulen *et al.*, 2005; van Dam *et al.*, 2006). The role of the pikas in this context has so far remained unexplored.

The taxonomy of fossil pikas is not very straightforward, which is mostly due to mosaic evolution, convergent and parallel trends and generally conservative evolutionary change, while having considerable intra-specific and ontogenetic variation. The comprehensive work of López-Martínez (1989) comprises a firm taxonomic framework for Spanish Miocene ochotonids and provides a wealth of information on the evolution of the group, which serves as the main starting point in the analysis of the several thousand ochotonid tooth elements from the Daroca-Villafeliche succession.

The focus of this thesis is fourfold, comprising:

1) A detailed analysis and description of the extensive new ochotonid material from the Daroca-Villafeliche succession and re-evaluation of the existing taxonomy and biostratigraphy (Chapters 2 & 3);
2) Analysis of the main evolutionary trends in the lineages with special attention to speciation and competition (Chapter 4);
3) Analysis of the role of pikas in the small-mammal primary consumer communities (e.g. rodents and pikas) in the succession and analysis of the community structure in terms of community membership ("residents" and "transients") and persistence-abundance patterns (Chapter 5);
4) Establishing the impact and effect of long-term climate changes on the small-mammal community composition and evolution of individual lineages by comparison to marine stable isotope records that serve as a proxy for changes in global climate (Chapter 6).

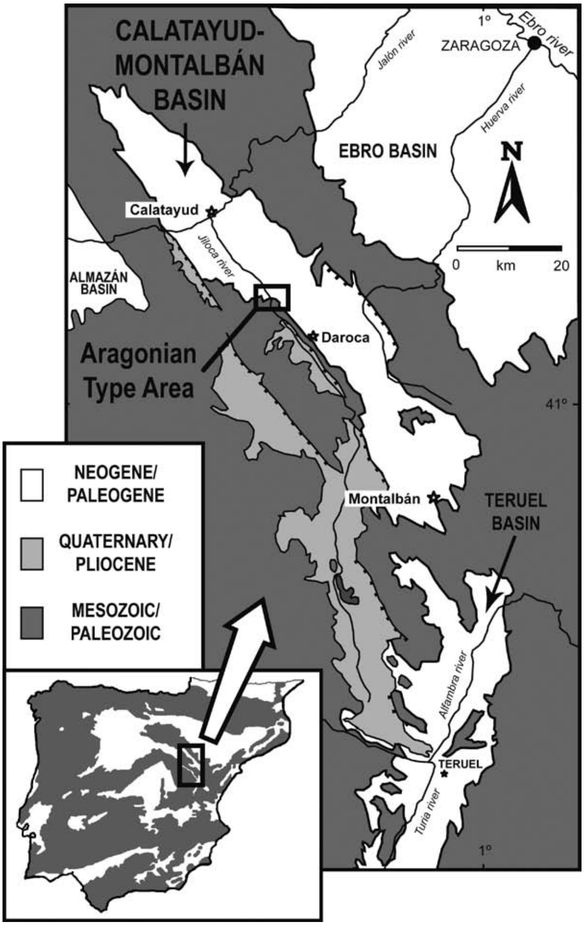


Figure 1.1: Location of the Calatayud–Montalbán Basin and synthetic geology of the surrounding region. The square box denotes the position of the studied succession near the village of Villafeliche. (Modified after García-Paredes *et al.*, 2010).

1.2 Summary

The high resolution mammal record in the Calatayud-Montalbán Basin provides an ideal setting for verifying and specifying the existing taxonomy and biostratigraphy of middle Miocene ochotonids. **Chapter 2** deals with the systematics of the two ochotonid lineages that were already present in the region during a significant part of the early Miocene: the *Lagopsis penai* – *L. verus* and the *Prolagus lopezmartinezae* n. sp. – *P. tobieni* lineage. The definition of the chronospecies has been refined both in terms of morphological characteristics and in the extent of their temporal ranges. The anagenetic transition in the *Lagopsis* lineage has been shifted to a level ~400 kyr older. The presence of *P. lopezmartinezae* marks the onset of the endemic evolution of this lineage and represents a different stage of evolution relative to *P. tobieni*.

Chapter 3 is focussed on the systematics of the two immigrant lineages in the area: the *Prolagus vargasensis* n. sp. – *P. major* and the well known *Prolagus oeningensis* lineages. Similar to Chapter 2, the morphological definition and temporal ranges of the chronospecies have been refined. It is demonstrated that *P. vargasensis* arrived ~2 Myr earlier than *P. oeningensis* into the area and that *P. major* evolved from *P. vargasensis* in the early late Aragonian, thereby rejecting earlier hypotheses on the phylogenetic origin of *P. major*.

In **Chapter 4** the intraspecific variation and interspecific disparity between the four lineages described in Chapters 2 & 3 is demonstrated by multivariate analyses of size and shape characteristics of the P_3. On the basis of our results we hypothesize that competition in combination with climate likely played a role in the evolutionary and co-existence patterns of the ochotonid lineages present in the Daroca-Villafeliche area. The first appearance of the endemic *P. vargasensis* n. sp. is inferred to be the result of parapatric speciation from a *P.* cf. *oeningenensis* stock from a more northern region. We deduce from our modelled disparity pattern between the morphologically similar *P. vargasensis*-*P. major* and *P. oeningensis* lineages that apart from climate, biotic mechanisms such as competitive exclusion of neighbouring allopatric species and limiting similarity between co-occurring species are likely to have significantly affected the evolution of these lineages.

The community-structure of the small-mammal primary consumers from the Calatayud-Montalbán Basin, comprising lagomorphs and rodents, is analyzed in **Chapter 5**. Our results consolidate the patterns established in earlier studies based on rodents, which are: 1. the recognition of two main groups on the basis of residence time, i.e. residents and transients of which the former can be further subdivided in a resident and long-term resident group respectively, 2. the preferential loss of newcomers during phases of community disassembly, 3. the recognition of temporal metacommunities. Three out of the four ochotonids represent core components of the small-mammal community in the basin. The generally rare or occasional ochotonid lineages are endemic to the Iberian Peninsula, while the locally common species are widespread in Western Europe. The most persistent species also show higher maximum abundances. The persistence-abundance patterns further suggest influence of phylogeny.

In **Chapter 6** we investigate the correlation between changes in the primary consumer community composition and evolutionary trends of individual lineages in the Calatayud-Montalbán Basin and the pronounced climate shifts and phases evidenced in the stable isotope records of ODP Site 1146 (South China Sea) and the Ras Il Pellegrin section (Malta). The results indicate a close connection between climate events and the local small-mammal record, in particular with regard to the sensitivity of the latter to changes in local humidity. The Miocene Climate Optimum coincides with significant aridification in Spain and marked impoverishment of the small-mammal community and is associated with an increase in the influence of the subtropical high pressure zone in Spain due to widening of the tropical belt. The Middle Miocene Climate Transition is correlated with a prolonged immigration phase, which is interpreted to reflect contraction of the tropical belt, and is characterized by distinct anagenetic evolution in various lineages. It ultimately results in a community turnover event following the onset of the "ice-house" climate state.

1.3 Background

1.3.1 Geological setting and age model

The Calatayud-Montalbán Basin is situated north-east of central Spain (Fig. 1) and is part of the Iberian Chain (Anadón & Moissenet, 1996; Daams *et al.* 1999a). The basin is a narrow north-west south-east trending depression that is flanked by Paleozoic basement rock. Its north-western part is a graben structure with normal faulting, while its south-eastern end is more complex, having strike-slip faults with low angle thrusts that confine the basin. The terrestrial sediments consist of alluvial fan, shallow lake and marsh deposits (Daams *et al.*, 1999a). A detailed overview of the tectonic and sedimentologic features is given by Anadón & Moissenet (1996) and Daams *et al.* (1999a).

The pikas from the study area are associated with various rodent and insectivore families in the small-mammal assemblages, part of which are still under study or are under taxonomic revision. The glirids and cricetids are the most abundant and/or diverse family groups and have therefore traditionally received most attention (Freudenthal, 1963; de Bruijn, 1966a, 1966b, 1967; Daams, 1981; Daams & Freudenthal 1988a; van der Meulen *et al.*, 2003; García-Paredes, 2006; López Guerrero *et al.*, 2008; Oliver Pérez *et al.*, 2008; García-Paredes *et al.*, 2009). Other small-mammal groups present in the assemblages are sciurids (de Bruijn, 1967; Cuenca-Bescos, 1988; Péalez-Campomanes, 2001), eomyids (de Bruijn, 1967; Álvarez Sierra, 1987), beavers (Daams *et al.*, 1988), and the insectivores (de Jong, 1988; van den Hoek Ostende, 2003; van den Hoek Ostende & Furió, 2005; van Dam, 2010). Previous work on Ochotonidae from the study area has been done by de Bruijn & van Meurs (1967) and López-Martínez (1977, 1989), of which several assemblages are included in this thesis as well.

Independent dating by means of magnetostratigraphy has been provided by Krijgsman *et al.* (1994, 1996), which is based on four partly overlapping Middle Miocene sections that include series of mammal localities. The combination of magnetostratigraphy, sedimentology, biostratigraphy and additional sampling later necessitated several re-interpretations of the initial magnetostratigraphic correlation (Daams *et al.*, 1999a, 1999b) and a revision of the biostratigraphic framework for the Miocene of central Spain (Daams *et al.* 1998). The age model provides generally accurate magnetostratigraphically calibrated age constraints for the mammal localities in the interval between ~16 and ~13 Ma. The ages of the localities older than ~16 Ma are estimated by extrapolation of the sedimentation rates in the section. The numerical age calibration of localities between 13 and 10 Ma is, however, less well constrained and is primarily based on biostratigraphic correlations.

Freudenthal (2006) strongly disagrees with the revised age model, but his correlation scheme is in conflict with the magnetostratigraphic data and the biostratigraphy of superposed faunas within sections (van der Meulen *et al.*, in review). The latter authors have refined the mammal zonation scheme and include recently updated absolute age estimates for the magnetostratigraphically calibrated localities by van Dam *et al.* (2006), which have been recalibrated with the current polarity reversal ages of the ATNTS2004 (Lourens *et al.*, 2005).

Correlations of Spanish material to the MN system follow Daams *et al.* (1999a); the numerical ages of MN-correlated Spanish assemblages are known to differ from those in central Western Europe (Kempf, *et al.*, 1997; Lindsay, 2001; van der Meulen *et al.*, in review).

1.3.2 Evolution and early history of pikas in Europe

Fossil evidence indicates that lagomorph-like mammals originated close to the Cretaceous-Paleogene boundary (Asher *et al.*, 2005). Since then, the lagomorphs have evolved as a successful order, having dispersed to all continents but Antarctica and Australia, until their introduction by humans on the latter. Crown lagomorphs are known from the Eocene (Meng *et al.*, 2005; Dawson, 2008; López-Martínez, 2008; Rose *et al.*, 2008).

Extant representatives of the order Lagopmorpha Brandt, 1855 comprise the families Leporidae Fischer, 1817, the rabbits and hares, and Ochotonidae Thomas, 1897, the pikas (Hoffmann & Smith, 2005). The Ochotonidae appear in the fossil record from the early Oligocene in Asia (Kraatz & Barnosky, 2004; Dawson, 2008; López-Martínez, 2008). Of the ~20 Neogene ochotonid genera listed by López-Martínez (2008), only two survived into historic times. The last remaining species of *Prolagus* Pomel, 1853 went extinct during the Holocene on the Mediterranean islands Corsica and Sardinia (Vigne *et al.*, 1981; Sondaar *et al.*, 1986; Vigne & Valladas, 1996; Lagomorph Specialist Group, 1996). All extant pika species (30) belong to the genus *Ochotona* Link, 1795 (Hoffmann & Smith, 2005). The geographical range of this genus is now restricted to Asia and to mountainous regions of western North-America (Smith, *et al.* 1990; Smith, 2008), but used to reach as far as Britain (Fisher & Yalden, 2004).

The origin of pikas is usually, yet tentatively, associated with the genus *Desmatolagus* Matthew & Granger 1923 (Dawson, 1967, 2008; López-Martínez, 1989; McKenna & Bell 1997; Kraatz & Barnosky, 2004). This genus has been grouped with either Leporidae (Matthew & Granger, 1923; Meng *et al.*, 2005) or Ochotonidae (López-Martinez, 1989; McKenna & Bell, 1997). Dawson (1967) indicated the possibility that some species included in *Desmatolagus* may be referable to Leporidae and others to Ochotonidae. McKenna (1982) considers *Desmatolagus* neither leporid nor ochotonid. Similarly, López-Martínez (2008) places this genus with an informal group of stem-lagomorphs, from which the ochotonids and leporids have arisen.

Martin (2004) concluded, on basis of the differences in incisor enamel, that the two species that were originally included in *Desmatolagus* by Matthew & Granger (1923) are most likely leporids. Therefore, with respect to this feature, the exact origin of the Ochotonidae would yet have to be determined.

Pikas successfully colonized Europe in the late Oligocene from an Asian source area (Tobien, 1963, 1986; López-Martínez, 2008). The timing of this event is possibly (in part) related to Oligocene basin rearrangements resulting in the closure of various shallow marine corridors in the Peri- and Paratethys realm, thereby connecting Western Europe with Eastern Europe and Asia (Meulenkamp & Sissingh, 2003; Popov *et al.*, 2004). Pikas became well established in the European peninsula. The Miocene encompasses their most successful epoch, during which their diversity was high and their geographic range expanded from Asia to North-America, Europe and parts of Africa (Dawson, 1967, 2008; López-Martínez, 1989).

The taxonomy of primitive European ochotonids has been scarcely studied during the last three decades, and has thus remained stable. McKenna (1982), López-Martínez (2008) and Angelone (2009) have shown that there is ample room for discussion. The works of Tobien (1974, 1975, 1986) and López-Martínez (1986) indicate that Miocene European ochotonid genera are probably related to a morphologically primitive genus like *Amphilagus* Pomel, 1853 or to a very similar form. This ancestor, that has rooted and relatively low crowned teeth, appears to have given rise to various evolutionary branches during the Late Oligocene that are characterized by increased hypsodonty.

The (immigrant) genera *Piezodus* Viret, 1929 and *Titanomys* von Meyer, 1843 represent the most prominent variants. During the Early Miocene, *Prolagus* evolved as a separate branch from *Piezodus*. *Marcuinomys* Lavocat, 1951 most likely branched from *Titanomys* and subsequently gave rise to *Lagopsis* Schlosser, 1884 and possibly *Albertona* López-Martínez, 1986, although the latter is uncertain and remains to be substantiated (López-Martínez, 1974, 1986, 1989; López-Martínez & Thaler, 1975; Tobien, 1963, 1974, 1975, 1978).

The origin of the hypselodont genera *Prolagus* and *Lagopsis*, i.e. having rootless and very high crowned teeth, represents a distinct stage in evolution in Europe during the Early Miocene. Hypselodonty evolved independently in both lineages, since both genera have a different direct ancestor with hypsodont rooted cheek teeth.

Similarly, the Miocene North American ochotonid genus *Oreolagus* Dice, 1917 also possessed rootless teeth during the Early Miocene (Kraatz & Barnosky, 2004). Asian ochotonid genera, such as *Sinolagomys* Bohlin, 1937, evolved rootless cheek teeth in the Late Oligocene (López-Martínez, 1986). The occurrence of these parallel evolutionary trends on different continents marks a conspicuous and ultimately very successful adaptation in the evolution of ochotonid lineages.

The primitive rooted ochotonids continued in Europe in the Miocene alongside the more evolved rootless forms, which is exemplified by the Middle Miocene relatively low-crowned genus *Eurolagus* López-Martínez, 1977, while the genera with rooted hypsodont teeth eventually went extinct during the Early Miocene. The fossil record of North America has revealed that morphologically primitive ochotonid genera continue to thrive during the Middle Miocene (Bair, 2006).

Lagopsis and *Prolagus* are the two most commonly found pika genera from the late early and middle Miocene of West-central and Southwestern Europe. The latter is by far the most extensively studied pika genus in Europe. *Prolagus* is species rich, representing numerous evolutionary lineages, and is widely distributed throughout Europe and ultimately extending to some parts of North Africa. Its stratigraphic range spans more than ~20 million years, from the early Miocene to the Holocene. Most *Prolagus* species have a limited geographic distribution, with the exception of widespread species such as *Prolagus vasconiensis* Viret, 1930 and *Prolagus oeningensis* (König, 1825). The high species diversity within the genus therefore comprises mainly endemic lineages. The most prominent radiation phases occurred during the late early Miocene and during the latest Miocene and Pliocene. The first phase is characterized by the evolution of lineages on the continent (López-Martinez, 1997), while the younger phase is mostly characterized by the evolution of island lineages in the Western Mediterranean (López-Martinez & Thaler, 1975; Angelone, 2005, 2007, 2008; *et al.*, 2008).

Lagopsis has had a wide geographic distribution throughout Western Europe, but not as widespread as *Prolagus*, since it has not reached North Africa and, apparently, the more eastern parts of Europe. Its stratigraphic range is early to middle Miocene, after which it went extinct in Spain at the end of the Middle Miocene. Its persistence elsewhere in Europe during the Late Miocene is unknown. However, a relict population may possibly have survived in (pen)-insular

Italy, since the Late Miocene genus *Paludotona* Dawson, 1959 from Tuscany has been suggested to be a descendant insular lineage (López-Martínez, 1986, 1989; Dawson, 2008).

López-Martínez (2001) has demonstrated a latitudinal difference in the relative abundance of *Prolagus* versus that of *Lagopsis* during the Miocene, where *Lagopsis* is the more abundant genus in Spain and *Prolagus* in Southern France. Mein (1984) and López-Martínez (*et al.*, 1987; 1989, 2001) have associated the gradient in their abundance pattern with latitudinal temperature and humidity gradients across Western Europe.

1.3.3 Systematics at the (sub)-family level – a brief discussion

Evolution in lagomorphs is relatively slow and conservative. Formally defining groups at the (sub)-family rank may create a false sense of diversity at a high taxonomic level, while this is not reflected in the morphological diversity, in particular in comparison to other small-mammal families, such as in the rodents.

Von Brandt (1855) introduced the subordinal name Lagomorphi Brandt, 1855. Gidley (1912) later elevated the rank of this name in his definition of the order Lagomorpha, and separated it from the order Rodentia Bowdich, 1821, in which it had previously been included. The former suborder Duplicidentata Illiger, 1811, which previously comprised the lagomorphs, is currently used at a higher taxonomic level and also includes other, currently extinct groups (Asher *et al.*, 2005).

In this thesis, the genera *Prolagus* and *Lagopsis* are included in the family Ochotonidae, without using subfamily ranks, which is in accordance with previous use by de Bruijn & van Meurs (1967), Dawson (1967, 1969, 2008), López-Martínez (1974, 1984, 1989, 2001), Bucher (1982), McKenna (1982), McKenna & Bell (1997), Angelone (2008, 2009) and Angelone & Sesé (2009). Characteristics of the Ochotonidae are summarized by Dawson (2008).

Erbajeva (1988) argues that the genus *Prolagus* represents a separate family group next to Ochotonidae and formally proposes to elevate the subfamily name Prolaginae Gureev, 1960 to the family rank. In their contribution to the latest edition of Wilson & Reeder's (2005) comprehensive and widely used classification of extant mammals, Hoffmann & Smith (2005) follow this proposal, but erroneously refer to Prolagidae Gureev, 1964 instead of 1960. At the same time, however, Hoffmann & Smith (2005) list Prolaginae Gureev, 1960 with the synonymy of Ochotonidae. As Erbajeva *et al.* (2006) note, there is no general agreement on the use of Prolagidae. Dawson (1967) disagrees with Gureev (1964) in using Prolaginae. Similarly, McKenna & Bell (1997) neither follow Gureev (1960) nor Erbajeva (1988), and synonymize Prolaginae and Prolagidae with Ochotonidae. Averianov & Tesakov (1998) and Fostowicz-Frelik (2010) place *Prolagus* in Prolaginae and in Ochotonidae.

López-Martínez (2001) specifies the close resemblance between the osteology of extant pikas (*Ochotona*) and those of fossil *Prolagus* as has been shown by Dawson (1969). Secondly, López-Martínez (2001) points out the marked similarity between the preserved soft tissue shape of a late Miocene *Prolagus* from France (Mein *et al.*, 1983) and the characteristics of extant pikas, in particular the shape and size of the ears, the general body proportions, and the lack of a tail. The dental formula and the diagnosis given by Erbajeva (1988: 15) for Prolagidae include an M_3, a view that is shared by Fostowicz-Frelik (2010) who states that the M_3 merged with the M_2. The presence of an M_3 in the diagnosis is rather puzzling, since one of the typical characteristics of the genus *Prolagus* is the absence of this element. The posterior lobe in the M_2 has been shown to represent the hypoconulid (Tobien, 1975; Ringeade, 1979). The genera included in Prolagidae are not explicitly indicated, but two figures shown by Erbajeva (1988: 198-199, fig. 41-42) suggest inclusion of *Prolagus* and *Ptychoprolagus* Tobien, 1975, but possibly exclude the closely related genus *Piezodus* Viret, 1929, which also lacks an M_3. The remaining features mentioned for this family are considered non-diagnostic. It is not clear whether Erbajeva (1988) originally intended to define this family on the basis of the absence of the M_3. However, following the reasoning of López-Martínez (2001), we regard this alternative criterion insufficient as a basis for a pika family. Tobien (1974) has shown that the presence and the degree of development of the M_3 are variable within representatives of *Amphilagus*, in which evolutionary reduction has taken place. The M_3 is lost in *Piezodus* (Tobien, 1975).

Similarly, the tooth formula in (extant) Leporidae is not entirely stable either. The presence of the M^3 varies within the extant monotypic genus *Pentalagus* Lyon, 1904 (Corbet, 1983; Yamada, 2008). Robinson & Matthee (2005) have shown that *Pentalagus* is closely related to the other relatively derived leporid genera within the monophyletic family Leporidae on the basis of cytogenetic, morphologic and molecular data. Von Koenigswald (1995, 1996) has shown that the incisor enamel structure of *Prolagus* is comparable to that of other pikas. This clearly separates it from Leporidae and does not prohibit its inclusion in Ochotonidae. For these reasons, we refrain from using the family Prolagidae next to Ochotonidae and Leporidae as is proposed by Erbajeva (1988, 1994) and endorsed by Hoffmann & Smith (2005).

Averianov (2000) proposed the subfamily Lagopsinae Averianov, 2000 in the family Ochotonidae for the genera *Lagopsis* Schlosser, 1884, *Marcuinomys* Lavocat 1951, *Paludotona* Dawson 1959, *Alloptox* Dawson, 1961 and *Albertona* López-Martínez, 1986. Averianov (2000) indicates that some of the characteristics given in the diagnosis for this subfamily do not apply to all included genera. Systematic use of this subfamily therefore seems to be problematic, although López-Martínez (1986) has shown that these genera may be closely related. Erbajeva (1994; *et al.*, 2006) include these five genera in the subfamily Ochotoninae Thomas, 1897 with other, Asian genera. In accordance with Dawson (2008), we will not use the subfamily rank.

CHAPTER 2

Systematics of resident species of *Lagopsis* and *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) from the late early and middle Miocene of north-eastern Central Spain

Kees Hordijk & Albert J. van der Meulen

2.1 Abstract

The evolution of the pika lineages *Prolagus vasconiensis-tobieni* and *Lagopsis penai-verus* during the late early Miocene to early late Miocene are described and reviewed on the basis of previously undisclosed material from the rich small mammal record from the Daroca-Villafeliche area in the Calatayud-Montalbán Basin.

Chronospecies recognized within these two lineages are refined, resulting in the definition of a new species, *Prolagus lopezmartinezae* n. sp., which represents a distinct endemic intermediate stage in the evolution of the lineage leading to *Prolagus tobieni* López, 1977.

The first occurrence of *Prolagus lopezmartinezae* n. sp. in the late Ramblian marks the beginning of endemic evolution in this lineage on the Iberian Peninsula. The exact timing of the anagenetic evolution to its the late Aragonian successor during the middle Aragonian could not be more narrowly constrained due to the rarity of this lineage in the study area in this time interval.

The *Lagopsis penai-verus* lineage shows a continuous presence throughout the late Ramblian and early late Aragonian, but declines strongly and ultimately disappears from the fossil record in the late Aragonian. This lineage, which is found throughout Western Europe, is characterized by a distinct shift in the proportion of P_3 morphotype frequencies that distinguishes *L. penai* Royo, 1928 from *L. verus* (Hensel, 1856) in the upper part of Iberian mammal zone Dd. In regions outside Spain the timing of this morphological transition is not yet precisely known.

The diagnoses of the genera *Lagopsis* Schlosser, 1884 and *Prolagus* Pomel, 1853 are emended on the basis of the new assemblages and revised published data. We propose to surpress the use of (sub)-family names Prolagidae Gureev, 1960 and Lagopsinae Averianov, 2000.

2.2 Introduction

Extensive research on Neogene mammals from the Daroca-Villafeliche area in the Calatayud-Montalbán Basin area that has been progressing for the last five decades has yielded a database comprising several tens of thousands of small-mammal teeth collected from over 100 mammal localities (Daams *et al*. 1999a). Previous work on the Ochotonidae from this area has been done by de Bruijn & van Meurs (1967) and López-Martínez (1977, 1989), but the bulk of the available material has until now remained unstudied and undescribed. The rich and well dated succession in the study area provides the opportunity to recognize and constrain evolutionary stages lineages more precisely, which is of significance for the definition of chronospecies and may be of value for biostratigraphy.

The objective of this paper is to deliver a detailed overview of the evolution of the early and middle Miocene *Lagopsis penai-verus* and *Prolagus vasconiensis-tobieni* lineages in Spain and is therefore focused on 1) re-evaluation of the existing taxonomy of these lineages, and 2) providing updated descriptions of the involved species based on the extensive new material. For this purpose, a selection of 40 localities with representative material from Iberian local biozones A to H (MN3-MN9) is used. This selection also includes ochotonid material from five previously published assemblages (de Bruijn & van Meurs, 1967; López-Martínez, 1977, 1989), which provide a reference for the new material and in which previously undescribed material is included.

Early representatives of the two lineages in question are already present in deposits of late Ramblian (early Miocene) age in the region (López-Martínez, 1984). They continue their stratigraphic range in the Aragonian for several million years. During the Aragonian other pika lineages immigrated into the basin area as well, whose systematics and evolution will be described in a separate paper (Chapter 3).

Prolagus Pomel, 1853 and *Lagopsis* Schlosser, 1884 are the most commonly found pika genera in mammal assemblages from the late early and middle Miocene of West-central and Southwestern Europe. Earlier work on these genera from this region and time interval has been done, among others, by Major (1899), Tobien (1963, 1975), de Bruijn & van Meurs (1967), López-Martínez (1974, 1977, 1984, 1988, 1989, 1997, 2001), López-Martínez & Thaler (1975), López-Martínez *et al.* (1977), Ringeade (1979), Huin (1979), Bucher (1982) and Angelone (2009). Both genera have been very successful, but *Prolagus* is distinctly richer in species, represents numerous evolutionary lineages, and is widely distributed throughout Europe and ultimately some parts of North Africa (López-Martinez, 2001). *Lagopsis*, on the other hand, shows a very different evolutionary pattern, being represented by an apparently single lineage. It has had a wide geographic distribution throughout Western Europe, but not as widespread as *Prolagus*, not having reached North Africa and the more eastern parts of Europe. A more detailed overview of their phylogenetic affinity and paleobiogeography is given in Chapter 4.

2.3 Material and methods

2.3.1 Repositories

The material studied is stored in the research collections of the following institutes.

IVAU: Instituut voor Aardwetenschappen Utrecht (Institute of Earth Sciences Utrecht), Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands.

MNCN: Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences), Department of Paleobiology, Madrid, Spain.

NCBN: Netherlands Centre for Biodiversity Naturalis (National Museum of Natural History Naturalis), Leiden, the Netherlands.

2.3.2 Sample treatment

The sediment containing the fossil material has been screen washed in the field using the basic sieve setup described in Daams & Freudenthal (1988b) with some improvements that have been implemented since. The residue was treated with acetic acid and wet sieved in the laboratory to remove the remaining carbonate matrix. The vertebrate fossil material was sorted manually from the siliciclastic residue aided by a binocular.

2.3.3 Material

The P_3, P^2 and P^3 are markedly the most distinctive elements for the studied pika lineages and are, with the exception of the P^2 in the time interval under consideration, usually diagnostic to the species level. The remaining upper and lower cheek teeth (P^4-M^2, P_4-$M_{2/3}$) can, the P_4 and M_1 excluded, be distinguished at the genus level, but are generally not or only slightly distinctive at the species level. Therefore these cheek teeth are not studied in detail for the purpose of this paper. Some relevant information is provided in the descriptions of the species. Angelone & Sesé (2009) suggest some additional measures for these elements that might provide taxonomic information in the absence of diagnostic teeth.

New ochotonid material is described from all 40 assemblages, 35 of which were previously undescribed. The repository of included specimens and the material of the other ochotonid lineages present in the assemblages are indicated in Table 2.1.

Material from five assemblages included in this study has been published by de Bruijn & van Meurs (1967) and López-Martínez (1977, 1989). These assemblages have been completed with previously unstudied material from the original samples. The *Lagopsis verus* material from Manchones is used as comparative material only, since its large collection has been extensively studied in previous publications. The locality of Armantes 7, which is not from the Aragonian type area (Daams *et al.*, 1977; Krijgsman *et al.*, 1994), has been included on the basis of the biostratigraphic value of the small mammal fauna. Part of its assemblage has been described earlier (López-Martínez, 1989) and the remainder of the material is included here.

Deciduous teeth are relatively well represented in the available assemblages. It is currently not yet possible to assign these elements to one of the four different lineages present in the study area with any reasonable degree of certainty. The total number of deciduous teeth present in the assemblages is indicated in Table 2.1.

2.3.4 Measurement technique

Tooth size measurements have been taken using a Reflex Microscope. A series of size measures has been defined for each of the diagnostic elements (i.e. P_3, P^2 and P^3) in order to capture changes in size and shape, and to include damaged specimens that miss a particular part of their original structure (Fig. 2.1). The Reflex Microscope measures distance coordinates. Tooth size measures are calculated from distances between predefined coordinates. All coordinates for a specimen are measured in a single run to ensure that the length and width measures are at right angles and to ensure that all measures correspond to exactly the same orientation of the specimen.

The tables showing measurements and morphological counts only include fully erupted teeth of young adults and older individuals. Teeth of unworn or very slightly worn juvenile specimens are excluded, because they strongly deviate from the general morphology and size.

Grayscale picture images are compiled from stacked images using a Leica MZ 16 FA stereomicroscope with a Leica DFC 420 C digital camera.

2.3.5 Nomenclature

The nomenclature of lagomorph tooth morphology employed here (Fig. 2.1) generally follows the descriptive terminology of López-Martínez (1974, 1989), Angelone (2007) and Angelone & Sesé (2009), but with several modifications.

Table 2.1: A listing of the analyzed assemblages. A: Locality names, repository, age estimates from Daams *et al.* (1999a) and van Dam *et al.* (2006), and the number of P^2, P^3 and P_3 specimens of the studied lineages. In case of two repository institutions, the first holds the original or largest collection. B: Total number of P^3, P_3, and deciduous teeth of all Ochotonidae along with the number of species present in the assemblages. The references indicate earlier publications on part of the assemblages under consideration: 1. de Bruijn & van Meurs (1967); 2. López-Martínez (1977); 3. López-Martínez (1989). Asterisk footnotes: * Included for comparative purposes. Additional material of *P. tobieni* has been included in the analysis; ** From outside the Aragonian type area, in the vicinity of the Armantes sections (Krijgsman *et al.*, 1994); *** Scanty material. The taxon is identified by other teeth than the P^3 or P_3; **** Comparative material. The original collection has been described by Mein (1958) and is stored at the Centre des Sciences de la Terre of the Université Claude Bernard Lyon 1.

A

Locality name	Locality code	Repository	MN zone correlation	Iberian local zone	Age (Daams *et al.* 1999)	Age (van Dam *et al.* 2006)	*L. penai* *L. verus*			*P. lopezmartinezae* n. sp. *P. tobieni*		
							P2/	P3/	p/3	P2/	P3/	p/3
Carrilanga 1	CAR1	NCBN	9	H	10,50	11,57				5	5	8
Nombrevilla 1	NOM1	IVAU	9	H	11,00	10,76					1	
Solera	SOL	NCBN	7/8	G3	11,75	12,01	7	11	15	26	42	43
Paje 2	PJE2	MNCN	7/8	G3	12,17	12,20				1	1	
Toril 3B	TOR3B	MNCN	7/8	G3	12,59	12,11	15	5	13	22	20	33
Toril 3A	TOR3A	MNCN	7/8	G3	12,60	12,12	1		1	25	24	25
Toril 1	TOR1	NCBN	7/8	G3	12,62	12,14		11	7		1	3
Borjas	BOR	NCBN	6	G2	13,20	13,26	5	5	7			
Manchones*	MAN	IVAU	6	G2	13,25	13,31	n.a.	198	283		3	5
Valalto 1B	VT1B	NCBN-MNCN	6	G1	13,30	13,36	2	6	5			
Valalto 1A	VT1A	MNCN	6	G1	13,35	13,41		10	14		2	2
Las Planas 5B	LP5B	NCBN-MNCN	6	G1	13,47	13,56	7	22	26			
Armantes 7**	ARM7	IVAU	6	F			18	18	31			
Valalto 2C	VT2C	NCBN	6	F	13,68	13,74	14	58	31		2	
Las Umbrias 22	LUM22	MNCN	6	F	13,73	13,76	4	10	7			
Las Planas 4BA	LP4BA	MNCN	5	E			4	13	8		1	1
Las Planas 4A	LP4A	IVAU-NCBN	5	E	13,96	13,98	19	36	27			
Las Umbrias 12	LUM12	MNCN	5	E	14,01	14,03	2	18	9			
Las Umbrias 10	LUM10	MNCN	5	Dd	14,07	14,09	3	12	7			
Las Umbrias 9	LUM9	MNCN	5	Dd	14,16	14,18	10	14	12			
Las Umbrias 3	LUM3	MNCN	5	Dd	14,37	14,37	9	30	17			
Valdemoros 3F	VA3F	MNCN	5	Dd	14,52	14,50	15	18	16	1	2	
Valdemoros 1A	VA1A	IVAU-NCBN	5	Dd	14,64	14,61	17	41	30			
Valdemoros 3B	VA3B	IVAU-MNCN	5	Dc	14,85	14,84	19	49	35			
Vargas 5	VR5	MNCN	5	Dc	15,32	15,32	10	45	39		2	2
La Col D	COL-D	MNCN	5	Db	15,87	15,84		9	11		1	
Fuente Sierra 3	FTE3	MNCN	5	Da	15,92	15,88	5	11	7			
Fuente Sierra 2	FTE2	MNCN	5	Da	15,93	15,89	2	11	6			
Olmo Redondo 9	OR9	NCBN	5	Da	15,95	15,91	6	13	14			
Vargas 2B	VR2B	MNCN	5	Da	15,96	15,92	2					
Vargas 2A	VR2A	MNCN	4	Cb	15,98	15,94	1	7	8			
Olmo Redondo 8	OR8	NCBN	4	Cb	15,99	15,95	9	8	10			
Vargas 1A	VR1A	NCBN	4	Cb	16,14	16,11	10	14	14		1	1
Vargas 4BB	VR4BB	MNCN	4	Cb	16,15	16,12	14	25	19		1	
Vargas 4A	VR4A	MNCN	4	Cb	16,18	16,15	6	35	18			
San Roque 3	SR3	MNCN	4	Ca	16,35	16,33	27	30	34		1	2
Villafeliche 2A	VL2A	IVAU	4	B	16,64	16,63	33	61	45	2	2	2
San Marcos	SAM	MNCN	4	B	16,70	16,69	82	84	98	14	26	28
Olmo Redondo 2	OR2	NCBN	4	B	16,73	16,72	32	71	59	5	13	2
San Roque 4A	SR4A	MNCN	3	A	17,02	17,00	7	26	22	4	6	12
Vieux-Collonges		IVAU****	4-5					9	10			

B

Locality code	*L. penai* *L. verus*	*P. lopezmartinezae* n. sp. *P. tobieni*	Other Ochotonidae	# deciduous teeth Ochotonidae	# species Ochotonidae present	References
	P3/ + p/3	P3/ + p/3	P3/ + p/3			
CAR1		13	300	10	2	
NOM1		1	17	3	2	1, 3
SOL	26	85	151	31	3	
PJE2		1	18	13	2	
TOR3B	18	53	13	42	3	
TOR3A	1	49	14	22	3	
TOR1	18	4	21	5	4	
BOR	12		23	2	2	
MAN	481	8	342	48	4	1, 2, 3
VT1B	11		10	4	3	
VT1A	24	4	10	19	4	
LP5B	48		30	23	3	
ARM7	49		11	5	2	1, 3
VT2C	89	2	9	6	3	
LUM22	17		11	4	2	
LP4BA	21	2	14	7	3	
LP4A	63		3	22	2	1, 3
LUM12	27		4	17	2	
LUM10	19		2	4	2	
LUM9	26		1	3	2	
LUM3	47		1	2	2	
VA3F	34	2		6	2	
VA1A	76			7	1	
VA3B	84	***0.5		24	2	
VR5	84	4	***0.5	3	3	
COL-D	20	1			2	
FTE3	18		3	3	2	
FTE2	17		12	5	2	
OR9	27		3	1	2	
VR2B	***0.5		2		2	
VR2A	15		1	3	2	
OR8	18		2	6	2	
VR1A	28	2	11	7	3	
VR4BB	44	1	8	4	3	
VR4A	53		9	2	2	
SR3	64	3		12	2	
VL2A	106	4		14	2	1, 3
SAM	182	54		14	2	
OR2	130	15		3	2	
SR4A	48	18		3	2	

In the P_3 of *Piezodus* Viret, 1929 and primitive *Prolagus* the protoconulid is either absent, incipient or very small. This results in the presence of only one main flexid on the antero-labial side. We consider this flexid to be the protoflexid, which is in agreement with López-Martínez (1986). In advanced *Prolagus*, López-Martínez (1989) denotes an anteroflexid and a protoflexid between the anteroconid and protoconid on the labial side of the P_3. These inflexions are separated by a protoconulid.

However, in our opinion the anteroflexid is a structure that is formed on the antero-labial side of the anteroconid in the P_3 and D_3, which is in agreement with the D_3 shown by Angelone (2007) and Angelone & Sesé (2009). In derived *Prolagus*, the protoconulid has expanded in the original protoflexid, thus dividing it in two parts. We name these two flexids protoflexid 1 and 2, respectively (Fig. 2.1). Additionally, the protoflexid of Angelone (2007) and Angelone & Sesé (2009) is the hypoflexid in our interpretation.

The centroflexid is an internal extension of the paraflexid (López-Martínez, 1986, 1989; Angelone, 2007). In our opinion, the metaflexus indicated by López-Martínez (1986) and the metafossette indicated by Angelone (2007) in upper cheek teeth are the mesoflexus and mesofossette, respectively, which is in agreement with López-Martínez (1974, 1989) and Angelone & Sesé (2009).

López-Martínez (1974) introduced the term isthmus to describe various narrow connections betweed cuspids in the P_3. For reasons of consistency, we choose to modify this term to isthmid, since it applies to a lower tooth.

We prefer the term anterolophid, used by López-Martínez (1989), over labial anteroisthmus, employed by López-Martínez (1974). The lingual anteroisthmus of López-Martínez (1974) is thus the anteroisthmid in our scheme. We consider the lagiloph in the D_3 of Angelone (2007) to be an incipient protoconulid with an anterolophid. The centroisthmus in the D_3 indicated by Angelone (2007) and Angelone & Sesé (2009) is equivalent to the protoisthmid in the P_3 as shown by López-Martínez (1974, 1989), Angelone (2007) and Angelone & Sesé (2009).

2.3.6 Morphological trends

A general evolutionary trend that is observed in Oligocene and Miocene European lagomorphs involves molarizaton of the premolars, presumably increasing the chewing efficiency of the tooth row. The degree of molarization in the deciduous teeth is more advanced compared to the adult teeth (Tobien, 1986). The shapes of the P_4 and P^4 are basically similar to those of the molars. The P_3 does not show molarization, while such a trend, although incomplete, is present in the P^3. Its mesial hyperloph is lengthened and folds over the lagicone toward the labial side. The degree of molarization of the P^3 differs between genera. A triangular shaped P^3 is less molarized compared to that of a trapezoid P^3.

A second general evolutionary trend is the reduction of labial enamel inflexions and fossettes in upper cheek teeth. Although reduction is more progressive toward the posterior end of the tooth row, the loss or reduction of these structures is independent from the process of molarization, because enamel inflexions and fossettes are present in both molars and premolars of stem lagomorphs. Contrary to the labial inflexions, the hypoflexus tends to deepen over time, which is more progressive in the posterior teeth.

The recognition of chronospecies and their transitions within ochotonid lineages are to a large extent based on statistical observations of morphologies, as has been described by López-Martínez (1984; *et al.*, 1987). The anagenetic evolution of these lineages is usually characterised by a frequency shift in the presence of distinctive characteristics between two chronospecies, while the morphotypes under consideration can be present in the total variability range of both. Species assignments based on small assemblages are consequently provisional or impossible. Although species assignment is obscured by limited material, assignment to an evolutionary lineage may, on the other hand, be possible with high confidence, provided that the characterizing features are

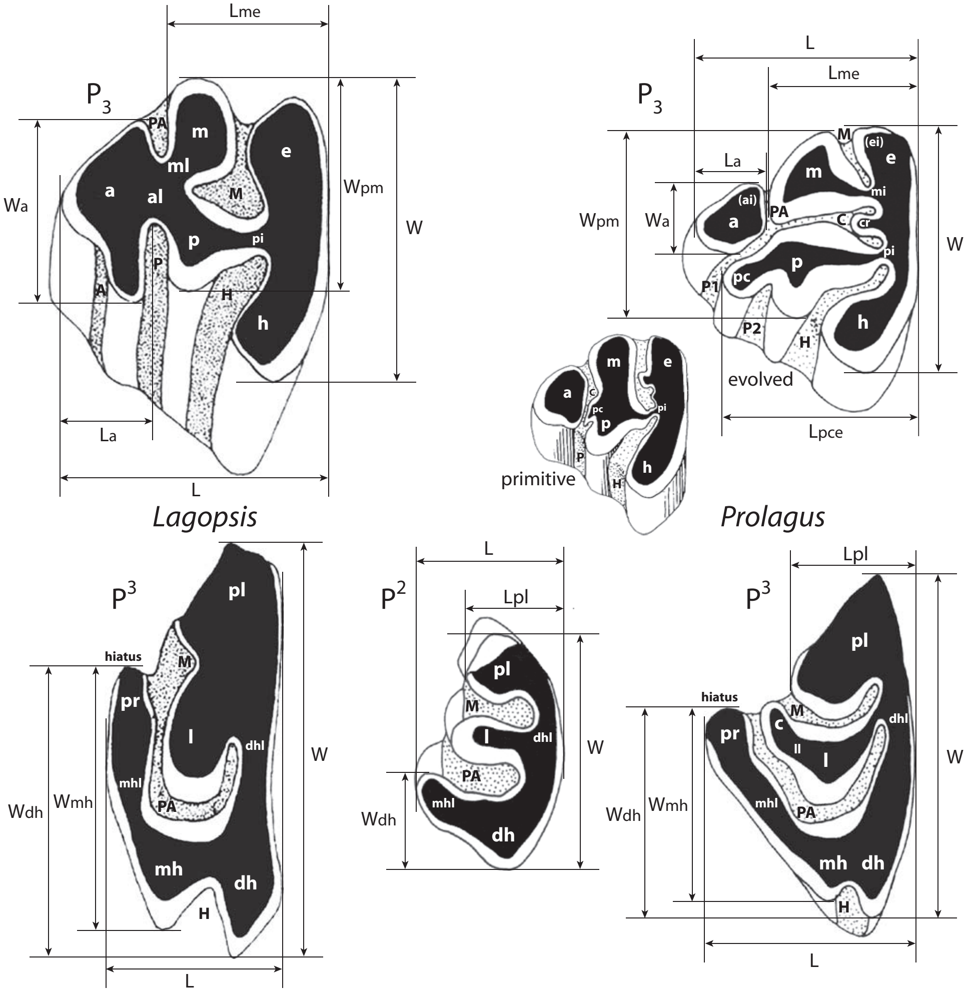


Figure 2.1: Nomenclature and size measurements for ochotonid teeth. The nomenclature generally follows the descriptive terminology of López-Martínez (1974, 1989), with some modifications (see text). The two *Prolagus* P$_3$'s represent primitive and derived forms. Tooth cusps and lophs (white letters). a: anteroconid; p: protoconid; m: metaconid; h: hypoconid; e: entoconid; pc: protoconulid; cr: crochet; al: anterolophid; ml: metalophid; mi: metaisthmid; ai: anteroisthmid; ei: entoisthmid; pi: protoisthmid; l: lagicone; ll: lagiloph; c: centrocone; pr: precone; pl: postlobus; mh: mesial hypercone; dh: distal hypercone; mhl: mesial hyperloph; dhl: distal hyperloph. Inflexions (black letters). A: anteroflexid; PA: paraflexus/-id; P: protoflexid (1 & 2); M: mesoflexus/-id; H: hypoflexus/-id; C: centroflexid. Fossettes represent closed equivalents of inflexions. Tooth size measurements. L: length; W: width; La: a length; Wa: a width; Lme: m-e length; Lpce: pc-e length; Wdh: pr-dh width; Wmh: pr-mh width. Tooth drawings are modified after López-Martínez (1988, 1989) and Álvarez Sierra *et al.* (1991).

preserved. In such a case we will use Drooger's (1952, 1993) designation *exemplum intercentrale* (ex. interc.) to indicate that identification at the species-level is unresolved and that the material belongs to either one of the two optional chronospecies given.

2.4 Systematic paleontology

The abbreviations used in the listing of synonymy follow Matthews (1973): v indicates material studied by the author; (v) designates material documented by good and expressive drawings or photos; vp denotes material studied by the author of which a part belongs to the species under consideration; the publication date in italics indicates that the taxon is only mentioned without further description or illustration; a point. marks an assignment with high confidence;? indicates a degree of uncertainty in the assignment; an asterisk * denotes the first description of a taxon to which the assignment of the specimens refer.

ORDER LAGOMORPHA BRANDT, 1855
FAMILY OCHOTONIDAE THOMAS, 1897

We refrain from using the family Prolagidae GUREEV, 1960 next to Ochotonidae and Leporidae FISCHER, 1817 as is proposed by Erbajeva (1988, 1994) and endorsed by Hoffmann & Smith (2005) (see Chapter 1). Likewise, we propose to subdue Lagopsinae AVERIANOV, 2000.

GENUS *LAGOPSIS* SCHLOSSER, 1884

* 1884 *Lagopsis* SCHLOSSER, 1884: 13, Schlosser
(v). 1899 *Lagopsis* SCHLOSSER, 1884: 460, Major
. *1941 Opsolagus* KRETZOI, 1941: 350, Kretzoi
. 1947 *Lagopsis* SCHLOSSER, 1884: 369, De Villalta & Crusafont Pairó
1955 *Heterolagus* CRUSAFONT, VILLALTA & TRUYOLS 1955: 146, Crusafont *et al.*
. 1958 *Lagopsis* SCHLOSSER, 1884: 60, Mein
v. 1967 *Lagopsis* SCHLOSSER, 1884: 118, De Bruijn & Van Meur.
1982 *Lagopsis* SCHLOSSER, 1884: 48, Bucher
(v). 1984 *Lagopsis* SCHLOSSER, 1884: 36, López-Martínez
(v). 1989 *Lagopsis* SCHLOSSER, 1884: 159, López-Martínez

TYPE SPECIES
Lagomys verus HENSEL, 1856, collected by Quenstedt from limonite rich deposits in Baden-Württemberg, "Bohnerzen der Schwäbischen Alp", Germany. Schlosser (1884) refers to the Molasse von Althausen for the origin of Hensel's *L. verus* material.
AGE
Middle Miocene.
ORIGINAL DIAGNOSIS
No formal diagnosis is given by Schlosser (1884: 13-14), but rather a description and comparison. Schlosser (1884) introduced *Lagopsis* as a subgenus of *Lagomys* CUVIER 1798. In modern literature

(McKenna & Bell, 1997; Hoffmann & Smith, 2005) *Lagomys* is listed with the synonymy of *Ochotona*.

Previous Emended Diagnosis

Bucher (1982): "Ochotonidé de taille intermédiaire entre *Amphilagus* et *Prolagus*. Courbure et torsion des dents jugales supérieures plus fortes que chez *Prolagus*, avec perte des structures archaïques (regression puis perte des mésoflexus et paraflexus, extension de l'hypoflexus). P^3 trapézoïdale. Hypoflexus très développé et cement parfois présent sur la face vestibulaire de P^4, M^1 et M^2. Dents jugales supérieures plus hypsodontes que chez *Marcuinomys*. Dents jugales inférieures complétement hypsodontes. P_3 trilobée, plus longue que chez *Marcuinomys*, avec antéroconide bien individualisé mais jamais isolé comme chez *Prolagus*. Persistance d'une M_3 unilobée."

Previous Emended Diagnosis

López-Martínez (1989): "Fórmula dentaria: 2/1, 0/0, 3/2, 2/3, Ochotonidae de talla media a grande. P^4 molariform. Ausencia de lagilofo en P^3. Sin fosetas en los dientes molariformes. P_3 provisto de anterocónido, siempre unido al protocónido. M_3 simple, unilobulada."

Emended Diagnosis

Tooth formula: (2, 0, 3, 2)/(1, 0, 2, 3). Ochotonid of moderate size having rootless and hypsodont teeth. The mesoflexus and paraflexus in the P^2 are distinct. The P^3 is trapezoidal shaped and lacks a lagiloph. Its hypoflexus is shallow and wide. The P^4 is molariform and the P^4-M^2 of fully adult specimens lack enamel fossettes. The hypoflexus in the P^4-M^2 is deep and is progressively deeper in the posterior elements. The P_3 has an anteroconid that is connected to the protoconid. The metaconid is usually connected to the protoconid and anteroconid, but may be isolated. The mesoflexid is well developed. It is generally wider interiorly, where its anterior end is usually more developed than the posterior. The lower molariform cheek teeth consist of two separate lobes that are connected with crown cement, and lack a hypoconulid. The M_3 is a single pillar.

Differential Diagnosis

Lagopsis differs from *Marcuinomys* Lavocat, 1951 by being rootless and lacking rudimentary enamel fossettes in fully adult molariform upper teeth. The centroflexid observed in the P_3 of *Albertona* López-Martínez, 1986 and *Alloptox* Dawson, 1961 is not present in *Lagopsis*. The mesoflexus in P^2 of *Albertona* is very shallow. *Paludotona* Dawson 1959 is larger, its P^2 has a very weak or absent mesoflexus and in its P_3 the paraflexid is absent. *Prolagus* differs in having an isolated anteroconid in the P_3 and in having a three-lobed M_2, which includes a hypoconulid, while lacking an M_3. The torsion and curvature of the P^4-M^2 are less strong compared to those of *Lagopsis*. These upper cheek teeth of adult *Prolagus* commonly have residual enamel fossettes, unlike those of *Lagopsis*. *Ptychoprolagus* Tobien, 1975 differs on the same characteristics as *Prolagus*, but also in having complex enamel crenulations that are absent in *Lagopsis*. The genera *Titanomys* Von Meyer, 1843, *Piezodus*, *Eurolagus* López-Martínez, 1977 and *Gymnesicolagus* Mein & Adrover, 1982 have rooted teeth and may have (residual) enamel fossettes in fully grown P^4-M^2. The lower molariform teeth of the latter genus have a hypoconulid, which is absent in *Lagopsis*.

Remarks

We consider the hypselodonty of *Lagopsis* an important diagnostic feature at the generic level representing a distinct stage in evolution and chose, therefore, to expand the diagnosis of López-Martínez (1989). Additionally, the morphology of the P^2 is added as a distinctive characteristic.

The genus *Lagopsis* is generally thought to have evolved in Europe from the early Miocene genus *Marcuinomys* (Bucher, 1982; López-Martínez 1984, 1989). The generic assignment of species in the transition phase between these genera has been subject to discussion. López-Martínez (1984) reassigned the species *spiracensis* Baudelot & Crouzel 1974 to the genus *Marcuinomys*. This species was originally described as a subspecies of *Lagopsis penai* (Royo, 1928) and later raised to the species level (Díaz Molina & López-Martínez 1979; Bucher 1982). The reassignment of *spiracensis* and, subsequently, the transition between the genera *Marcuinomys* and *Lagopsis* remains to be resolved, but is beyond the scope of this study, since it precedes the studied time interval. The emended diagnosis provided here may therefore require further emendation in the future, in particular with regard to the presence and persistence of rudimentary enamel fossettes in the upper cheek teeth.

Lagopsis penai (Royo, 1928)

* 1928 *Lagomys penai* Royo, 1928:39, from Alcalá de Henares, *in* Royo Gómez
1930 *Lagopsis cadeoti* Viret, 1930: 589, from Estrepouy, *in* Roman & Viret.
1934 *Lagopsis cadeoti* Viret, 1930: 26, from Estrepouy, *in* Roman & Viret.
1947 Lagopsis penai (Royo, 1928): 369, from Alcalá de Henares, *in* de Villalta & Crusafont Pairó
? 1955 *Heterolagus albaredae* Crusafont, Villalta & Truyols, 1955: 146, from Molí Calopa, *in* Crusafont *et al.*
. 1958 *Lagopsis* cf. *penai* (Royo, 1928): 60, from Vieux-Collonges, *in* Mein
v. *1967 Lagopsis penai* (Royo, 1928): 205-210, from Ateca 1 & 3, Armantes 1 & 3, Munebrega 1 & 3, Torralba 1, *in* de Bruijn
v. 1967 *Lagopsis penai* (Royo, 1928): 118, from Ateca 3, Villafeliche 2A, Valdemoros 3B & Munebrega 1, *in* de Bruijn & van Meurs
1972 *Lagopsis verus* (Hensel, 1856): 311, from Vermes *in* Engesser
v. *1977 Lagopsis penai* (Royo, 1928): 49 & 51 & 53, from Villafeliche 2A, Valdemoros 3B, Ateca 1 & 3, Valtorres 1, Munebrega 1, Torralba 1 & Armantes 1 & 3, *in* Daams *et al.*
1981 *Lagopsis verus* (Hensel, 1856): 912, from Vermes 1 & 2, *in* Engesser *et al.*
1982 *Lagopsis cadeoti* Viret, 1930: 50, from Estrepouy, *in* Bucher
(v). 1984 *Lagopsis penai* (Royo, 1928): 36, from Moratilla 1, Bañon 2 & 11, *in* López-Martínez
v. 1989 *Lagopsis penai* (Royo, 1928): 159, from Villafeliche 2 & 4 & Ateca 3, *in* López-Martínez
1992 *Lagopsis verus* (Hensel, 1856): 159, from Hüllistein, *in* Bolliger
1993 *Lagopsis penai* (Royo, 1928): 141, from Vermes 1, *in* Kälin
1993 *Lagopsis verus* (Hensel, 1856): 141, from Vermes 2, *in* Kälin
1997 Lagopsis penai (Royo, 1928): 530, Table 2, from Buchberg, *in* Kälin
1997 Lagopsis penai-verus transitional form: 530, Table 2, from Hubertingen, Eiboden, Vermes 1 & 2, *in* Kälin
1997 Lagopsis verus (Hensel, 1856): 530, Table 2, from Oberkulm-Sämlen, Hüllistein, Hotwiel & Froberg, *in* Kälin
2009 *Lagopsis verus* (Hensel, 1856): 1782, from Untereichen-Altenstadt 540m & 565m, *in* Prieto *et al.*
. 2009 *Lagopsis* cf. *penai* (Royo, 1928): 71, from Sandelzhausen, *in* Angelone *et al.*
2009 *Lagopsis* cf. *penai* (Royo, 1928): 252, from Oggenhausen 2, *in* Böttcher *et al.*

TYPE SPECIES

Lagomys penai Royo 1928, from Alcalá de Henares, Madrid Basin, Spain.

AGE

MN4, Early Miocene.

ORIGINAL DIAGNOSIS

"Semejante a *L. verus* (Hensel, 1856) de La Grive, pero de mucho menor tamaño; P^3 es más estrecho por delante, con los senos más pronunciados y con los lóbulos externos más cortos, mientras que los internos están muy extendidos. El último molar es también más anguloso." (Royo Gómez, 1928, *in* López-Martínez 1989).

PREVIOUS EMENDED DIAGNOSIS

López-Martínez (1989): "*Lagopsis* de talla pequeña, con P^4 sin molarizar completamente, con hipoflexo incompleto en M^{1-2}, con anterocónido y metacónido reducidos en P_3."

EMENDED DIAGNOSIS

Lagopsis of relatively small to medium size. Enamel fossettes are completely absent in slightly worn and worn P^4-M^2, but may be briefly present in juvenile individuals. The hypoflexus in P^4-M^2 is deep, but not reaching the labial side of the tooth. The anteroconid in P_3 is well developed and larger than the metaconid in a majority of specimens, but simple in shape, being rounded, oval or triangular. A distinct anteroflexid in the anteroconid is often absent. Shallow or more distinct anteroflexids may be present in the assemblage. A deep anteroflexid with cement is always less frequently present than an anteroconid without a distinct anteroflexid.

DIFFERENTIAL DIAGNOSIS

Lagopsis penai differs from the Ramblian *Lagopsis* aff. *penai* (as listed by López-Martínez 1984) in having a well developed anteroconid in P_3 that is larger than the metaconid ("type C" *in* López-Martínez, 1984), instead of a small anteroconid. *L. penai* is different from *Lagopsis verus* (Hensel, 1856) in the structure of the anteroconid in its P_3. In *L. verus* a distinct anteroflexid with cement in the anteroconid of P_3 is present more frequently than P_3's lacking a distinct anteroflexid, which is opposite to *L. penai*. The occlusal area or wear surface of the P_3 appears to be slightly less developed in *L. penai* compared to *L. verus*. *L. penai* teeth appear somewhat less robust. Although there is significant size overlap, *L. verus* can be slightly larger than *L. penai*.

MATERIAL AND MEASUREMENTS

The material analysed is indicated in Table 2.1. Quantified morphological features are summarized in Table 2.2 & 2.3. Scatter diagrams of tooth sizes are shown in Figs. 2.2-2.4. Summarized measurements are listed in Appendices 2.A1-2, 2.B1-2 and 2.C. Photographed specimens are shown in Plates 2.1-2.2.

DESCRIPTION

P^2 (Plate 2.2): The paraflexus and mesoflexus are narrow and oblique, with their apices pointing in a postero-labial direction. The lagicone is short, but well developed and may be similar in length to the hypercone. A mesial hyperloph is absent. In a few anomalous specimens, however, a distinct accessory cusp is present, which is positioned anterior to the lagicone. The antero-labial side appears compressed. The postlobus is wedge-shaped and narrow. Its mesial tip is pointing in an antero-lingual direction. In the vast majority of specimens the hypercone length forms the most anterior part and determines the largest length of the P^2. In some specimens the postlobus is the most anterior part of the tooth. The lingual side of the hypercone is usually smooth, lacking a hypoflexus or incipient hypoflexus, but in some cases a weak inflexion or shallow groove is present (Table 2.3). The shape of the distal hyperloph varies, being rather straight or being curved near the lagicone where the hypercone is bent in a more anterior position.

P^3 (Plate 2.2): The P^3 is slightly molariform, having a trapezoidal-like shape instead of a triangular shape. Its mesial hyperloph is more or less parallel to the distal hyperloph and the precone reaches to the position of the mesoflexus. The mesial hyperloph is generally thickest in its center part. It is slightly compressed close to the mesial hypercone due to the presence of the paraflexus. Its labial endpoint or precone is mostly of similar thickness or is slightly compressed. In some cases the thickest part of the mesial hyperloph is the labial endpoint, thus showing a distinctly developed precone (Table 2.3). The paraflexus is well developed in a distinct J-shape. Its lingual portion consists of relatively straight parts that are connected by two sharp bends. A very shallow mesoflexus is present in the vast majority of specimens (Table 2.3), marking the distinction of the lagicone and the postlobus. The mesoflexus is developed as a straight inflexion that points toward the posterior in some, usually ontogenetically younger, specimens. On a few occasions, mostly with large and more worn specimens, the mesoflexus is absent. The hypoflexus is distinct, but shallow and wide, and clearly separates the distal and mesial hypercones. Crown cement is present in the para-, meso- and hypoflexus, but is not always preserved in the latter two due to poor preservation. The lagicone is large and oval, and lacks a lagiloph and centrocone. It is oriented in a lingual to slightly antero-lingual direction. The postlobus usually extends widely on the labial side. It is damaged in many specimens. The P^3 becomes wider with wear, which is due to the lateral curvature of the tooth (Fig. 2.3 D-E).

P^4-M^2: The mesoflexus and paraflexus are absent, except in unworn or very slightly worn specimens of young adults, in which shallow remnants of these structures may still be visible. The hypoflexus is deep, but does not reach the labial side of the molar. The P^4-M^2 are very much alike and their distinction in isolated teeth is generally difficult. The P^4 is usually slightly wider than the M^1 and M^2, and the anterior lobe of the M^2 can be wider than its posterior lobe.

P_3 (Plate 2.1): The anteroconid is well developed and is generally wide and roughly triangular in shape. In the assemblages from zones A to Ca, a simple diamond shaped anteroconid is observed in several specimens. The paraflexid and protoflexid are generally well developed and mark the separation between the anteroconid and the proto- and metaconid. The anteroconid is larger than the metaconid in the vast majority of adult specimens (Table 2.2). The anteroconid tends to be slightly narrower in ontogenetically younger than in older specimens. It is always connected to the protoconid by the anterolophid and is usually connected to the metaconid, forming a triple junction. In a few specimens, both ontogenetically young and older specimens, the metaconid is isolated (Table 2.2). The mesial side of the anteroconid has a relatively variable shape. A wide but distinct anteroflexid may be present or absent on the antero-labial side. In some of the specimens with an anteroflexid, crown cement is present. The specimens lacking an anteroflexid or showing only a weak undulation are always more frequent than specimens with a cement-filled anteroflexid (Table 2.2). Besides normal variation within an assemblage, the ontogenetic stage plays a role as well. The rare specimens with a cement-filled anteroflexid are generally ontogenetically older individuals, while the ones with the simple anteroconids lacking anteroflexids usually represent younger individuals. Weak inflexions on the lingual side of the anteroconid are mostly absent, but may also be present, in which case they are very shallow and lack cement. The metaconid is relatively small and has a rounded rectangular to slightly oval shape. Its width is generally larger than its length and the metaconid represents the most lingual extension of the tooth. The entoconid and hypoconid form the posterior lobe that has more or less equal width. This lobe is slightly curved on its labial side, placing the hypoconid in a more anterior position compared to the entoconid. The protoisthmid, connecting the protoconid and the entoconid-hypoconid lobe is present in all specimens. With the exception of one specimen from VA3F that has a metaisthmid,

Table 2.2: Counted morphologies in the P_3 of *L. penai* and *L. verus*. Juvenile specimens are excluded.

p/3					Anteroconid				Anteroflexid			Protoconulid			Centroflexid			Crochet			Connections							Relative size		
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	(sub)round	ellipsoid	flattened/broad/triangular	diamond shaped	distinct with cement	distinct inflexion	absent/weak/incipient inflexion	absent	incipient/small	developed	absent	incipient/superficial	deep	absent	incipient/small	developed	metaconid isolated	anterolophid	metalophid	protoisthmid present	protoisthmid absent	metaisthmid	anteroisthmid	anteroconid < metaconid	anteroconid = metaconid	anteroconid > metaconid
7/8	G3	SOL	*L. verus*	15			13		2	8	3	15			15			15			1	15	14	15						13
7/8	G3	TOR3B	*L. verus*	9			9		3	6		9			9			9				9	9	9					1	8
7/8	G3	TOR3A	*L. verus*	1								1			1			1				1	1	1						
7/8	G3	TOR1	*L. verus*	5			5		4		1	5			5			5				5	5	5						5
6	G2	BOR	*L. verus*	7			5		1	2	2	7			7			7				7	7	7						5
6	G1	VT1B	*L. verus*	5			5		4			5			5			5				5	5	5						5
6	G1	VT1A	*L. verus*	14			13		9	3		12			14			14				14	14	14					1	10
6	G1	LP5B	*L. verus*	26			19		16	4		26			26			26				26	26	26					1	19
6	F	ARM7	*L. verus*	31			23		7	10	6	29			31			31				31	31	31		1			1	22
6	F	VT2C	*L. verus*	31			26		13	8	5	31			31			30	1			31	31	31		1	1		2	23
6	F	LUM22	*L. verus*	4	1		3		1	1	2	4			4			4				4	4	4				1		3
5	E	LP4BA	*L. verus*	8			7		7			8			8			8				8	8	8						6
5	E	LP4A	*L. verus*	27			21		12	8	4	27			27			27			1	27	26	26						21
5	E	LUM12	*L. verus*	9			7		4	2	2	9			9			9				9	9	9						6
5	Dd	LUM10	*L. verus*	7			6		3	2	1	7			7			7				7	7	7						6
5	Dd	LUM9	*L. verus*	11			7	1	5	1	1	11			11			11				11	11	11						8
5	Dd	LUM3	*L. penai*	15			10		1	4	6	13			15			14			1	15	14	14						11
5	Dd	VA3F	*L. penai*	12			9			4	5	11			12			12				11	12	11		1				11
5	Dd	VA1A	*L. penai*	30			30		9	8	11	30			30			30			1	30	29	30						30
5	Dc	VA3B	*L. penai*	34			34		5	10	17	34			34			34			1	34	33	34						34
5	Dc	VR5	*L. penai*	37			27		4	7	15	37			37			37			1	37	36	37						25
5	Db	COL-D	*L. penai*	11			11		2	7	2	11			11			11				11	11	11						11
5	Da	FTE3	*L. penai*	7			7		1	3	3	7			7			7				7	7	7						7
5	Da	FTE2	*L. penai*	6			6		1	1	4	6			6			6				6	6	6						6
5	Da	OR9	*L. penai*	12			10		2	5	4	12			12			12				12	12	12						10
5	Da	VR2B	*L. penai*	0																										
4	C	VR2A	*L. penai*	5			4			3	1	5			5			5				5	5	5						4
4	C	OR8	*L. penai*	9			8			3	5	8			9			9			1	9	8	9						9
4	C	VR1A	*L. penai*	12			11	1	2	3	7	12			12			12			2	12	10	12						12
4	C	VR4BB	*L. penai*	19			16		1	8	7	19			19			19				19	19	19						16
4	C	VR4A	*L. penai*	18			17		3	7	7	18			18			18				17	18	18					1	15
4	C	SR3	*L. penai*	33			28	1	1	9	19	32			33			33				33	33	22					1	29
4	B	VL2A	*L. penai*	44			37	2	7	15	17	44			44			44				44	44	44						38
4	B	SAM	*L. penai*	92			82	4		51	34	92			92			92			3	91	89	92					7	75
4	B	OR2	*L. penai*	55			49	2	9	18	23	54			55			55				55	55	55				1	2	46
3	A	SR4A	*L. penai*	22			15	3	1	4	12	22			22			22				22	22	22						17
4-5		Vieux-C.	*L. penai*	10			10			1	9	10			10			10			2	10	8	10					2	8

the mesoflexid is always open, thus separating the metaconid and entoconid. Its internal, most labial extension is generally wider than at the opening on the lingual side. The inflexion extends very little in a posterior direction, but generally extends further in the anterior direction. A crochet is absent in the mesoflexid.

P_4-M_2: With the exception of the M_2, these tooth elements are non-diagnostic at the genus level. Their shape is generally indistinguishable from that of other contemporaneous hypselodont European ochotonids of roughly similar size, such as *Prolagus*. The teeth consist of two separate lobes of approximately similar width and are fused together by crown cement. The posterior walls of the lobes have thick enamel. The trigonid has a rhomboid shape. The talonid is more compressed and somewhat wedge shaped; its labial side is thicker and attaches to the trigonid. The position of the talonid is slightly more labial than that of the trigonid. The crown of the P_4 is a more or less straight column. That of the M_1 is slightly curved posteriorly and the M_2 shows yet stronger posterior curvature.

M_3: A single prism or lobe with an ellipsoid occlusal surface. Its crown height is markedly less than that of the M_2.

Remarks

The size measurements of *L. penai* indicate that this species has a stable size through time, although the variability within assemblages is large. Comparative material is shown in Plate 2.9. The older assemblages are characterized by the occurrence of a small percentage of P_3 specimens that have a simple diamond shaped anteroconid and do not have a large wide and more triangular anteroconid. Additionally, the hypercone of the P^2 more frequently shows a shallow hypoflexus in the form of a weak undulation.

The words “molarized” and “reduced” used in the emended diagnosis for *Lagopsis penai* by López-Martínez (1989) require a minor modification. The supposed incomplete molarization of the P^4 does not agree with the (emended) diagnosis for the genus *Lagopsis* given by López-Martínez (1989), which states that the P^4 is molariform. In our emended diagnosis the P^4 shape of *L. penai* is considered molariform as well. The term reduction may imply that the primitive P_3 form of *Lagopsis* has a large and well developed anteroconid and metaconid, while this is not the case, in particular for the anteroconid.

López-Martínez (1984) has shown that the relative frequencies of P_3 morphologies, in particular the stage of development of the anteroconid in *Lagopsis*, indicate a distinct anagenetic evolutionary trend during the Ramblian (early Miocene) in Spain. In accordance with López-Martínez (1984), we include assemblages in which >50% of the specimens have a large and well developed, but somewhat anteriorly compressed anteroconid that is clearly larger than the metaconid, in *L. penai*. This morphology corresponds to López-Martínez’s (1984) “Type C” morphotype.

López-Martínez (1984) assigned assemblages with dominance of the more primitive morphotypes to *Lagopsis* aff. *penai*. These more primitive morphotypes are “Type A”, in which the anteroconid is rounded and equal to or smaller than the metaconid, and “Type B”, in which the anteroconid is rounded and somewhat larger than the metaconid. In agreement with López-Martínez (1984), we consider *L.* aff. *penai* to belong to a separate chronospecies in the *Marcuinomys-Lagopsis* lineage. A possible reassignment of this material to the more primitive species *Lagopsis spiracensis* or to a new species remains to be investigated, but is beyond the scope of this paper.

De Villalta & Crusafont Pairó (1947) include *Lagopsis cadeoti* Viret, 1930 from Estrepouy (MN3, France) in *L. penai*. Similarly, López-Martínez (1984) has indicated that the morphological

Table 2.3: Counted morphologies in the P^3 and P^2 of *L. penai* and *L. verus*. Juvenile specimens are excluded.

P3/					Mesoflexus			Precone		Lagilophe			P2/	Hypoflexus			
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	absent	incipient	developed	indistinct (mhl = pr)	distinct (precone thicker than mhl)	long	short	absent (only lagicone)	Ntotal (excl. juveniles)	absent	incipient/superficial	distinct	with cement
7/8	G3	SOL	*L. verus*	11	2	8	1	11				11	7	6	1		
7/8	G3	TOR3B	*L. verus*	4		1	3	4				4	14	14			
7/8	G3	TOR3A	*L. verus*	0									1	1			
7/8	G3	TOR1	*L. verus*	10	1	5	1	8				10	0				
6	G2	BOR	*L. verus*	5	1	3		4				5	5	4			
6	G1	VT1B	*L. verus*	6		5		3	1			6	3	2			
6	G1	VT1A	*L. verus*	10	1	6		9				10	10	9			
6	G1	LP5B	*L. verus*	22	2	15	1	13	1			22	7	5			
6	F	ARM7	*L. verus*	18		14		13	1			16	18	11	2		
6	F	VT2C	*L. verus*	56	1	44	4	40	6			55	14	11	2		
6	F	LUM22	*L. verus*	9		6	1	6	1			9	2	2			
5	E	LP4BA	*L. verus*	13	2	9		11				13	5	5			
5	E	LP4A	*L. verus*	34		27	3	29	2			34	16	9			
5	E	LUM12	*L. verus*	16	3	8	1	10	2			16	2	2			
5	Dd	LUM10	*L. verus*	12	2	9	1	10				12	3	2	1		
5	Dd	LUM9	*L. verus*	14	1	10		7	2			14	10	10			
5	Dd	LUM3	*L. penai*	26	4	14	3	17	2			25	7	7			
5	Dd	VA3F	*L. penai*	16	1	10	4	8	4			16	13	9	2	1	
5	Dd	VA1A	*L. penai*	43	1	35	2	29	9			43	15	10	1		
5	Dc	VA3B	*L. penai*	49	4	37	5	45	4			49	17	15			
5	Dc	VR5	*L. penai*	45		34	3	29	7			45	10	7	2		
5	Db	COL-D	*L. penai*	9		9		7	1			9	0				
5	Da	FTE3	*L. penai*	10	2	8		8	1			10	5	2	3		
5	Da	FTE2	*L. penai*	10	1	8	1	10				10	3	3			
5	Da	OR9	*L. penai*	13		5	1	7				13	6	3		1	
5	Da	VR2B	*L. penai*	0									2				
4	Cb	VR2A	*L. penai*	7		4	2	5	1			7	1	1			
4	Cb	OR8	*L. penai*	7		5	1	6	1			7	9	6	3		
4	Cb	VR1A	*L. penai*	14	2	10	1	12	1			14	10	7	2		
4	Cb	VR4BB	*L. penai*	22	3	14		16	2			22	14	8	6		
4	Cb	VR4A	*L. penai*	33	2	23	1	23	2			32	6	3	3		
4	Ca	SR3	*L. penai*	29	4	18	3	22	3			29	26	20	6		
4	B	VL2A	*L. penai*	57	2	43	3	45	2			56	33	24	4	1	1
4	B	SAM	*L. penai*	81	7	55	5	80				80	82	61	15	1	1
4	B	OR2	*L. penai*	66	6	44	3	59	3			66	32	25	6	1	1
3	A	SR4A	*L. penai*	25		10		21				25	7	7			
4-5		Vieux-C.	*L. penai*	7		4	2	4				7	0				

variation of the *L. cadeoti* type material significantly overlaps with the variation range of *L. penai* and recommends including the former species in *L. penai*. We have not studied the *Lagopsis* material from Estrepouy, but here will follow López-Martínez (1984).

We refrain from including the material assigned to *L. cadeoti* by Ginsburg *et al.* (2000) in *L. penai*. The morphological features reported by these authors, a primitive shape of the anteroconid in P_3 and P^4 with a remnant paraflexus, suggest a more primitive stage of evolution compared to *L. penai*.

Murelaga *et al.* (2004) described *L. penai* from three early Miocene localities (Ramblian) from the Ebro Basin. The plates and description provided by these authors indicate that these assemblages do not show the “Type C” P_3 morphology defined by López-Martínez (1984), but a more primitive morphology. We therefore exclude these assemblages from *L. penai*.

Kälin (1997) notes transitional forms between *L. penai* and *L. verus* in various localities from the Upper Freshwater Molasse (Switzerland). This interval of taxonomic uncertainty is also indicated by Bolliger (1997). Although we have not studied the Swiss *Lagopsis* material, we provisionally assign the *L. verus* material listed by Kälin (1997: 530, table 2) to *L. penai* on the basis of the drawings shown by Engesser (1972), Engesser *et al.* (1981), Bolliger (1992) and Kälin (1993), which show a simple anteroconid morphology in the P_3.

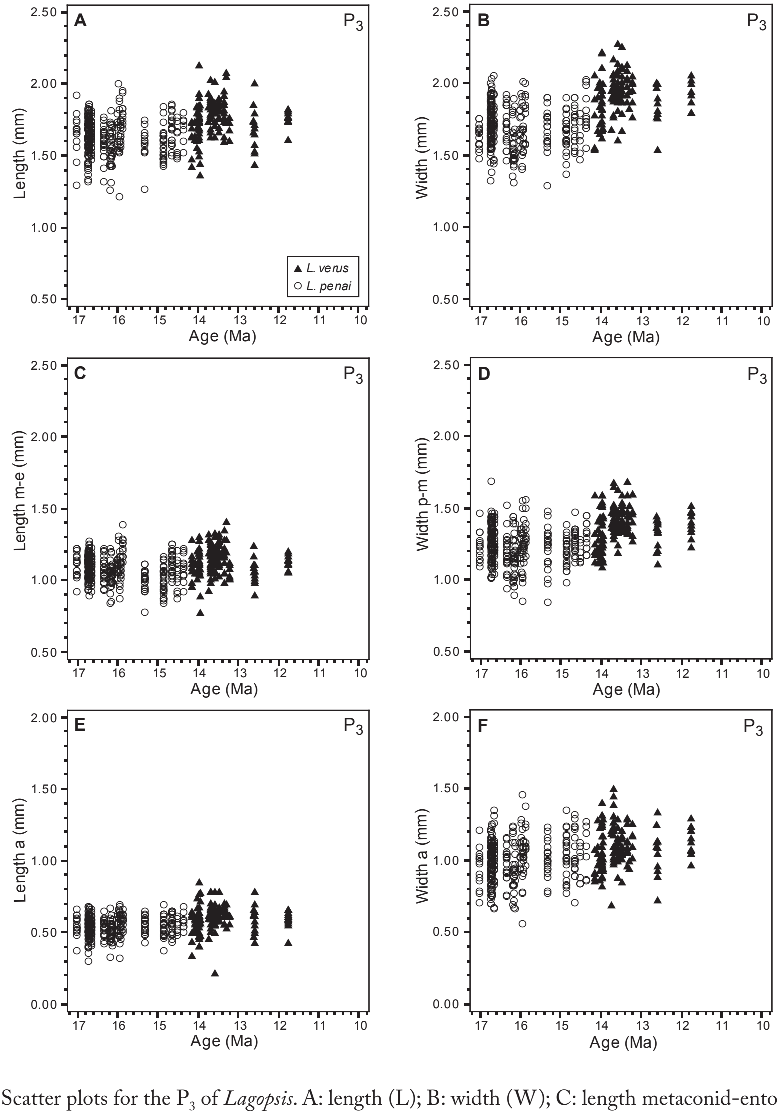


Figure 2.2: Scatter plots for the P_3 of *Lagopsis*. A: length (L); B: width (W); C: length metaconid-entoconid (Lme); D: width protoconid-metaconid (Wp-m); E: length of the anteroconid (La); and F: width of the anteroconid.

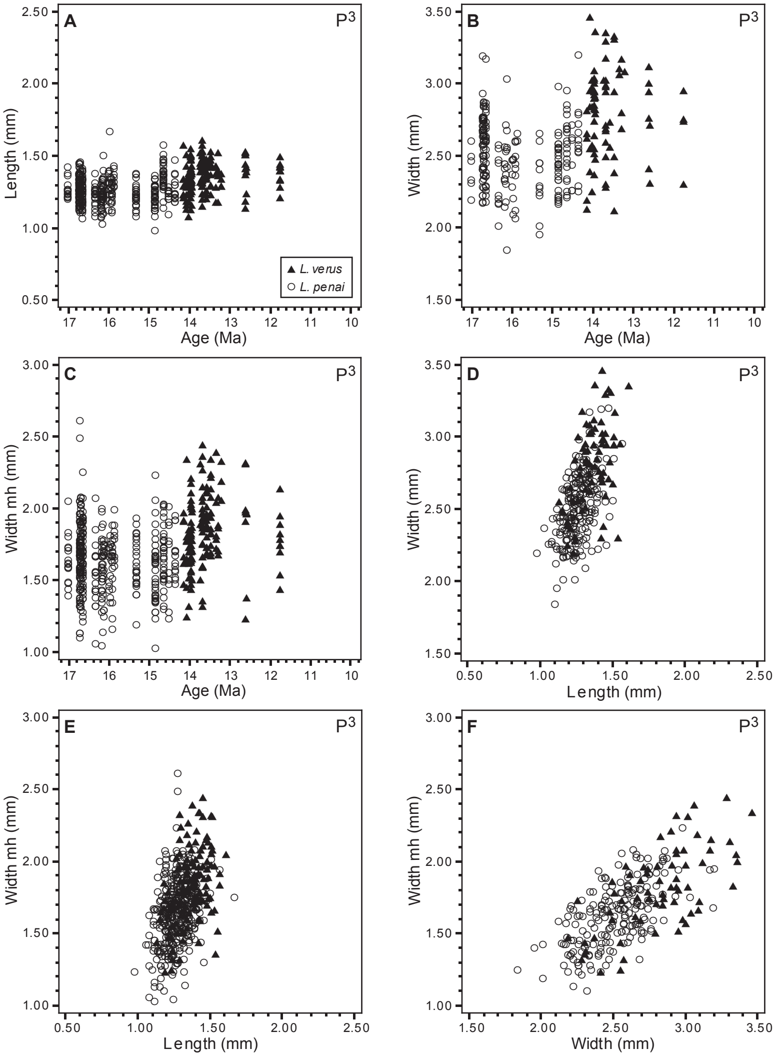


Figure 2.3: Scatter plots for the P^3 of *Lagopsis*. A: length (L); B: width (W); C: width mesial hyperloph (Wmh); D: width (W) versus length (L); E: width mesial hyperloph versus length (L); and F: width mesial hyperloph versus width (W).

Prieto *et al.* (2009) have assigned the assemblages from Untereichen-Altenstadt (UA 540m & UA 565m) to *L. verus*, but indicate that the anterior flexid structures of P_3 are reduced compared to the younger assemblages described by Engesser (1972). Their conclusion appears to contradict the argument given, since the absence or weak presence of an anteroflexid is generally associated with *L. penai*. Comparing the sizes and the drawings provided by Prieto *et al.* (2009) with our Spanish material lead us to conclude that the UA assemblages should probably be assigned to *L. penai*.

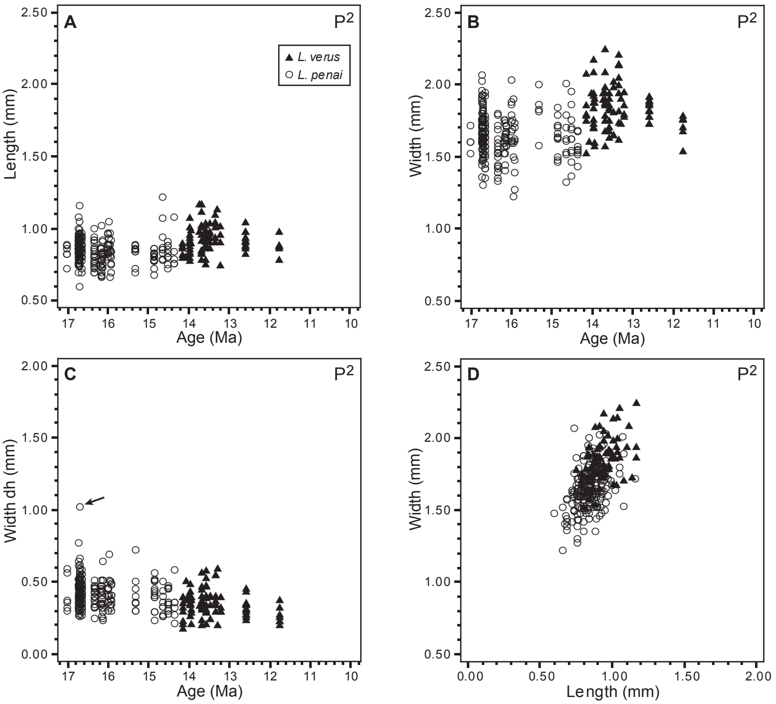


Figure 2.4: Scatter plots for the P^2 of Lagopsis. A: length (L); B: width (W); C: width distal hyperloph (Wdh); D: width (W) versus length (L). The arrow in diagram C indicates a specimen with a long mesial hyperloph that extends over the paraflexus. Its mesial accessory cusp (precone?) is fused with the mesial hyperloph.

Angelone (2009) has adopted López-Martínez's (1989) model for the recognition of two intermediate stages in the evolution from *L. penai* to *L. verus* in the species assignment of *Lagopsis* from Sandelzhausen (MN5, Germany) and assigned this material to *L.* cf. *penai*. Böttcher *et al.* (2009) have followed this conclusion for their limited material from Oggenhausen 2 that has a similar age. On the basis of our data we consider these intermediate stages no longer tenable, in particular with respect to the suggested high potential as a biochronologic marker (Angelone, 2009), and we include the material from Sandelzhausen and Oggenhausen 2 in *L. penai*. This conclusion is in full agreement with the tooth sizes and morphological characteristics provided by Angelone (2009), which include the presence of an incipient anteroflexid in the anteroconid in the P_3 of which only 10% contains cement.

Lagopsis verus (Hensel, 1856)

* 1856 *Lagomys verus* Hensel, 1856: 688, Hensel.
1884 *Lagomys* (*Lagopsis*) *verus* Hensel, 1856: 13, Schlosser.
1899 *Lagopsis verus* (Hensel, 1856): 460, from La Grive, *in* Major.
1958 *Lagopsis verus* (Hensel, 1856): 60, from La Grive, *in* Mein.
1963 *Lagopsis verus* (Hensel, 1856): 26, from La Grive, *in* Tobien

v. *1967 Lagopsis verus* (Hensel, 1856): 211, from Armantes 7, *in* de Bruijn
v. 1967 *Lagopsis penai* (Royo, 1928): 118, from Las Planas 4A & 4B, *in* de Bruijn & van Meurs
v. 1967 *Lagopsis verus* (Hensel, 1856): 122, from Armantes 7, Arroyo del Val 6 & Manchones, *in* de Bruijn & van Meurs
(v). 1972 *Lagopsis verus* (Hensel, 1856): 309, from Anwil & La Grive, *in* Engesser
v. *1977 Lagopsis penai* (Royo, 1928): 49, 51, 53, from Las Planas 4A, *in* Daams *et al.*
v. *1977 Lagopsis verus* (Hensel, 1856): 49, 51, 53, from Armantes 7, Arroyo del Val 6 & Manchones, *in* Daams *et al.*
1982 *Lagopsis verus* (Hensel, 1856): 59, from Anwil & La Grive, *in* Bucher
v. 1989 *Lagopsis* cf. *verus* (Hensel, 1856): 179, from Armantes 7, Arroyo del Val 6 & Manchones, *in* López-Martínez.
1994 Lagopsis aff. *verus* (groß!): 243, 250, from Petersbuch 6 & 18, *in* Bolliger & Rummel
1997 Lagopsis verus (Hensel, 1856): 509, fig. 4, from the Mettlen, Helsighausen & Anwil assemblage zones, *in* Bolliger
2000 *Lagopsis penai* (Royo, 1928): 115, from Somosaguas Sur, *in* Luis & Hernando
v. *2004 Lagopsis verus* (Hensel, 1856): 273, from Toril 3A & 3B, *in* Azanza *et al.*
2005 *Lagopsis* sp.: 116, from Somosaguas Norte, *in* Cuevas Gonzáles
2005 *Lagopsis penai* (Royo, 1928): 116, from Somosaguas Sur, *in* Cuevas Gonzáles
v. 2007 *Lagopsis* n. sp. Prieto, 2007: 100, from Petersbuch 6 & 18, *in* Prieto (unpublished thesis)
v. *2009 Lagopsis* n. sp. Prieto, 2007: 1782, from Petersbuch, *in* Prieto *et al.*

Type Species

Lagomys verus Hensel, 1856, (see genus type *Lagopsis*).

Age

MN7/8, Middle Miocene

Original Diagnosis

Hensel (1856): "I nenne die Art *Lagomys verus*, weil sie sich durch die Zahl ihrer fünf Backenzähne, durch die Stellung des Foramen mentale und durch den ersten unteren Backenzahn, der nur aus einem Cylinder besteht, als ein ächter *Lagomys* ausweist."

Previous Emended Diagnosis

Schlosser (1884): No formal diagnosis is given, but rather a description and comparison.

Previous Emended Diagnosis

Bucher (1982): "La plus grande espèce du genre. Antéroconide de P_3 s'inscrivant dans un triangle. Forte variabilité morphologique de l'antéroconide par rapport à *L. penai*. Protoconulide plus développé que chez *L. penai*. Amplitude très variable du paraflexide. P^3 avec hypoflexus et mésoflexus développés. Forte torsion et plus grand degree d'hypsodontie des dents jugales supérieures que chez *L. penai*."

Previous Emended Diagnosis

López-Martínez (1989): "*Lagopsis* de talla grande. P^4 molarizado. Hipoflexo completo en los molares superiores. P_3 con anterofléxido y anteroconúlido generalmente diferenciado; metacónido cuadrangual provisto de un vértice en su ángulo postero-labial."

Emended Diagnosis

Lagopsis of relatively large size. The proportion of P_3's with a distinct cement-filled anteroflexid in the anteroconid is >50% relative to that of P_3's without a distinctly developed anteroflexid in the anteroconid. The metaconid is relatively short and wide, approaching a rectangular shape. The teeth have a robust appearance. The hypoflexus in upper cheek teeth is deep.

Differential Diagnosis

The main distinction between *Lagopsis penai* and *Lagopsis verus* is made on the basis of the higher proportion of the presence of a cement-filled anteroflexid versus the absence of a distinct anteroflexid in the anteroconid of the P_3. The reverse situation corresponds to *L. penai*. Additionally, the anteroconid is generally slightly better developed in *L. verus* compared to *L. penai*. The molars of *L. verus* tend to be more robust in appearance and may be marginally larger, in particular with respect to tooth width. *Lagopsis* aff. *penai* (as listed by López-Martínez, 1984) has a distinctly less developed anteroconid in the P_3 compared to *L. verus*, in particular with respect to its shape and to its relative size compared to the metaconid.

Material And Measurements

The material analysed is shown in Table 2.1. Quantified morphological features are summarized in Table 2.2 & 2.3. Scatter diagrams of tooth sizes are shown in Figs. 2.2-2.4. Summarized measurements are listed in Appendices 2.A1-2, 2.B1-2 and 2.C. Photographed specimens are shown in Plates 2.3-2.4.

Description.

P^2 & P^4-M^2 (Plate 2.4): The morphology is generally identical to that of *L. penai* (Plates 2.2, 2.9).

P^3 (Plate 2.4): The P^3 morphology and size are highly similar to that of *L. penai* (Plates 2.2, 2.9, Fig. 2.4, App. 2.B1-2). The smallest values of the mesial hyperloph width of *L. verus* are not as small as those from *L. penai* (Fig. 2.3 C,E-F). Similar to *L. penai*, the width increases with wear due to the lateral curvature of the tooth (Fig. 2.3 D). A small round premolar foramen is present lingual to the P^3 in a maxilla from VT1B.

P_3 (Plate 2.3): The P_3 of *L. verus* is basically similar to that of *L. penai*, but shows some marked differences. It appears slightly more robust in comparison to *L. penai* and its anteroconid appears slightly more massive as well. The size largely overlaps with that of *L. penai*, but its width can tend to be somewhat larger (Fig. 2.2). The occurrence of an isolated metaconid in adult specimens is rare. As in *L. penai*, the shape of the mesial side of the anteroconid is relatively variable. A distinct anteroflexid on the antero-labial side of the anteroconid can be present or absent. The number of specimens in an assemblage with a distinct cement-filled anteroflexid is higher than the number of specimens without or with a very weak anteroflexid (Table 2.2). Both morphologies can occur in ontogenetically young individuals of *L. verus*. In a small number of P_3 specimens the paraflexus may be slightly reduced to a shallower depth, thereby broadening the connection of the anteroconid with the metaconid and protoconid. The metaconid is approximately rectangular and represents the most lingual extension of the tooth. Its postero-labial corner is usually angular, while the lingual side may be slightly more rounded. The entoconid and hypoconid form a posterior lobe that has more or less equal width along the tooth. The hypoconid is slightly more rounded at its labial side compared to the flatter entoconid on the lingual side. The hypoconid has a slightly more anterior position compared to the entoconid. The mesoflexid is open, but can be closed by a metaisthmid on rare occasions. Its internal part of the mesoflexid is widest, as in *L. penai*. On one occasion, a very small crochet-like structure is present in the mesoflexid (Table 2.2).

P_4-M_3: The morphology of the P_4-M_3 is identical to that of *L. penai*.

Remarks

Lagopsis verus is a chronospecies. In order to consistently distinguish it from its predecessor *L. penai* a well specified characteristic is required, because these species have many characteristics in common. The dense fossil record form Calatayud-Daroca reveils that the previous diagnosis (López-Martínez, 1989) resulted in a relatively long interval in which the species-assignment remains tentative or unresolved, despite the availability of extensive fossil material.

López-Martínez (1989) dealt with this problem by using *cf.* to designate intermediate stages of development in the gradual change in size and morphology observed in the *Lagopsis penai-verus* lineage. López-Martínez (1989) assigned the *Lagopsis* material from Armantes 7, Arroyo del Val 6 (Plate 2.9) and Manchones to *L.* cf. *verus* instead of *L. verus* on the basis of the somewhat smaller tooth size of these assemblages compared to *L. verus* from La Grive and Anwil. Similarly, *Lagopsis* from Las Planas 4A was assigned to *L.* cf. *penai*, because their size was larger than that of *L. penai*, but smaller than that of *L.* cf. *verus*. The anteroconid in the P_3 was also reported to be more developed in *L.* cf. *penai* compared to that of *L. penai*.

Royo Gómez (1928) and López-Martínez (1989) indicated tooth size as one of the distinctive criteria for distinguishing between *L. penai* and *L. verus* in the diagnosis of *L. penai*. However, the measurements in Appendices 2.A-2.C and Figs. 2.2-2.3 show that size is an insufficient argument to distinguish *L. penai* from *L. verus*. *L. verus* tends to be slightly larger compared to *L. penai*, but sizes mostly overlap. The transition between these species therefore requires a morphological argument other than size.

Various characteristics for distinguishing between *L. verus* and *L. penai* have been used in previous studies, of which the tooth size and the presence of a distinct anteroflexid in the anteroconid of the P_3 are the most commonly used features (de Bruijn & van Meurs, 1967; Engesser, 1972; Bucher, 1982; López-Martínez, 1989; Bolliger, 1992; Kälin, 1993; Murelaga *et al.*, 2004; Cuevas-González, 2005). In practice, however, the identification of these characteristics has not been tightly constrained and they have therefore been loosely applied. For instance, size measurements are not provided in the descriptions of *Lagopsis* from Switzerland (Engesser, 1972; Bolliger, 1992; Kälin, 1993). The range in the variability of the possible taxonomic assignment may as a result be quite large and to such a degree that the timing of species transition is largely unclear or is interpreted differently by different researchers, while the actual characteristics of the fossil material may not be necessarily different. The lack of stable constraints of the criteria and the resulting variability and taxonomic uncertainty may lead to less accurate biostratigraphic correlations and comparisons between different regions.

Beside large size variation, the morphology is quite variable as well, which also depends on ontogenetic development. These circumstances require relatively large assemblages to make consistent taxonomic assignments. During the last decades, the number of assemblages from different stratigraphic levels has grown considerably in comparison to the record that was available to López-Martínez (1989). This provides the means for an emended diagnosis for *L. verus* that constrains and refines the transition of chronospecies more precisely.

Table 2.2 shows that our definition for distinguishing between *L. verus* and *L. penai*, (i.e. the proportion between the presence of a cement filled anteroflexid in the P_3 and the absence of a distinct anteroflexid), is fairly consistent in the study area and is in general agreement with the supposed stratigraphic arrangement of localities. It therefore appears to be suitable for the characterization of this species.

As a consequence of our definition, *L.* cf. *penai* from Las Planas 4A & 4B (zone E) described by López-Martínez (1989) are included in *L. verus*. The *cf.* designations used previously for indicating intermediate forms are no longer consistently applicable in the Calatayud-Daroca record.

The assemblages from Las Umbrías 22, Borjas and Solera fail to meet the P_3 anteroflexid criterion for *L. verus* by a very small margin. There are several reasons that may have caused this offset. One is small sample size. The dominant presence of relatively young individuals may play a role as well. Additionally, the effect of differences in preservation quality cannot be ruled out as well, because the presence of crown cement in the anteroflexid partly depends on preservation. The width and depth of the anteroflexid determine whether or not crown cement was present in the first place, but also influence whether the cement was preserved. Cement may not always have been preserved in relatively wide and shallow anteroflexids, as these are more succeptible to damage. It is not known in how many specimens the crown cement has been lost and the total number of specimens with crown cement may be slightly underestimated. Their total number therefore represents a minimum. With the criterion employed here, an assemblage is assigned to *L. verus* when this minimum number is higher than the number of individuals without a distinct anteroflexid. The specimens in which the cement is lost are included in the category with a distinct anteroflexid without cement (Table 2.2).

Prieto *et al.* (2009) report the presence of a third and new *Lagopsis* species (Prieto, 2007) in a younger part of the German fossil record (Petersbuch) that is considered to be distinctly larger than *L. verus* and *L. penai*. This *Lagopsis* from Petersbuch 6 & 18 is large indeed, but its size range (Prieto, 2007) almost completely overlaps with that of large sized *L. verus* from Spain. Direct comparison of our *Lagopsis* material with that from Petersbuch 18 has shown no appearent difference. In our opinion the species from the latter assemblage can thus be referred to *L. verus*. López-Martínez (1989) indicated that *L. verus* from La Grive and Anwil, which have been used as alternative reference assemblages for this species instead of the type specimen, are also large, although sizes have not been specified.

GENUS *PROLAGUS* POMEL, 1853

* *1853 Prolagus* POMEL, 1853: 43, *in* Pomel
. 1856 *Myolagus* HENSEL, 1856: 695, *in* Hensel
(v). 1899 *Prolagus* POMEL, 1853: 449, *in* Major
(v). 1974 *Prolagus* POMEL, 1853: 38, *in* López-Martínez
(v). 1975 *Prolagus* POMEL, 1853: 851, *in* López-Martínez & Thaler
(v). 1975 *Prolagus* POMEL, 1853: 143, *in* Tobien
(v). 1979 *Prolagus* POMEL, 1853: 113-114, *in* Ringeade
(v). 1989 *Prolagus* POMEL, 1853: 110, *in* López-Martínez

TYPE SPECIES
Lagomys sansaniensis LARTET 1851, from Sansan (Gers, France). Major (1899) included the species *Lagomys sansaniensis* in *Anoema oeningensis* KÖNIG 1825 from Öhningen (Upper Freshwater Molasse, Baden-Württemberg, Germany) and included *Anoema oeningensis* in the genus *Prolagus*.
AGE
MN6 (Sansan), MN7/8 (Öhningen), Middle Miocene.

ORIGINAL DIAGNOSIS

Pomel (1853: 43), *in* Hensel, 1856: 701-702): "Ceux de Sansan diffèrent encore comme sousgenre, par la dernière molaire inférieure qui a trois prismes par réunion de la cinquième molaire à la quatrième. Du reste, la première est aussi triangulaire. On pourrait nommer l'espèce *Prolagus sansaniensis*."

PREVIOUS EMENDED DIAGNOSIS

Tobien (1975): "Zahnformel: P(2, 3, 4)/(3, 4), M(1, 2)/(1, 2). Vollhypsodonte obere und untere P und M. P^3 mit schlingenartigem Mittelelement, P^4 stets mit Resten der Außen- und Mittelsynkline. M^1 und M^2 mit allmählichem Verlust dieser Altstrukturen. P_3 mit Vorderpfeiler und kleinem Synklinid im Vorderaußenelement. Vordersynklinid flach oder tief, fast bis zur Hinterwand des Zahnes reichend. M_2 mit drittem Lobus, teilweise oder gänzlich von zweiten Lobus isoliert."

PREVIOUS EMENDED DIAGNOSIS

López-Martínez & Thaler (1975): "Ochotonidé de taille petite à grande, dents à croissance continue, sans trace de racines. Hypoconulide exclusivement à la M_2 inférieure. P_3 inférieure à trois sillons externes, par addition d'un protoconulide, et deux sillons internes."

PREVIOUS EMENDED DIAGNOSIS

Ringeade (1979): "Prémolaires et molaires inférieures totalement hypsodontes. Prémolaires supérieures présentant soit une hypsodontie incomplete chez les formes primitives soit une hypsodontie complete chez les formes récentes. Molaires supérieures totalement hypsodontes. P^4 montrant toujours des restes de synclinal median et externe. M^1 et M^2 perdant, après usure totale, ces structures primitives. P_3 avec un pilier antérieur. Synclinide antérieur peu profond chez les formes primitives, profond chez les formes récentes où il attaint la muraille postérieure. Petit synclinide à l'elément antéro-externe, rare ou absent chez les formes primitives, constant chez les formes récentes. M_2 avec un troisième lobe non isolé initialement et en partie ou totalement isolé chez les formes jeunes."

EMENDED DIAGNOSIS

Tooth formula: (2, 0, 3, 2)/(1, 0, 2, 2). Ochotonids of small to large size. Adult teeth are hypsodont and rootless. The anteroconid in the P_3 is isolated in the vast majority of specimens, but an occasional connection to the protoconid or metaconid is possible. A protoconulid may be absent, incipient or well developed. The centroflexid in P_3 can be absent, shallow or deep. The trigonid and talonid of the P_4 and M_1 form two lobes of similar width. A third lobe, the hypoconulid, is always and exclusively present in M_2, and is partly or completely isolated from the hypoconid-entoconid lobe. The M_3 is always absent. The P^2 has a distinct meso- and paraflexus and the mesial hyperloph can be very short to well developed. The P^3 has a well developed paraflexus and mesoflexus and a shallow and relatively narrow hypoflexus may be present. The P^4 is molariform and usually includes one or more rudimentary enamel fossettes. Enamel fossettes in the M^1-M^2 may be present or absent and may reduce or become lost with wear. The reduction of fossettes in P^4-M^2 is more progressive towards the posterior, while the depth of the hypoflexus increases.

DIFFERENTIAL DIAGNOSIS

Prolagus differs from other Miocene European ochotonid genera, except *Piezodus* and *Ptychoprolagus*, in lacking the M_3 and having a hypoconulid in the M_2 instead. *Prolagus* differs from *Piezodus*, *Titanomys* and *Marcuinomys* in having rootles teeth. The paraflexus and/or mesoflexus in *Prolagus* P^4-M^2 are generally more reduced and isolated from the molar outline (fossettes), while in *Piezodus* these features are more developed and open on the labial side of the molar outline. *Ptychoprolagus* differs from *Prolagus* by the strong crenulation of the thinner parts of the meso- and paraflexus enamel walls in P^3-M^2. *Lagopsis*, *Albertona* and *Alloptox* do not have an isolated anteroconid in the P_3 and their mesoflexus in the P^3 is reduced and/or less consistently well developed. The adult P^4-M^2 of *Lagopsis* and *Alloptox* lack the fossettes that are often present in *Prolagus*. The torsion and curvature of the P^4-M^2 in *Lagopsis* is stronger. *Eurolagus* is larger and rooted, as is *Gymnesicolagus*.

REMARKS

In the emended diagnosis provided here the main characteristics given in previous diagnoses are compiled, some features are corrected or updated and a range of characteristic morphologies is specified. *Prolagus* has originally been designated as a subgenus of *Lagomys* by Pomel (1853) and was later raised to the genus level by Major (1899). Major (1899) included the generic type assemblage from Sansan in the species *P. oeningensis* from Öhningen. López-Martínez (1974) later assigned the forms from Sansan and Öhningen to subspecies: *P. oeningensis sansaniensis* and *P. oeningensis oeningensis*. We do not follow the subspecies assignment (see chapter 3). The question regarding the homogeneity of *P. oeningensis* in the Miocene of Central Europe, mentioned by López-Martínez (1989), is beyond the scope of this study and remains to be investigated.

PROLAGUS LOPEZMARTINEZAE N. SP.

v. 1967 *Prolagus vasconiensis* VIRET, 1930: 128, from Ateca 3 & Villafeliche 2A, de Bruijn & van Meurs
v. *1977 Prolagus vasconiensis* VIRET, 1930: 49, 51, 53, from Ateca 3 & Villafeliche 2A, *in* Daams *et al.*
1984 *Prolagus* aff. *tobieni* LÓPEZ, 1977: 30, 36, from Moratilla 1, *in* López-Martínez
v. 1989 *Prolagus vasconiensis* VIRET, 1930: 110, from Ateca 3, *in* López-Martínez
v. 1989 *Prolagus* cf. *tobieni* LÓPEZ, 1977: 53, 122, from Villafeliche 2A, *in* López-Martínez
2009 Prolagus aff. *tobieni* LÓPEZ, 1977: 82, from Moratilla 1, *in* Angelone & Sesé
v. *2009 Prolagus* cf. *tobieni* LÓPEZ, 1977: 82, from Villafeliche 2, *in* Angelone & Sesé

TYPE LOCALITY
San Marcos, Calatayud-Daroca Basin, Spain.

AGE
local zone B, MN4, Early Miocene.

HOLOTYPE
P_3: SAM – L6B-07 (MNCN) (Plate 2.5, fig. 9).

PARATYPES
Associated diagnostic elements from San Marcos (MNCN): 27 P_3 (L6A-06 – L7B-06); 26 P^3 (L12B-01 – L13B-10); 14 P^2 (L18B-01 – L19A-08).

STRATIGRAPHIC RANGE
Early Miocene to Middle Miocene. Upper part of local zone A (MN3) to at least zone Cb (MN4); zone Da to G1 (MN5 – MN6) uncertain.

DERIVATIO NOMINIS
This species is named after Prof. Dr. Nieves López-Martínez in recognition of her extensive contribution to the knowledge of Neogene European lagomorphs.

DIAGNOSIS

Prolagus of small size and primitive appearance. The lagiloph in the P^3 is reduced in the majority of the specimens, being either short or absent (leaving only a lagicone). The precone is developed as a thickened labial endpoint of the mesial hyperloph in the majority of the population. The P^2 is similar to that of *Prolagus vasconiensis*, having three short lophs or cusps and having two inflexions with their apices pointing straight toward the posterior side of the tooth. A distinct hypoflexus may be present. The occlusal surface of the P_3 has a triangular outline, with a (sub)-round to slightly anterioly compressed or triangular anteroconid. The protoconid and metaconid are always connected. A shallow but distinct centroflexid is present in part of the assemblage, while it is very weak or absent in the remainder. The prototonulid is small/incipient, but distinctly visible. The mesoflexid is deep and curved sharply toward the posterior side, in which a crochet may be present at the inner bend. A protoisthmid is usually present, but can be lacking in rare cases. The metaisthmid is absent.

DIFFERENTIAL DIAGNOSIS

Prolagus lopezmartinezae n. sp. differs from *Prolagus vasconiensis*, its evolutionary ancestor, in having a P^3 lagicone without a long lagilophe. The mesoflexus in P^3 of *P. lopezmartinezae* is generally shorter and curved less than in *P. vasconiensis*. The parafossette and mesofossette in the P^4-M^2 of *P. lopezmartinezae* are slightly reduced compared to those in *P. vasconiensis*.

Prolagus praevasconiensis RINGEADE, 1979 is more primitive compared to *P. vasconiensis*, and differs from *P. lopezmartinezae* in similar features as *P. vasconiensis*. Additionally, the hypoconulid of the M_2 of *P. lopezmartinezae* is well developed along the full height of the crown and its enamel is isolated from the hypoconid-entoconid lobe, unlike that of *P. praevasconiensis*.

Prolagus fortis LÓPEZ-MARTÍNEZ & SESÉ, 1991 differs from *P. lopezmartinezae* by its larger size and by its P^3 with a long lagiloph. *Prolagus schnaitheimensis* TOBIEN, 1975 and *Prolagus aguilari* LÓPEZ-MARTÍNEZ, 1997 are larger and more robust compared to *P. lopezmartinezae*, and have a distinctly larger and wider anteroconid in the P_3. The metaisthmid and/or the complete separation of the protoconid and metaconid are present in some P_3 of *P. aguilari*, but absent in *P. lopezmartinezae*.

Prolagus tobieni LÓPEZ, 1977, which is considerd to be the evolutionary successor of *P. lopezmartinezae*, differs from the latter in having a slightly more evolved P_3 morphology. Its anteroconid is triangular, wide and/or anteriorly compressed instead of more (sub)-round instead. *P. lopezmartinezae* has a more distinct, although shallow/incipient, centroflexid compared to *P. tobieni*. Absence of the protoisthmid in the P_3 is a common condition in *P. tobieni*, while it is rare or mostly absent in *P. lopezmartinezae*. The P_3 tends to be slightly wider in *P. tobieni*. The lagiloph in the P^3 is more consistently and progressively reduced in *P. tobieni*. The hypercone of the P^2 of *P. tobieni* is generally more massive and thick.

Prolagus oeningensis (KÖNIG, 1825) and *Prolagus major* LÓPEZ, 1977 differ from *P. lopezmartinezae* by their well developed centroflexid in the P_3. The lagiloph in their P^3 is long and not reduced, in contrast to that of *P. lopezmartinezae*. *Prolagus major* is distinctly larger than *P. lopezmartinezae*. *P. lopezmartinezae* differs from all currently known late Miocene to Holocene *Prolagus* species, from *Prolagus crusafonti* LÓPEZ, 1975 up to *Prolagus sardus* (WAGNER, 1829) by the absence of a well developed centroflexid in its P_3, i.e. its protoconid and metaconid are connected.

MATERIAL AND MEASUREMENTS

The material analysed is shown in Table 2.1. Quantified morphological features are shown in Table 2.4 & 2.5. Scatter diagrams of tooth sizes are shown in Figs. 2.5-2.7. Summarized measurements are listed in Appendices 2.D1-2, 2.E1-2 and 2.F. Photographed specimens are shown in Plates 2.5-2.6.

DESCRIPTION

P^2 (Plate 2.6): The mesoflexus and paraflexus are distinctly developed and straight with their apices pointing in a posterior direction. The hypercone forms the largest length of the tooth. Its shape varies from relatively short and thick to more elongate and less thick. The distal hyperloph is usually slightly curved or rounded. One specimen from San Marcos has an accessory cuspid. A hypoflexus is absent in most cases, but can is distinctly present in a few specimens, with or without crown cement (Table 2.5).

P^3 (Plate 2.6): The lagicone and lagiloph have a variable shape. The lagiloph is reduced in well over half of the assemblage, forming either a short lagiloph or being absent (Table 2.5). The lagicone has a simple shape and smooth outline, apart from a few exceptions that show a weak indentation at the base of the lagiloph. The postlobus is well developed and extends distinctly on the labial side of the tooth. The mesoflexus is deep and is moderately curved or quite straight. The precone is distinct in the majority of specimens, forming a thickened tip on the distal end of the mesial hyperloph. A shallow cement-filled hypoflexus is present in all specimens. The distal hypercone is more developed than the mesial hypercone, which is slightly reduced in some cases, leaving a very shallow hypoflexus.

P^4-M^2 (Plate 2.6): These teeth have residual enamel fossettes that are progressively more reduced towards the posterior end of the tooth row. Both the parafossette and mesofossette are present in the P^4. The latter is lost during wear. The hypoflexus is more developed in the more posterior cheek teeth. It reaches to about one third of the tooth width in the P^4. The M^1 has a J-shaped parafossette, while the mesofossette is lost. Its hypoflexus is deeper than that of the P^4, reaching to between one and two third of the width of the tooth. The M^2 has a very small oval or slightly curved parafossette. Its hypoflexus covers about two third of the tooth width.

P_3 (Plate 2.5): The occlusal surface of the P_3 has a triangular outline of which the labial side is slightly longer than the lingual side. The tooth is slightly concave on its posterior side along the height of the crown. The anteroconid has a variable shape, being somewhat triangular with flattened anterolabial and anterolingual sides, or being slightly anteriorly compressed or more (sub)-round. One specimen from San Marcos shows a narrow anteroflexid with crown cement and some show a very weak inflexion. The protoconid and metaconid are always broadly connected. A shallow but distinct centroflexid is present in part of the population, while it is very weak or absent in the remainder. The protoconid is smaller than the metaconid. The prototonulid is very small or incipient, but is distinct. The hypoconid is placed slightly forward with respect to the posterior wall. The hypoconid and the entoconid are thick, while the loph connecting them is very narrow. The hypoconid is more oval and the entoconid has a more rectangular shape. The mesoflexid and hypoflexid are deep. The latter is more or less straight and points in a postero-lingual direction, while the former is sharply curved. The lingual part of the mesoflexid is parallel to the posterior wall. The apex of the mesoflexid is pointing in a posterior direction, which accentuates the antero-labial angle of the entoconid. A small incipient or well developed crochet may be present at the bend of the mesoflexid (Table 2.4). A protoisthmid is always present in the assemblages under consideration (Table 2.4). The metaisthmid is absent.

P_4-M_1: The P_4 and M_1 are generally indistinguishable from the lower molars of other similar sized and high crowned ochotonids in Europe, such as *Lagopsis*.

M_2 (Plate 2.5): The hypoconulid is fully developed and isolated from the talonid along the total height of the crown. Its posterior enamel wall is flattened, resulting in a shape similar to that of

Table 2.4: Counted morphologies in the P_3 of *P. lopezmartinezae* and *P. tobieni*. Juvenile specimens are excluded.

p/3					Anteroconid				Anteroflexid			Protoconulid			Centroflexid			Crochet			Connections							Size		
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	(sub)round	ellipsoid	flattened/broad/triangular	diamond shaped	distinct with cement	distinct inflexion	absent/weak/incipient inflexion	absent	incipient/small	developed	absent	incipient/superficial	deep	absent	incipient/small	developed	metaconid isolated	anterolophid	metalophid	protoisthmid present	protoisthmid absent	metaisthmid	anteroisthmid	anteroconid < metaconid	anteroconid = metaconid	anteroconid > metaconid
9	H	CAR1	*P. tobieni*	8			5			2	3	2	6		7	1		6	2				8	7	1					5
9	H	NOM1	*P. tobieni*	0																										
7/8	G3	SOL	*P. tobieni*	41			16				18	18	20		36	3		33	3	1			41	32	9			8	6	2
7/8	G3	PJE2	*P. tobieni*	0																										
7/8	G3	TOR3B	*P. tobieni*	32		1	28			1	29	12	8		28	2		28	4				32	16	15	1	1	5	18	6
7/8	G3	TOR3A	*P. tobieni*	23			22			1	21	8	14		21	2		17	5				23	12	13			5	10	3
7/8	G3	TOR1	*P. tobieni*	3			3				3	1	2		3			3					3	3				1	2	
6	G2	MAN	*P. tobieni*	4			4				4	2	2		4			3	1				4	2	2				1	2
6	G1	VT1A	*Prolagus* ex. interc.	2			2				2		2		1	1		2					2	2					1	1
6	F	VT2C	*Prolagus* ex. interc.	0																										
5	E	LP4BA	*Prolagus* ex. interc.	1																										
5	Dd	VA3F	*Prolagus* ex. interc.	0																										
5	Dc	VR5	*Prolagus* ex. interc.	2	1		1				2		2			2		2					2	2						1
5	Db	COL-D	*Prolagus* ex. interc.	0																										
4	Cb	VR1A	*P. lopezmartinezae*	1			1				1		1			1		1					1	1				1		
4	Cb	VR4BB	*P. lopezmartinezae*	0																										
4	Ca	SR3	*P. lopezmartinezae*	2	2						2		2			2		1		1			2	2					1	1
4	B	VL2A	*P. lopezmartinezae*	2		1	1			1	1		2			2		1	1				2	2					2	
4	B	SAM	*P. lopezmartinezae*	28	5	5	13		1		22	9	17	2	17	11		8	7	12			28	28				4	9	8
4	B	OR2	*P. lopezmartinezae*	2			1				1		2			2		2					2	2						1
3	A	SR4A	*P. lopezmartinezae*	12	4						4		12		1	10		2	4	5			12	12					1	

the second lobe (talonid). The prisms are strongly curved, with their base pointing in a posterolabial direction.

Remarks

López-Martínez (1984) described the marked change in the morphology of the P^3 of *Prolagus vasconiensis* from a Spanish succession of Ramblian age in which the lagiloph is reduced. Moratilla 1 is the oldest locality in this particular succession in which this derived P^3 *P. tobieni*-like morphology is dominantly present. López-Martínez (1984) therefore assigned this assemblage to *P.* aff. *tobieni*. Similarly, López-Martínez (1997) indicated the increased commonness of the *tobieni*-like morphology in the P_3 from Moratilla 1 as well.

In our opinion, the material from San Marcos, supported by the assemblages from Olmo Redondo 2 and San Roque 4A, provides a good basis for the description of a new species, *P. lopezmartinezae*, to which the material from Moratilla 1 can be assigned as well. The combination of features such as the derived P^3 morphology with the reduced lagiloph, the slightly reduced enamel fossettes in the upper molars and the relatively primitive morphology of the P_3 and P^2 can be recognized as a distinct intermediate chronospecies in the evolution of *P. vasconiensis* to *P. tobieni*.

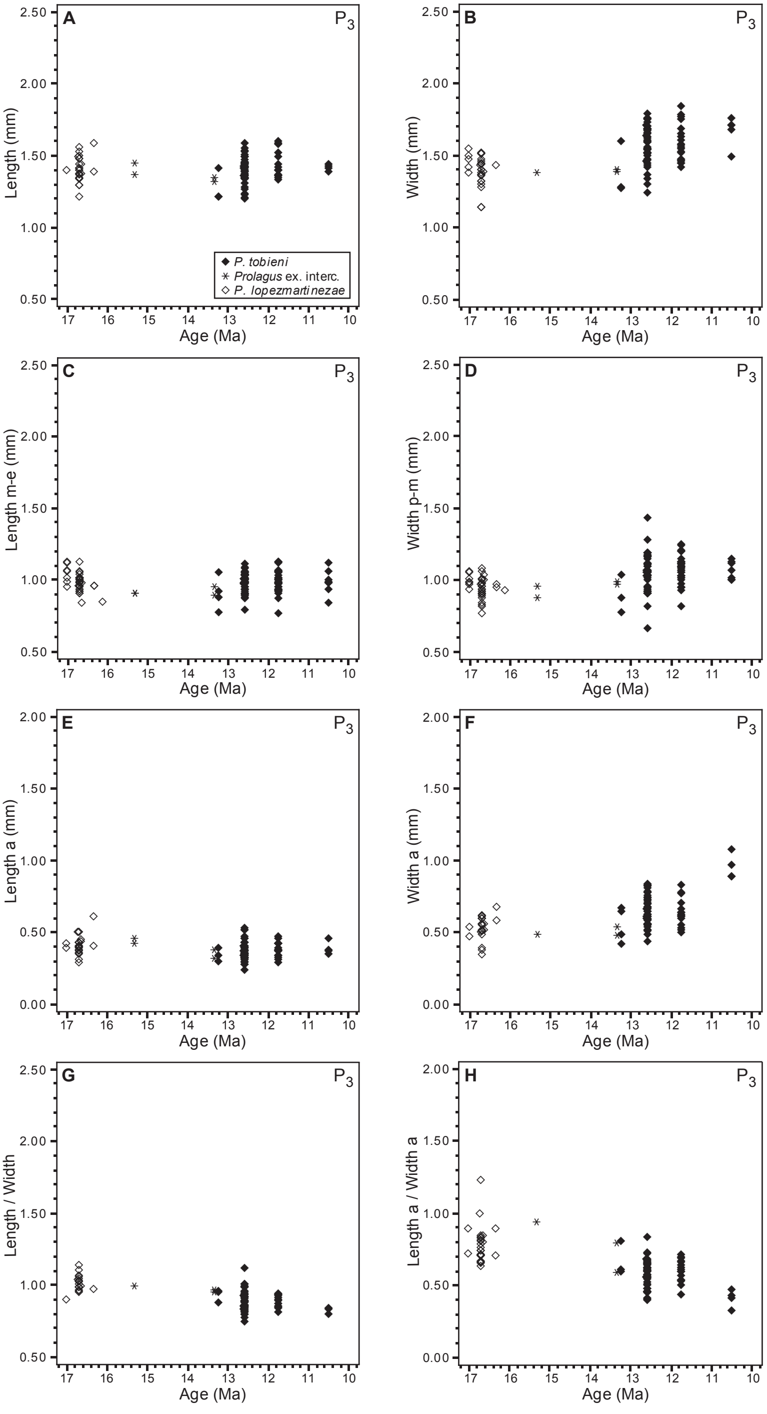
In contrast to the material from San Marcos (Table 2.5), a shallow hypoflexus in the P^2 is common in the assemblage from Moratilla 1 (López-Martínez, 1984). This feature is also present in a few specimens from San Roque 4A and Olmo Redondo 2 (Table 2.5, Plate 2.6).

De Bruijn & van Meurs (1967) and López-Martínez (1989) assigned the *Prolagus* assemblage from Ateca 3 (collection IVAU) to *P. vasconiensis*. Although the material has a slightly more primitive appearance than that of San Marcos, the lagiloph of its P^3 clearly (Plate 2.10) shows reduction in the majority of specimens: Two specimens are without a lagiloph, seven have a short lagiloph, and two have a long lagiloph. This leads to our conclusion that the Ateca 3 material can be included in *P. lopezmartinezae*.

In addition to the reduced lagiloph, one out of the 17 P_3 specimens from Ateca 3 lacks a protoisthmid, which is also seen in Moratilla 1. Although the type assemblage from San Marcos does not contain this particular morphotype, we consider its presence possible within this species.

A crochet on the entoconid in the mesoflexid of the P_3 is a relatively common feature in the assemblages from San Marcos and San Roque 4A (Table 2.4, Plate 2.5). This structure appears to be equivalent to the crochet seen in *P. oeningensis*, since it looks very similar and is placed on the approximately same position, but it is not necessarily homologous. In some cases there appear to be more than one crochet-like structure present, albeit incipient or developed. In general, a crochet in *P. lopezmartinezae* may possibly be a potential proto-metaisthmid, although the metaisthmid is absent in the studied assemblages. On the other hand, this crochet may be identical to the crochet present in the centroflexid of *P. oeningensis*, in which the metaisthmid is generally present.

The relative abundance of *P. lopezmartinezae* with respect to *L. penai* is distinctly lower in the localities of the studied succession. An opposite situation has been reported for the assemblage from Moratilla 1, in which *Prolagus* is slightly more abundant compared to *Lagopsis*. Contrary to the relative abundances of *Prolagus* and *Lagopsis* listed in López-Martínez (1989: 115) and figured by López-Martínez (2001: 223), the relative abundance of *P. lopezmartinezae* in the assemblage from Ateca 3 is significantly smaller compared to that of *L. penai* (*Lagopsis*: 110 P^3 & 96 P_3; *Prolagus* 11 P^3 & 17 P_3), which is in agreement with the figure shown by López-Martínez (1989: 114).


A
P3
Length (mm)
2.50
2.00
1.50
1.00
0.50
P. tobieni
Prolagus ex. interc.
P. lopezmartinezae
17
16
15
14
13
12
11
10
Age (Ma)
B
Width (mm)
C
Length m-e (mm)
D
Width p-m (mm)
E
Length a (mm)
0.00
F
Width a (mm)
G
Length / Width
H
Length a / Width a

← *Figure 2.5:* Scatter plots for the P_3 of *Prolagus*. A: length (L); B: width (W); C: length metaconid-entoconid (Lme); D: width protoconid-metaconid (Wp-m); E: length of the anteroconid (La); and F: width of the anteroconid; G: length/width ratio (L/W); and H: length/width of the anteroconid (La/Wa).

Table 2.5: Counted morphologies in the P^3 and P^2 of *P. lopezmartinezae* and *P. tobieni*. Juvenile specimens are excluded.

P3/					Mesoflexus			Precone		Lagilophe			**P2/**	Hypoflexus			
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	absent	incipient	developed	indistinct (mhl = pr)	distinct (precone thicker than mhl)	long	short	absent (only lagicone)	Ntotal (excl. juveniles)	absent	incipient/superficial	distinct	with cement
9	H	CAR1	*P. tobieni*	5			5	1	3		1	4	5			5	4
9	H	NOM1	*P. tobieni*	1			1		1			1	0				
7/8	G3	SOL	*P. tobieni*	39			39		30		13	25	26	15	6	5	7
7/8	G3	PJE2	*P. tobieni*	1			1	1			1		1	1			
7/8	G3	TOR3B	*P. tobieni*	18			17		17		5	12	20	2	6	10	10
7/8	G3	TOR3A	*P. tobieni*	24			24		23		2	21	24	5	8	7	9
7/8	G3	TOR1	*P. tobieni*	2			2		2		1	1	0				
6	G2	MAN	*P. tobieni*	3			3		3			3	0				
6	G1	VT1A	*Prolagus* ex. interc.	2			2		2		2		0				
6	F	VT2C	*Prolagus* ex. interc.	2			2		2			2	0				
5	E	LP4BA	*Prolagus* ex. interc.	1			1	1			1		0				
5	Dd	VA3F	*Prolagus* ex. interc.	1			1		1			1	1	1			
5	Dc	VR5	*Prolagus* ex. interc.	2			2		1		1	1					
5	Db	COL-D	*Prolagus* ex. interc.	1			1		1			1	0				
4	Cb	VR1A	*P. lopezmartinezae*	1			1					1	0				
4	Cb	VR4BB	*P. lopezmartinezae*	1			1		1		1		0				
4	Ca	SR3	*P. lopezmartinezae*	1			1	1			1		0				
4	B	VL2A	*P. lopezmartinezae*	2			2	1	1			2	2	1			
4	B	SAM	*P. lopezmartinezae*	26			26	1	21	8	11	7	14	13	1		
4	B	OR2	*P. lopezmartinezae*	13			13	2	8	1	9	3	4	3		1	1
3	A	SR4A	*P. lopezmartinezae*	6			6		5	2	4		4	2		2	2

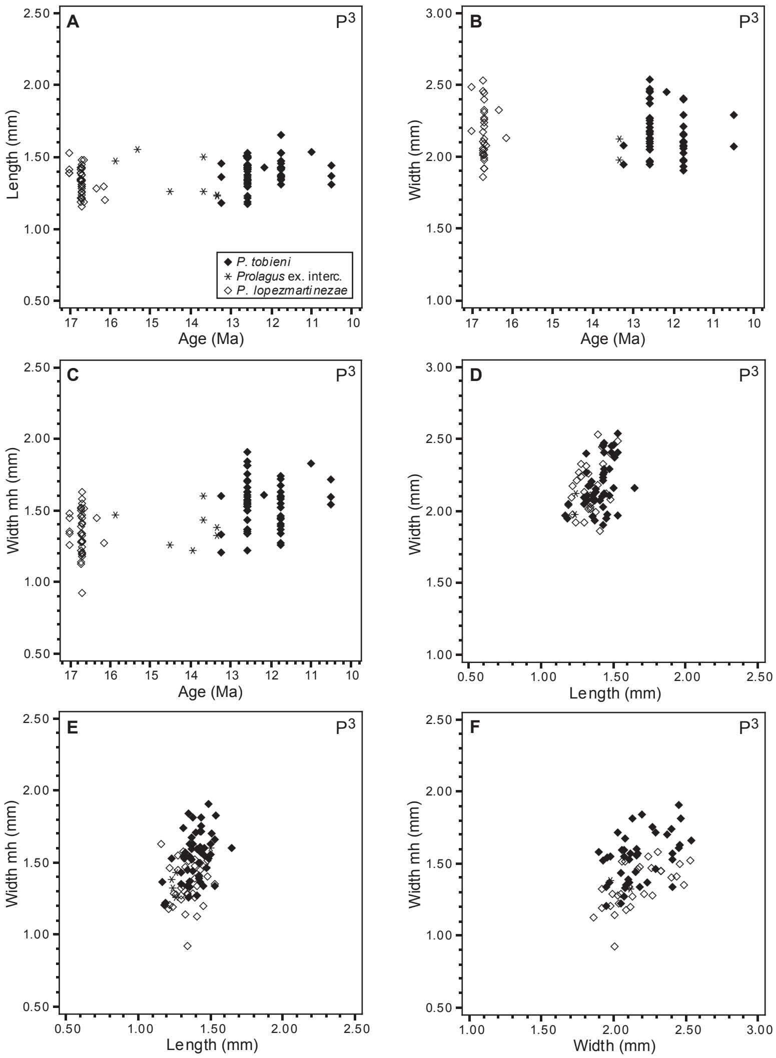


Figure 2.6: Scatter plots for the P^3 of *Prolagus*. A: length (L); B: width (W); C: width mesial hyperloph (Wmh); D: width (W) versus length (L); E: width mesial hyperloph versus length (L); and F: width mesial hyperloph versus width (W).

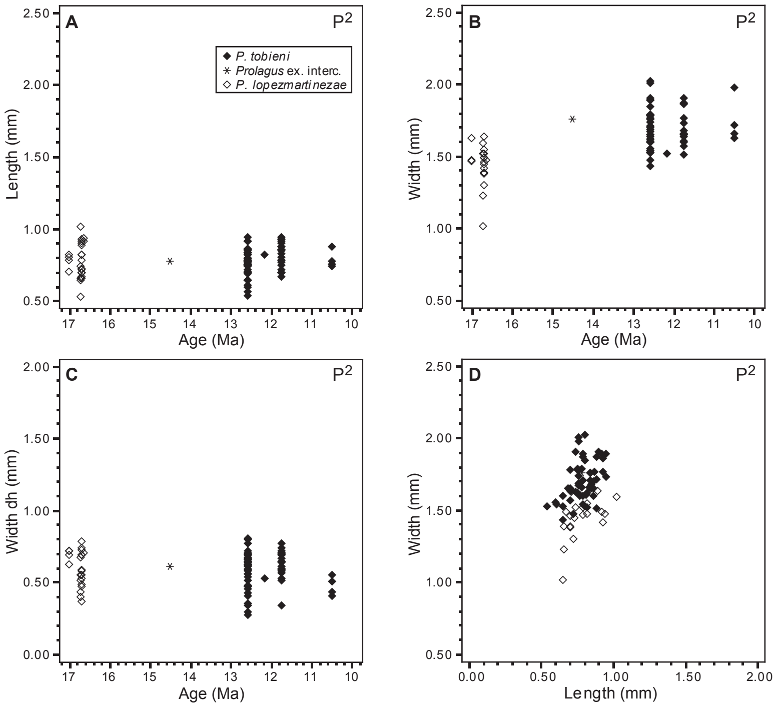


Figure 2.7: Scatter plots for the P^2 of *Prolagus*. A: length (L); B: width (W); C: width distal hyperloph (Wdh); D: width (W) versus length (L).

PROLAGUS EX. INTERC. *LOPEZMARTINEZAE-TOBIENI*

v. 1989 *Prolagus* cf. *tobieni* López, 1977: 53, 122, from Villafeliche 4, *in* López-Martínez

v. *2009 Prolagus* cf. *tobieni* López, 1977: 82, from Villafeliche 4, *in* Angelone & Sesé

Stratigraphic Range

The interval of unresolved species assignment covers zone Da (MN5) to G1 (early MN6), Middle Aragonian, Middle Miocene.

Material And Measurements

The material analysed is shown in Table 2.1. Quantified morphological features are shown in Table 2.4 & 2.5. Scatter diagrams of tooth sizes are shown in Figs. 2.5-2.7. Summarized measurements are listed in Appendices 2.D1-2, 2.E1-2 and 2.F. Photographed specimens are shown in Plate 2.7.

Description

The two P_3 specimens from Valalto 1A both have a protoisthmid and triangular anteroconids. One (broken) has both a shallow but distinct centroflexid and a mesoflexid that weakly extends anteriorly, while these features are not present in the other. The two P^3 specimens from Valalto 1A have a very short incipient lagiloph and a well developed precone. The distinct precone and absence of a lagiloph in the two P^3 specimens from Valalto 2C show a very close resemblance to the morphology of *P. tobieni*. The two P_3 from Vargas 5, on the other hand, have a relatively narrow anteroconid and a protoisthmid. One of the two P^3 specimens from Vargas 5 has a short lagiloph, while it is absent in the other. These features appear to be more similar to *P. lopezmartinezae*. The P_3 from Las Planas 4BA is damaged and the P^3 has a short lagiloph. The P^3 specimens from Valdemoros 3F (incl. 1 juvenile) and La Col-D have no lagiloph, of which the latter does show a small hint. The damaged P^2 from the former locality lacks a hypoflexus. The Valdemoros 3B only contains a few non-diagnostic P^4-M^2 elements that fit the morphology and size of the lineage.

REMARKS

The scanty tooth material from La Col-D, Vargas 5, Valdemoros 3B & 3F, Las Planas 4BA, Valalto 2C and Valalto 1A does not allow for reliable identification at the species level. The evolution from *P. lopezmartinez* to *P. tobieni* involves several changes in the frequency and stage of development of features in the P_3, P^2 and P^3, of which we consider the frequency of the absence of the protoisthmid in the P_3, in combination with the relative width of the tooth and the anteroconid, as the most important characteristics for the distinction of these species. The assignment to the *P. lopezmartinezae-tobieni* lineage can be firmly established on the basis of the distinct morphological characteristics of this lineage, such as the reduced lagiloph in the P^3 (Plate 2.7).

Despite the unresolved taxonomy in this interval, the two chronospecies represent distinct recognizable stages in the evolution of this lineage. It is not yet known whether their transition was relatively gradual, or whether it occurred in a short period of time. New material of from other regions in Iberia in which this lineage is less rare is required to more precisely determine the manner and timing of the evolution from *P. lopezmartinezae* to *P. tobieni*.

PROLAGUS TOBIENI LÓPEZ, 1977

v. 1967 *Prolagus vasconiensis* VIRET, 1930: 128, from Manchones, *in* de Bruijn & van Meurs
vp. 1967 *Prolagus oeningensis* (KÖNIG, 1825): 129, specimen NOM-335 (IVAU) from Nombrevilla, specimens AR6-3021, AR6-3029, AR6-3044 (IVAU) from Arroyo del Val 6, *in* de Bruijn & van Meurs
*(v). 1977 *Prolagus tobieni* LÓPEZ, 1977: 65, from Escobosa I (type locality), Escobosa M & G2, *in* López-Martínez *et al.*
(v). 1989 *Prolagus tobieni* LÓPEZ, 1977: 120, from Escobosa de Calatañazor, *in* López-Martínez
v. 1989 *Prolagus* cf. *tobieni* LÓPEZ, 1977: 122, from Manchones, *in* López-Martínez
(v). 2009 *Prolagus tobieni* LÓPEZ, 1977: 82, from Escobosa de Calatañazor, *in* Angelone & Sesé
v. 2009 *Prolagus* cf. *tobieni* LÓPEZ, 1977: 82, from Manchones, *in* Angelone & Sesé

TYPE SPECIES
Prolagus tobieni LóPEZ, 1977, *in*: López-Martínez *et al.* 1977, Escobosa I (Spain).
AGE: local zone G3, MN7/8, Late Aragonian, Middle Miocene.
HOLOTYPE
P_3: Es. I-1 (C.S.I.C. Madrid).
STRATIGRAPHIC RANGE
Middle Miocene to early Late Miocene; zone G1 to I (MN6 – MN9); zone Da to G1 (MN5 – MN6) uncertain.
ORIGINAL DIAGNOSIS

López-Martínez *et al.* (1977): „*Prolagus* de talla pequeña, P_3 con anterocónido comprimido y ensanchado, protoconúlido muy reducido y protolófido constante. P^2 con sinclinales fuertemente oblicuos. P^3 sin lagilofo. Talónidos de P_4 y M_1 fuertemente comprimidos."

PREVIOUS EMENDED DIAGNOSIS

Angelone & Sesé (2009): Small-sized *Prolagus*; P_3 with flattened anteroconid, extremely reduced protoconulid and protolophid always present; talonids of P_4 – M_2 very flattened. Posterior mandibular foramen lying under m2. Flattened P^2 with oblique synclines and marked hypoflexus; P^3 without lagiloph and with enlarged precone; fish-tail shaped P^4 without mesofossette and hypoflexus depth about 60% of tooth width. Small, round premolar foramen lying next to P^3.

EMENDED DIAGNOSIS

Prolagus of relatively small size. The P_3 has a usually triangular, relatively short and wide anteroconid, and a very small or indistinct protoconulid. The protoconid and metaconid are well connected in all specimens. The mesoflexid is deep and is regularly connected to the hypoflexid due to the absence of the protoisthmid. A shallow anteriorly extending inflexion in the mesoflexid usually delimits the metaconid from the protoconid. The P^3 is generally lacking a lagiloph and has a distinct precone at the end of a relatively long mesial hyperloph. Its mesoflexus is near-straight or only weakly curved. The P^2 generally has a short and thick hypercone, which can be divided by a shallow hypoflexus, either with or without crown-cement. Its mesoflexus may be in a slightly oblique orientation in part of the population, while in the remainder it is oriented antero-posteriorly similar to the paraflexus. A posterior mandibular foramen is positioned below the M_2. A small and round premolar foramen is positioned next to the P^3.

DIFFERENTIAL DIAGNOSIS

Prolagus tobieni differs from *Prolagus praevasconiensis* and *Prolagus vasconiensis* and *Prolagus fortis* in having a strongly reduced or absent lagiloph in the P^3 and having a wide, anteriorly compressed and triangular anteroconid in the P_3 instead of a more rounded anteroconid. The enamel fossettes in the P^4-M^2 of *P. tobieni* are more reduced as well. *P. fortis* is also larger than *P. tobieni*. *P. tobieni* is smaller and less robust in comparison to *Prolagus aguilari* and *Prolagus schnaitheimensis*. The latter species have a distinctly larger and wider anteroconid in the P_3. The separation of the protoconid and metaconid that is present in some P_3 of *P. aguilari*, is absent in *P. tobieni*.

P. tobieni differs from *Prolagus lopezmartinezae*, which is considered to be its predecessor, mostly in having a more derived P_3 stucture. The protoisthmid is regularly absent in *P. tobieni*, while this condition is rare in *P. lopezmartinezae*. The P_3 and the anteroconid of *P. tobieni* are slightly wider than those in *P. lopezmartinezae*. The latter species generally has a more distinct, although shallow/incipient, centroflexid compared to *P. tobieni*. The internal anterior inflexion in the mesoflexid of the P_3 of *P. tobieni* is generally absent or less pronounced in *P. lopezmartinezae*. *P. tobieni* has a more consistently and progressively reduced lagiloph in the P^3. The hypercone in the P^2 of *P. tobieni* is generally more massive and thick, in contrast to that of *P. lopezmartinezae*.

P. tobieni differs from *Prolagus oeningensis*, *Prolagus major* and all late Miocene to Holocene *Prolagus* species in lacking a deep centroflexid and a well developed protoconulid in the P_3 and having a reduced or absent lagiloph in the P^3.

MATERIAL AND MEASUREMENTS

The material analysed is shown in Table 2.1. Quantified morphological features are shown in Table 2.4 & 2.5. Scatter diagrams of tooth sizes are shown in Figs. 2.5-2.7. Summarized measurements are listed in Appendices 2.D1-2, 2.E1-2 and 2.F. Photographed specimens are shown in Plates 2.7-2.8.

DESCRIPTION

P^2 (Plate 2.8): The hypercone, lagicone and postlobus are well developed, but short. The hypercone represents the largest length of the tooth and is usually quite thick. A shallow hypoflexus is variably, but quite commonly present (Table 2.5), in some cases dividing the hypercone in a mesial and distal part. The specimens with a narrow hypoflexus have crown cement, while this may be absent in the wider ones. The mesoflexus and paraflexus are well developed. The mesoflexus is relatively narrow and tends to be slightly oblique in part of the population, running in a slightly antero-lingual to posterolabial direction. The paraflexus is slightly wider and generally runs in an antero-posterior direction similar to that in *P. oeningensis* and *P. lopezmartinezae*, but a slightly oblique direction occurs as well.

P^3 (Plate 2.8): The lagiloph is reduced in all specimens, in the majority it is even absent (Table 2.5). The lagicone has a simple shape and smooth outline. It is relatively narrow, leaving room for a relatively wide paraflexus on the lingual side of the tooth. The postlobus does not extend widely from the labial outline of the tooth. The mesoflexus is deep and nearly straight, but can show slight curvature. The precone is distinctly developed. A shallow hypoflexus is present in all specimens. The distal hypercone is more developed and extends further on the lingual side than the mesial hypercone. In a few cases the mesial hypercone is somewhat reduced, leaving a very shallow hypoflexus.

P^4-M^2: The P^4-M^2 morphology is generally identical to that of *P. lopezmartinezae*.

P_3 (Plate 2.7): The occlusal surface of the P_3 has a triangular outline. The width of the tooth is larger than its length. Similarly, its anteroconid is wider than long and is usually triangular. The P_3's from Carrilanga 1 have the widest anteroconids. However, the length of the anteroconids and the width of the whole tooth fit well with that of the other assemblages. The anteroconid is isolated in all but one specimen from Toril 3B that shows a connection with the metaconid. This particular specimen also has a metaisthmid, which is absent in all other specimens. The anteroconid is worn down to a conspicuously lower level than the rest of the crown. The protoconid and metaconid are always broadly connected, but the connection can be slightly narrowed by a shallow anterior extension of the mesoflexid. The protoconid is smaller than the metaconid. The protoconulid is very small. The metaconid is well developed and may approach a somewhat rectangular shape, with its length axis in an antero-posterior direction. The hypoconid and the entoconid are thick, while the loph connecting them is narrow. The hypoconid is more oval, while the entoconid has a more rectangular shape. The hypoconid is placed slightly forward with respect to the posterior wall and its anterior tip has thinner enamel compared to its sides. A centroflexid is indistinct in most specimens or is very shallow in some. The mesoflexid and hypoflexid are deep and are connected because of the absence of the protoisthmid in a significant part of the assemblages (Table 2.4). The hypoflexid is near straight or curved. In the latter case, the protoconid is slightly compressed on its postero-labial side. The mesoflexid is sharply curved. Most specimens lack a crochet, but a small incipient or more developed crochet may be present at the inner bend of the mesoflexid. The mesoflexid generally shows a conspicuous internal anterior extension that protrudes into and narrows the protoconid-metaconid connection.

P_4-M_1: The P_4 and M_1 are morphology generally undistinguishable from other *Prolagus* or *Lagopsis* species, having two lobes without any characteristic features. The M_1 generally shows slightly stronger curvature compared to the P_4.

M_2: The M_2 morphology is identical to that of *P. lopezmartinezae*.

REMARKS

The main reasons for the emendations in the diagnosis of *Prolagus tobieni* are the inclusion of the common absense of the protoisthmid and the shallow anterior extension of the mesoflexid in the P_3, the more specified morphology of the P^2 and the exclusion of the strongly compressed talonid in the P_4 and M_1 mentioned by López-Martínez *et al.* (1977). This latter feature has not been confirmed in the material studied here, while its assignment to *P. tobieni* is straight forward. The specified P_3 morphology provides a better distinction from *P. lopezmartinezae*.

The protoisthmid connects the hypoconid-entoconid lobe to the protoconid in the P_3. Even though it may be very narrow in many species, it is a generally very stable character in Neogene European pikas. However, in the *Prolagus lopezmartinezae-tobieni* lineage this stable morphology has become variable. López-Martínez (1984) has shown a single specimen from Moratilla 1, which we assign to *P. lopezmartinezae*, in which the protoisthmid is absent. In *P. tobieni* the absence of the protoisthmid appears to be a common characteristic that is also observed in the holotype (López-Martínez, 1977: 64, fig. 3.2). We consider the increased commonness of this feature as an evolutionary trend within the *P. lopezmartinezae-tobieni* lineage.

The total number of P^2 specimens in the assemblages of Solera and Carrilanga 1 may potentially be slightly underestimated (Table 2.1 & 2.5) due to the fact that the range in the P^2 morphology of *P. tobieni* overlaps with that of *P. oeningensis* (Plate 2.10). The latter species is present in large numbers at these localities. P^2 specimens with a relatively narrow hypercone, without a slightly oblique mesoflexus and lacking a hypoflexus, may possibly have been misidentified.

Our study of the ochotonid material from Nombrevilla 1 (Plate 2.8) and Arroyo del Val 6 (Plate 2.10) (de Bruijn & van Meurs, 1967; López-Martínez, 1989), has shown that the P^3 of *P. tobieni* is present in these assemblages as well, in which they have previously been included in *P. oeningensis*. Nombrevilla 1 therefore contains two ochotonid lineages, *P. oeningensis* and *P. tobieni*, and Arroyo del Val 6 contains four, *L. verus*, *P. oeningensis*, *P. major* and *P. tobieni*, similar to Manchones.

Recently, Angelone & Sesé (2009) provided an emended diagnosis of *P. tobieni* based on the type assemblage and the additional material from Escobosa de Calatañazor described earlier by López-Martínez *et al.* (1977). We consider their diagnosis somewhat too restrictive, not allowing for the variation in the P^2 morphology visible our material. The much flattened talonids of the P_4-M_2, in particular in comparison to those of *P. oeningensis*, is not evident from their drawings (Angelone & Sesé, 2009: 83, fig. 4) and is not confirmed in our material, as is the so-called fishtail shape of the P^4. On the other hand, their diagnosis introduces characteristics of the maxilla and mandible. Although these osteological features could not be verified in our *P. tobieni* and *P. lopezmartinezae* material and in our comparative material of *P. vasconiensis*, we consider these characteristics to possibly have taxonomic importance at the species level. However, the intraspecific variability and the diagnostic value of these morphologies with respect to the other early and middle Miocene *Prolagus* species and remains to be investigated, as has also been noted by López-Martínez (1985).

The presence of a premolar foramen is a synapomorphy of the Ochotonidae (McKenna, 1982; Dawson, 2008). López-Martínez (1974) described a small premolar foramen next to the P^3 and P^2 in *Piezodus branssatensis* VIRET, 1929, which is confirmed by Angelone & Sesé (2009), indicating that the morphology observed in *P. tobieni* is primitive. This also suggests that the position and size of the premolar foramen in *P. vasconiensis*, which is the evolutionary ancestor of all early and middle Miocene *Prolagus* lineages and the last common ancestor in the evolution leading to *P. tobieni* and *P. oeningensis*, is likely to be similar to that of *P. branssatensis* and *P. tobieni* as well. A similar configuration of the premolar foramen is present in *Lagopsis verus* (Plates 2.4 & 2.9).

2.5 Results

The rich succession of small-mammal localities in the study area provides better insight in the evolution of the pika lineages present. The data indicate that the evolution of *Lagopsis penai-verus* and *Prolagus lopezmartinezae-tobieni* is anagenetic.

The evolution of *L. penai* from *L.* aff. *penai* in local zone A (late early Miocene) is characterized by the gradual enlargement and subsequent flattening of the anteroconid in the P_3 (López-Martínez, 1984). The sequence studied here documents the evolution that closely follows after this evolutionary transition in time. *L. penai* shows relatively large variation in size throughout its range and its average size stays fairly unchanged (Figs. 2.2-2.4).

In the top of zone Dd the proportion of P_3's with a cement-filled anteroflexid in the anteroconid consistently exceeds that of anteroconids without a well developed anteroflexid in younger levels. This type of gradual morphological change is very similar to that seen in the late early Miocene. The morphological shift is interpreted as the anagenetic evolution from *L. penai* to *L. verus*.

The presence of the anteroflexid and the presence of crown cement in the anteroflexid do not only depend on evolution and ontogeny, but also on preservation. It is not known in how many of the specimens having the anteroflexid the crown cement has been lost. The category of P_3's that have a distinct anteroflexid, but lack cement, are therefore a possibly a mix. The total number of specimens in an assemblage that originally had cement in the anteroflexid may therefore be slightly underestimated.

Shortly after the morphological transition between *L. penai* and *L. verus*, the width of the P_3 and P^2-P^3 slightly increased (Figs. 2.2B, 2.3B, 2.4B). The largest sizes are recorded between 14 and 13 Ma, after which a slight decrease occurred. This size decrease coincides with a marked decrease in the relative abundance of this lineage. Overall, there is large size overlap between *L. penai* and *L. verus*. The minimum and maximum extremes of *L. penai* and *L. verus*, respectively, do indicate a small difference. However, although some previous studies suggested otherwise, the very modest size difference between these two chronospecies is not large enough to confidently discriminate them on the basis of this characteristic alone.

Similar to the *Lagopsis* lineage, *P. lopezmartinezae* evolved from *P. vasconiensis* in local zone A (López-Martínez, 1984). Unlike *Lagopsis*, which showed evolutionary change in the P_3 and appears to have completely replaced its ancestor, the emergence of *P. lopezmartinezae*, which is at present only known from Spanish localities, is mostly characterized by the morphological evolution of the P^3, while its ancestor, *P. vasconiensis*, was widespread throughout Western Europe where it gave rise to other species as well (López-Martínez, 1997). The origin of *P. lopezmartinezae* is therefore interpreted as being the result of endemic evolution.

The size of *P. lopezmartinezae* teeth does not change in zones B and C (Figs. 2.5-2.7). In zones Da to G1, the record of this lineage is very poor. Therefore, the timing of the anagenetic transition from *P. lopezmartinezae* to *P. tobieni* can not be narrowly constrained. The transition between these two chronospecies is characterized by a change in the morphology, which is most appearent in the P_3. The size appears to change slightly later than the morphology. The size of *P. tobieni* from Manchones (zone G2) fits within the range of both species (Fig. 2.5 & 2.6), but appears to be slightly more similar to that of *P. lopezmartinezae*, while its morphology is characteristic of *P. tobieni*. *P. tobieni* from younger levels are characterized by a slightly wider P_3, P^3 and P^2 (Figs. 2.5B, 2.6B, 2.7B).

The studied record just postdates the early Miocene evolutionary originations of *L. penai* and *P. lopezmartinezae* in zone A. At present it can not be verified whether or not both transitions are simultaneous or in succession. The following anagenetic transition between *L. penai* and *L. verus* is relatively well constrained in time, contrary to the transition between *P. lopezmartinezae* and *P. tobieni*. It is therefore not known whether or not the latter precedes, coincides with or postdates the morphological change observed in *Lagopsis*. The last occurrence of *Lagopsis verus* in the study area is in zone G3. *P. tobieni*, on the other hand, continues into the Vallesian.

2.6 Discussion and conclusions

The *Prolagus vasconiensis – P. lopezmartinezae – P. tobieni* lineage is endemic to Spain. The reduction of the lagiloph in the P^3 observed in *P. lopezmartinezae* marks the onset of endemic evolution in the top of local zone A, which is appearently approximately coincident with the anagenetic evolution within *Lagopsis* to *L. penai*.

The rooted teeth of primitive ochotonids and stem lagomorphs show very significant ontogenetic stages in morphology and size (Tobien, 1974, 1978; Bair, 2007). The variability within an ochotonid population or species with high crowned teeth is partly due to ontogenety as well, although to a significantly lesser degree. López-Martínez (1974) has shown that tooth size is influenced by ontogeneny in *Prolagus*, which is also the case in other high crowned ochotonids, such as *Lagopsis*. The stronger curvature of upper molars of *Lagopsis* results in relatively wider teeth in older individuals in comparison to *Prolagus*.

In evolution, morphological characteristics like the presence of a cement-filled anteroflexid in the P_3 of *Lagopsis* develop in increasingly younger individuals, while it initially formed at a later ontogenetic stage. Since this particular characteristic is considered to be of taxonomic interest, ontogenic stage needs to be taken into account.

The high abundance of *Lagopsis* on the Iberian Peninsula and its consistent presence during the late early and middle Miocene in combination with the observed gradual change in the morphology suggests that it is reasonable to infer that the transition from *L. penai* to *L. verus* in zone Dd reflects evolution and not immigration. A more abrupt change would be expected in case of the latter. Although it cannot be excluded entirely that *L. verus* evolved in a more peripheral region in the range of *L. penai* and subsequently migrated to Spain to replace *L. penai*, it appears plausible that gene flow within *Lagopsis* was possible throughout Western Europe and that *L. penai* evolved to *L. verus* throughout its range.

The new material from the Calatayud-Daroca Basin confirms the view that the evolutionary transition from *L. penai* to *L. verus* is characterized by a shift in morphotype frequency similar to the evolution of *L.* aff. *penai* to *L. penai* from the Ramblian. Such a trend depends on statistical observation and thus requires relatively large assemblages. Species assignments based on small assemblages, such as material from the Madrid Basin (zone E) described by Luis & Hernando (2000) and Cuevas Gonzáles (2005), are consequently provisional.

Although it has generally been used as a distinctive criterion, the rich record from the Daroca-Villafeliche area shows that tooth size alone is a poor discriminating factor for *L. penai* and *L. verus* in the Spanish record. The modest increase in size in Spain may be larger in other areas. López-Martínez (1989) notes that *L. verus* from Anwil and La Grive in central Europe are slightly larger than their equivalents from Spain. On the other hand, the relatively large *Lagopsis* reported by Bolliger & Rummel (1994) and Prieto (2007; *et al.*, 2009) from Petersbuch 6 and 18, cannot be distinguished from *L. verus* from Spain. This suggests that size by itself is probably not a reliable discrimitating factor for *L. penai* and *L. verus* in central Europe as well.

López-Martínez (1989) has indicated that the evolutionary transition from *L. penai* to *L. verus* in Spain occurs between the localities Las Planas 4A and Armantes 7 from local zones E and F, respectively. Cuevas Gonzáles (2005) uses this evolutionary transition as a biostratigraphic criterion for discriminating between these zones. A similar approach is seen in Peláez-Campomanes *et al.* (2003) and Sesé (2006). The middle/upper Aragonian boundary, which is biostratigraphically drawn between zones E and F, has been linked to the major East Antarctic ice-sheet expansion of the Middle Miocene Climate Transition that is reflected in the marine stable oxygen isotope record (van der Meulen & Daams, 1992; Krijgsman *et al.*, 1994).

The relatively high resolution of the data presented here in combination with the refined definition of chronospecies show that the evolutionary succession of *L. penai* to *L. verus* occurs several hundred thousand years earlier than previously thought, in zone Dd (~14.18 Ma; Table 2.1). This evolutionary step therefore precedes the Mi3b oxygen isotope shift in marine benthic foraminifera that marks the main cooling step in the Middle Miocene Climate Transition, which has been dated at ~13.82 Ma in the Mediterranean (Abels *et al.*, 2005). Based on this conclusion, earlier species assignments of *Lagopsis* in Spain in the interval between Dd and F may require revision, as well as related biostratigraphic correlations to the boundary of zones E and F that were based on *Lagopsis*.

Bolliger (1997) and Kälin (1997) indicated a transitional interval in the morphology and size between *L. penai* and *L. verus* in Switzerland. Bolliger (1992) noted that the different stages of development and the high morphological variability within an assemblage require cautious interpretation. Chronospecies assignments are therefore tentative. In comparison to the Spanish record, these authors recognize the transition between *L. penai* and *L. verus* at a distinctly older level, somewhere between 16.5 and 15 Ma (Bolliger, 1997; Kälin, 1997). However, this difference in age may be due to a difference in the application of the characteristics for species assignment. In our opinion, the *L. penai-verus* transition in Switzerland is not necessarily older than that in Spain. Based on published drawings, we consider some of the older assemblages that were assigned to *L. verus* by Kälin (1997) as *L. penai*, as is indicated in the synonymy lists. The exact timing of the succession with respect to our criteria is unclear in the Swiss record, due to the absence of measurement data and detailed morphological information. On the basis of the resemblance between the *Lagopsis* material described in this paper and the available information on *Lagopsis* from Switzerland accompanied with the numerical age estimates provided by Bolliger (1997) and Kempf *et al.* (1997), we hypothesize that the *L. penai-verus* transition in Switzerland possibly occurred in the upper part of the Sagentobel assemblage zone (*sensu* Bolliger, 1997) or the boundary interval of the Rümikon-Öschgraben assemblage zones (*sensu* Kälin & Engesser, 2001; Kälin & Kempf, 2009).

It remains to be investigated in detail whether there are differences in the morphology and size of *Lagopsis* between different regions (e.g. Spain and central Europe) through time. Our small scale comparison between Spanish and German material has not indicated any clear difference between the regions. The presence of *L. penai* at the locality of Sandelzhausen reported by Angelone (2009), which can be dated to around 15.1 Ma on the basis of rodent biostratigraphy in comparison to the partly numerically dated Swiss record, is in agreement with our hypothesis as well. To verify the presence or absence of regional patterns, rich mammal records with excellent time control are required. A detailed overview of the evolution of the *Lagopsis* lineage through time in central Europe is currently unavailable and thus prohibits a detailed comparison with the Spanish record.

Plates chapter 2

Plate 2.1

Lagopsis penai
1. P_3 inv. SR4A-L1A-09; San Roque 4A
2. P_3 SRA4-L1B-06; San Roque 4A
3. P_3 SR4A-L1B-01; San Roque 4A
4. P_3 inv. SR4A-L2A-01; San Roque 4A
5. P_3 SAM-L1B-10; San Marcos
6. P_3 inv. VL2A-VL-91; Villafeliche 2A
7. P_3 inv. SR3-1008; San Roque 3
8. P_3 RGM-433842; Vargas 1A
9. P_3 inv. RGM-433844; Vargas 1A
10. P_3 VR2-L1A-03; Vargas 2A
11. P_3 inv. VR2-L1A-07; Vargas 2A
12. P_3 VR5-L1A-01; Vargas 5
13. P_3 VR5-L1B-01; Vargas 5
14. P_3 VA1A-1A-01; Valdemoros 1A
15. P_3 inv. VA1A-1B-07; Valdemoros 1A
16. P_3 VA1A-1A-04; Valdemoros 1A
17. P_3 LUM3-L1A-03; Las Umbrías 3
18. P_3 inv. LUM3-L1B-01; Las Umbrías 3
19. P_3 inv. LUM3-L1B-02; Las Umbrías 3
20. P_3 inv. LUM3-L1B03; Las Umbrías 3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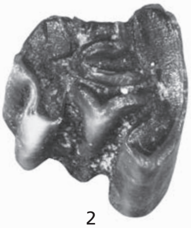
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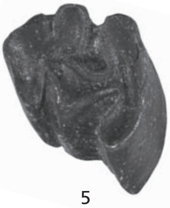
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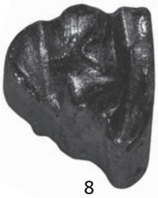
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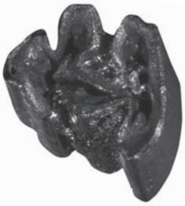
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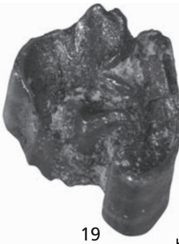
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Plate 2.2

Lagopsis penai
1. P^3 SR4-L3B-05; San Roque 4A
2. P^3 inv. SR4-L4A-08; San Roque 4A
3. P^3 VR2A-L1B-05; Vargas 2A
4. P^3 VA1A-2B-01; Valdemoros 1A
5. P^3 VA1A-2B-06; Valdemoros 1A
6. P^3 inv. SAM-L11B-05; San Marcos
7. P^3 SAM-L9A-03; San Marcos
8. P^3 SAM-L9B-05; San Marcos
9. P^3 SAM-L9A-04; San Marcos
10. P^3 RGM-433860; Vargas 1A
11. P^2 SAM-L16A-02; San Marcos
12. P^2 SAM-L16A-06; San Marcos
13. P^2 RGM-433881; Vargas 1A
14. P^2 RGM-433883; Vargas 1A
15. P^2 inv. RGM-433887; Vargas 1A
16. P^2 inv. VR2B-L1A-05; Vargas 2B
17. P^2 VA1A-4B-01; Valdemoros 1A
18. P^2 inv. VA1A-5A-03; Valdemoros 1A
19. P^2 inv. VA1A-5A-01. Valdemoros 1A

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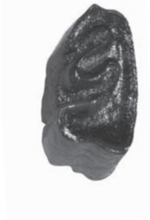

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Plate 2.3

Lagopsis verus

1. P_3 inv. LUM9-L1B-02; Las Umbías 9
2. P_3 inv. LUM9-L1B-03; Las Umbías 9
3. P_3 inv. LUM12-L1A-06; Las Umbías 12
4. P_3 RGM-434309; Valalto 2C
5. P_3 RGM-434310; Valalto 2C
6. P_3 RGM-434313; Valalto 2C
7. P_3 inv. ARM7-58-808; Armantes 7
8. P_3 inv. ARM7-58-804; Armantes 7
9. P_3 inv. ARM7-58-806; Armantes 7
10. P_3 VT1A-L1A-02; Valalto 1A
11. P_3 VT1A-L1A-04; Valalto 1A
12. P_3 MAN-6008B; Manchones
13. P_3 MAN-6007B; Manchones
14. P_3 inv. TOR3B-L1A-08; Toril 3B
15. P_3 TOR3B-L1A-01; Toril 3B
16. P_3 TOR3B-L1A-02; Toril 3B
17. P_3 RGM-435345; Solera
18. P_3 inv. RGM-435354; Solera


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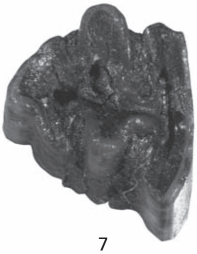
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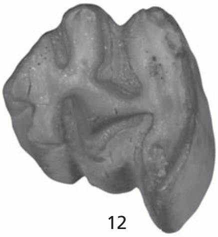
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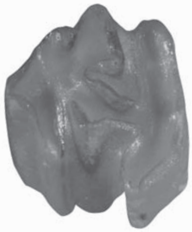
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Plate 2.4

Lagopsis verus
1. P^3 LUM9-L2A-01; Las Umbías 9
2. P^3 RGM-434347; Valalto 2C
3. P^3 inv. ARM7-58-867; Armantes 7
4. P^3 VT1A-L3A-02; Valalto 1A
5. P^3 inv. VT1A-L3B-02; Valalto 1A
6. P^3 MAN-6106A; Manchones
7. P^3-M^2 inv. RGM-434670; Valalto 1B
8. P^3 TOR3B-L4A-03; Toril 3B
9. P^3 TOR3B-L4A-01; Toril 3B
10. P^3 TOR3B-L4A-02; Toril 3B
11. P^3 TOR3B-L4A-04; Toril 3B
12. P^3 RGM-435494; Solera
13. P^2 LUM9-L3A-01; Las Umbías 9
14. P^2 inv. VT1A-L5A-09; Valalto 1A
15. P^2 MAN-6288A; Manchones
16. P^2 inv. TOR3B-L6B-02; Toril 3B
17. P^2 RGM-435610; Solera


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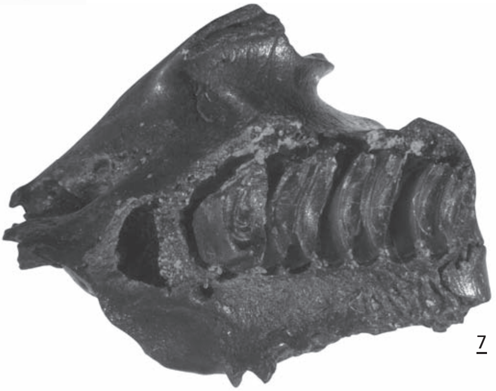
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Plate 2.5

Prolagus lopezmartinezae n. sp.
1. P_3 SR4A-L2B-01; San Roque 4A
2. P_3 inv. SRA4-L3A-01; San Roque 4A
3. P_3 inv. SRA4-L3A-02; San Roque 4A
4. P_3 SAM-L6A-06; San Marcos
5. P_3 SAM-L6A-07; San Marcos
6. P_3 SAM-L6B-01; San Marcos
7. P_3 SAM-L6A-06; San Marcos
8. P_3 SAM-L6B-06; San Marcos
9. P_3 SAM-L6B-07; holotype; San Marcos
10. P_3 inv. SAM-L7A-02; San Marcos
11. P_3 inv. SAM-L7A-07; San Marcos
12. P_3 inv. SAM-L7A-09; San Marcos
13. P_3 inv. SAM-L7A-10; San Marcos
14. P_3 SR3-1009; San Roque 3
15. P_3 inv. RGM-433859; Vargas 1A
16. M_2 inv. SAM-L20B-01; San Marcos


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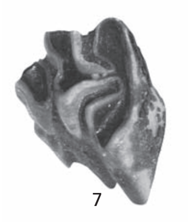
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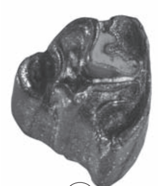
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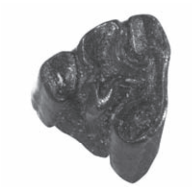
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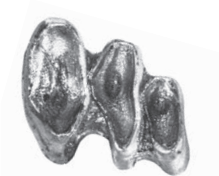
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Plate 2.6

Prolagus lopezmartinezae n. sp.
1. P^3 SR4A-L5A-01; San Roque 4A
2. P^3 SR4A-L5A-02; San Roque 4A
3. P^3 inv. SR4A-L5A-09; San Roque 4A
4. P^3 SAM-L12B-01; San Marcos
5. P^3 SAM-L12B-05; San Marcos
6. P^3 SAM-L12B-06; San Marcos
7. P^3 inv. SAM-L13B-02; San Marcos
8. P^3 inv. SAM-L13B-04; San Marcos
9. P^3 inv. RGM-433878; Vargas 1A
10. P^2 SR4A-L6A-02; San Roque 4A
11. P^2 SR4A-L6A-03; San Roque 4A
12. P^2 SAM-L18B-03; San Marcos
13. P^2 SAM-L18B-05; San Marcos
14. P^2 SAM-L18B-06; San Marcos
15. P^2 inv. SAM-L19A-01; San Marcos
16. P^2 inv. SAM-L19A-01; San Marcos
17. P^2 inv. SAM-L19A-01; San Marcos
18. P^4 SAM-L20B-03; San Marcos
19. P^4 SAM-L20B-04; San Marcos
20. M^1 inv. SAM-L20B-05; San Marcos
21. M^2 inv. SAM-L20B-07; San Marcos
22. M^2 inv. SAM-L20B-08; San Marcos


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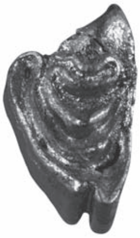
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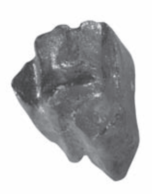
Plate 2.7

Prolagus tobieni
1. P_3 MAN-1341; Manchones
2. P_3 MAN-1342; Manchones
3. P_3 inv. RGM-434175; Toril 1
4. P_3 inv. RGM-434176; Toril 1
5. P_3 TOR3B-L1B-07; Toril 3B
6. P_3 TOR3B-L1B-07; Toril 3B
7. P_3 inv. TOR3B-L2B-01; Toril 3B
8. P_3 inv. TOR3B-L2B-03; Toril 3B
9. P_3 inv. TOR3B-L2B-06; Toril 3B
10. P_3 inv. TOR3B-L3A-01; Toril 3B
11. P_3 inv. TOR3B-L3A-04; Toril 3B
12. P_3 RGM-435457; Solera
13. P_3 RGM-435459; Solera
14. P_3 RGM-433394; Carrilanga 1
15. P_3 RGM-433393; Carrilanga 1
16. P_3 RGM-433395; Carrilanga 1

Prolagus ex. interc. *lopezmartinezae-tobieni*
17. P_3 inv. VR5-L3A-09; Vargas 5
18. P_3 COLD-L2A-07; La Col D
19. P_3 RGM-434407; Valalto 2C
20. P_3 inv. VT1A-L4B-07; Valalto 1A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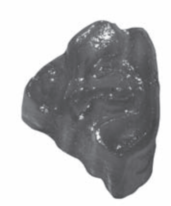
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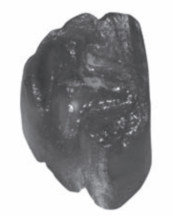
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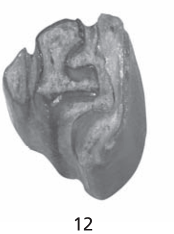
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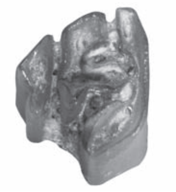
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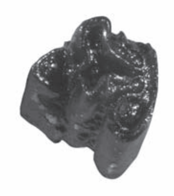
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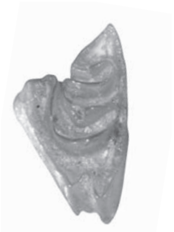
Plate 2.8

Prolagus tobieni
1. P^3 MAN-6241B; Manchones
2. P^3 inv. MAN-1294; Manchones
3. P^3 TOR3B-L4A-07; Toril 3B
4. P^3 TOR3B-L4A-08; Toril 3B
5. P^3 TOR3B-L4A-09; Toril 3B
6. P^3 TOR3B-L4B-03; Toril 3B
7. P^3 inv. TOR3B-L4B-10; Toril 3B
8. P^3 inv. TOR3B-L5A-01; Toril 3B
9. P^3 inv. TOR3B-L5A-05; Toril 3B
10. P^3 inv. PJE2-L3A-08; Paje 2
11. P^3 inv. RGM-435599; Solera
12. P^3 inv. NOM1-NO-335; Nombrevilla 1
13. P^3 inv. CAR- RGM-433536; Carrilanga 1
14. P^3 inv. CAR- RGM-433538; Carrilanga 1
15. P^2 TOR3B-L6B-08; Toril 3B
16. P^2 TOR3B-L6B -09; Toril 3B
17. P^2 inv. TOR3B-L7B -01; Toril 3B
18. P^2 inv. TOR3B-L7B -03; Toril 3B
19. P^2 inv. TOR3B-L7B -04; Toril 3B
20. P^2 inv. TOR3B-L7B -05; Toril 3B
21. P^2 inv. TOR3B-L7B -06; Toril 3B
22. P^2 inv. RGM-435654; Solera
23. P^2 inv. RGM-435636; Solera
24. P^2 RGM-433748; Carrilanga 1
25. P^2 inv. RGM-433780; Carrilanga 1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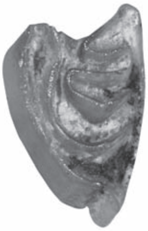
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Plate 2.9: Comparative material

Lagopsis penai
1. P_3 inv. AT3-51-503; Ateca 3
2. P_3 AT3-51-505; Ateca 3
3. P_3 AT3-51-507; Ateca 3
4. P_3 inv. AT3-51-509; Ateca 3
5. P_3 inv. VICO-1A-08; Vieux-Collonges
6. P_3 inv. VICO-1A-07; Vieux-Collonges
7. P_3 inv. TRB1-18-11; Torralba 1
8. P^3 VICO-2B-06; Vieux-Collonges
9. P^3 AT3-51-673; Ateca 3
10. P^2 AT3-51-804; Ateca 3

Lagopsis verus
11. P^3-M^2 inv. AR6-AR-3019; Arroyo del Val 6
12. P_3 AR6-AR-3002; Arroyo del Val 6
13. P_3 AR6-AR-3001; Arroyo del Val 6
14. P_3 AR6-AR-3006; Arroyo del Val 6


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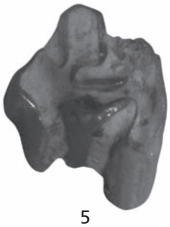
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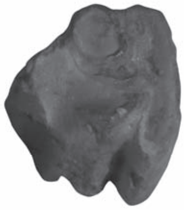
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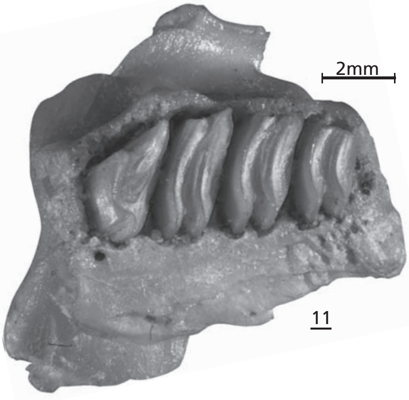

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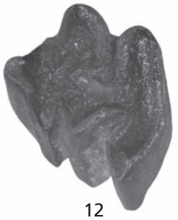
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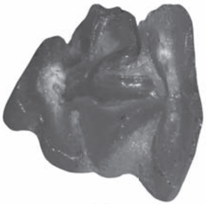
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1mm

Plate 2.10: Comparative material

Prolagus lopezmartinezae
1. P_3 AT3-51-604; Ateca 3
2. P_3 inv. AT3-51-603; Ateca 3
3. P^3 inv. AT3-51-753; Ateca 3
4. P^3 inv. AT3-51-754; Ateca 3

Prolagus tobieni
5. P^3 AR6-AR-3029; Arroyo del Val 6
6. P^4 inv. AR6-unregistered; Arroyo del Val 6

Prolagus oeningensis
7. P_3 SANS-1A-02; Sansan
8. P^3 inv. SANS-2A-04; Sansan
9. P^2 SANS-2B-01; Sansan


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Appendix chapter 2

2A: 1) P_3 size measurements (L, W, Lme, Wpm) of *L. penai* and *L. verus*

P/3 (excl. juveniles)			Length (mm)						Width (mm)						Length m-e (mm)						Width p-m (mm)					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	SOL	*L. verus*	11	1,62	1,77	1,83	0,018	0,058	8	1,80	1,93	2,06	0,035	0,098	11	1,06	1,13	1,21	0,015	0,051	12	1,23	1,40	1,52	0,025	0,086
G3	TOR3B	*L. verus*	8	1,44	1,62	1,80	0,042	0,120	7	1,54	1,81	2,00	0,054	0,143	8	0,90	1,03	1,11	0,023	0,064	8	1,11	1,30	1,42	0,037	0,105
G3	TOR3A	*L. verus*	1		2,01				0						0						1		1,39			
G3	TOR1	*L. verus*	4	1,67	1,76	1,86			4	1,77	1,94	2,01			5	1,06	1,13	1,24	0,032	0,072	4	1,19	1,36	1,45		
G2	BOR	*L. verus*	4	1,61	1,70	1,77			6	1,77	1,94	2,05	0,043	0,104	7	1,01	1,06	1,13	0,018	0,049	7	1,27	1,45	1,60	0,049	0,129
G1	VT1B	*L. verus*	3	1,73	1,95	2,08			2	1,83		1,94			3	1,20	1,30	1,41			3	1,32	1,43	1,52		
G1	VT1A	*L. verus*	11	1,60	1,79	1,95	0,034	0,111	8	1,87	2,01	2,13	0,030	0,085	11	0,99	1,17	1,35	0,033	0,108	10	1,32	1,44	1,69	0,038	0,122
G1	LP5B	*L. verus*	16	1,67	1,81	1,90	0,017	0,066	16	1,67	1,97	2,26	0,035	0,141	22	1,03	1,20	1,32	0,015	0,072	18	1,34	1,44	1,59	0,018	0,078
F	ARM7	*L. verus*	14	1,63	1,81	2,02	0,024	0,091	16	1,61	1,97	2,28	0,038	0,153	22	1,02	1,16	1,33	0,017	0,082	20	1,19	1,38	1,63	0,020	0,089
F	VT2C	*L. verus*	17	1,63	1,82	2,03	0,024	0,099	17	1,77	1,97	2,17	0,026	0,107	25	0,99	1,15	1,27	0,015	0,077	23	1,29	1,44	1,68	0,021	0,099
F	LUM22	*L. verus*	3	1,74	1,84	1,94			3	1,68	1,84	1,95			4	0,93	1,18	1,32			3	1,37	1,41	1,47		
E	LP4BA	*L. verus*	3	1,37	1,56	1,86			2	1,69		2,00			4	0,78	0,95	1,08			6	1,13	1,31	1,45	0,049	0,120
E	LP4A	*L. verus*	22	1,50	1,75	2,13	0,029	0,137	17	1,62	1,88	2,22	0,043	0,178	23	1,04	1,15	1,31	0,015	0,071	22	1,09	1,32	1,59	0,034	0,160
E	LUM12	*L. verus*	6	1,56	1,73	1,85	0,050	0,123	6	1,65	1,87	2,01	0,063	0,153	8	1,01	1,09	1,21	0,021	0,060	8	1,16	1,31	1,52	0,047	0,133
Dd	LUM10	*L. verus*	3	1,62	1,67	1,74			3	1,67	1,85	1,97			4	1,05	1,09	1,13			6	1,12	1,26	1,41	0,043	0,106
Dd	LUM9	*L. verus*	7	1,43	1,62	1,74	0,046	0,122	6	1,54	1,73	2,06	0,088	0,217	9	0,96	1,09	1,29	0,036	0,109	8	1,13	1,27	1,59	0,051	0,144
Dd	LUM3	*L. penai*	7	1,52	1,69	1,80	0,036	0,096	12	1,55	1,80	2,02	0,043	0,148	13	0,92	1,09	1,22	0,024	0,087	13	1,17	1,31	1,45	0,027	0,096
Dd	VA3F	*L. penai*	8	1,48	1,61	1,77	0,042	0,118	6	1,47	1,62	1,79	0,050	0,124	11	0,87	1,03	1,21	0,032	0,105	6	1,12	1,19	1,28	0,028	0,068
Dd	VA1A	*L. penai*	21	1,50	1,68	1,86	0,023	0,107	17	1,51	1,71	1,90	0,030	0,125	25	0,99	1,13	1,25	0,015	0,076	21	1,12	1,27	1,47	0,018	0,082
Dc	VA3B	*L. penai*	26	1,43	1,58	1,84	0,021	0,106	28	1,37	1,65	1,90	0,022	0,117	31	0,84	1,00	1,16	0,016	0,091	24	0,98	1,20	1,38	0,020	0,097
Dc	VR5	*L. penai*	14	1,27	1,59	1,75	0,030	0,113	20	1,29	1,68	1,90	0,032	0,145	23	0,78	1,00	1,11	0,015	0,072	24	0,84	1,22	1,48	0,030	0,148
Db	COL-D	*L. penai*	10	1,69	1,81	1,95	0,027	0,086	8	1,57	1,81	2,00	0,055	0,156	11	1,13	1,23	1,39	0,023	0,077	9	1,16	1,34	1,56	0,041	0,124
Da	FTE3	*L. penai*	5	1,60	1,67	1,75	0,027	0,061	5	1,52	1,59	1,68	0,027	0,060	5	1,01	1,07	1,16	0,029	0,065	7	1,12	1,23	1,37	0,031	0,082
Da	FTE2	*L. penai*	6	1,56	1,65	1,74	0,030	0,073	6	1,53	1,73	2,01	0,070	0,172	6	1,07	1,10	1,13	0,011	0,028	6	1,20	1,28	1,42	0,034	0,084
Da	OR9	*L. penai*	8	1,22	1,63	1,90	0,081	0,230	6	1,40	1,63	1,91	0,091	0,223	8	0,87	1,04	1,20	0,042	0,119	12	0,85	1,18	1,55	0,061	0,211
Da	VR2B	*L. penai*	0						0						0						0					
C	VR2A	*L. penai*	4	1,54	1,73	2,00			3	1,55	1,75	1,93			5	1,05	1,15	1,31	0,060	0,135	3	1,05	1,24	1,35	0,095	0,165
C	OR8	*L. penai*	6	1,58	1,69	1,79	0,033	0,082	7	1,60	1,71	1,81	0,032	0,086	8	1,01	1,11	1,15	0,017	0,048	7	1,11	1,23	1,35	0,034	0,090
C	VR1A	*L. penai*	9	1,43	1,59	1,71	0,032	0,096	7	1,47	1,59	1,84	0,052	0,136	9	0,99	1,05	1,11	0,015	0,045	10	1,03	1,19	1,39	0,031	0,099
C	VR4BB	*L. penai*	12	1,31	1,54	1,81	0,038	0,133	13	1,31	1,52	1,89	0,038	0,138	15	0,85	1,04	1,20	0,022	0,086	14	0,89	1,09	1,32	0,030	0,111
C	VR4A	*L. penai*	13	1,26	1,55	1,73	0,038	0,137	11	1,35	1,63	1,81	0,047	0,154	14	0,84	1,04	1,22	0,026	0,096	13	0,98	1,21	1,44	0,050	0,179
C	SR3	*L. penai*	23	1,32	1,60	1,77	0,021	0,103	20	1,46	1,71	1,92	0,029	0,131	26	0,93	1,07	1,22	0,016	0,081	23	0,94	1,18	1,52	0,026	0,126
B	VL2A	*L. penai*	31	1,47	1,66	1,81	0,017	0,093	25	1,44	1,73	2,05	0,029	0,147	38	0,92	1,09	1,23	0,011	0,068	27	1,04	1,26	1,46	0,021	0,108
B	SAM	*L. penai*	73	1,49	1,67	1,86	0,011	0,092	68	1,38	1,74	2,03	0,015	0,122	80	0,89	1,11	1,27	0,008	0,074	74	1,04	1,28	1,46	0,011	0,095
B	OR2	*L. penai*	45	1,32	1,61	1,83	0,021	0,138	44	1,32	1,69	2,00	0,021	0,138	50	0,93	1,09	1,21	0,011	0,076	53	1,01	1,26	1,69	0,019	0,136
A	SR4A	*L. penai*	14	1,30	1,65	1,92	0,039	0,147	15	1,48	1,63	1,75	0,021	0,083	18	0,92	1,11	1,22	0,020	0,085	14	1,09	1,23	1,46	0,027	0,099
	Vieux-C.	*L. penai*	6	1,60	1,72	2,00	0,066	0,162	4	1,59	1,69	1,82			5	1,02	1,11	1,19	0,028	0,063	8	1,03	1,28	1,73	0,074	0,209

2A: 2) P_3 size measurements (La, Wa, L/W, La/Wa) of *L. penai* and *L. verus*. Juvenile specimens are excluded.

P/3 (excl. juveniles)			Length a (mm)						Width a (mm)						Length / Width						Length a / Width a					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	SOL	*L. verus*	13	0,43	0,60	0,66	0,017	0,062	11	0,97	1,15	1,30	0,030	0,100	8	0,85	0,93	1,02	0,018	0,052	11	0,45	0,54	0,63	0,016	0,053
G3	TOR3B	*L. verus*	8	0,43	0,57	0,70	0,031	0,087	8	0,73	1,05	1,34	0,064	0,180	7	0,84	0,89	0,94	0,011	0,029	8	0,44	0,55	0,70	0,029	0,083
G3	TOR3A	*L. verus*	1		0,79				1		0,89				0						1		0,89			
G3	TOR1	*L. verus*	4	0,47	0,60	0,66			4	1,10	1,15	1,25			4	0,87	0,91	0,94			4	0,42	0,52	0,60		
G2	BOR	*L. verus*	4	0,56	0,60	0,62			5	1,02	1,15	1,26	0,040	0,090	4	0,84	0,87	0,89			4	0,53	0,54	0,55		
G1	VT1B	*L. verus*	3	0,53	0,62	0,70			2	0,95		1,00			2	1,06		1,14			2	0,56		0,70		
G1	VT1A	*L. verus*	11	0,56	0,63	0,71	0,016	0,055	11	0,96	1,14	1,30	0,032	0,107	8	0,82	0,90	0,97	0,021	0,058	11	0,44	0,56	0,64	0,017	0,055
G1	LP5B	*L. verus*	16	0,58	0,65	0,79	0,013	0,050	14	0,85	1,10	1,21	0,025	0,095	13	0,81	0,93	1,11	0,021	0,076	14	0,51	0,59	0,78	0,019	0,070
F	ARM7	*L. verus*	17	0,50	0,62	0,79	0,017	0,070	14	0,88	1,10	1,29	0,027	0,100	12	0,81	0,91	1,01	0,017	0,058	14	0,49	0,56	0,65	0,013	0,049
F	VT2C	*L. verus*	20	0,51	0,64	0,79	0,016	0,070	20	0,98	1,20	1,50	0,034	0,153	13	0,85	0,91	1,01	0,014	0,049	19	0,44	0,53	0,64	0,013	0,056
F	LUM22	*L. verus*	3	0,46	0,56	0,62			3	0,69	1,03	1,21			3	0,97	1,00	1,04			3	0,50	0,56	0,67		
E	LP4BA	*L. verus*	5	0,48	0,63	0,78	0,054	0,121	6	0,93	1,08	1,29	0,057	0,141	2	0,81		0,93			5	0,52	0,58	0,62	0,018	0,040
E	LP4A	*L. verus*	23	0,41	0,58	0,85	0,022	0,106	20	0,82	1,09	1,41	0,037	0,167	16	0,81	0,94	1,11	0,021	0,082	18	0,42	0,56	0,77	0,023	0,097
E	LUM12	*L. verus*	6	0,51	0,62	0,74	0,034	0,084	6	0,87	1,01	1,23	0,050	0,122	6	0,85	0,93	1,03	0,024	0,060	6	0,52	0,62	0,67	0,022	0,054
Dd	LUM10	*L. verus*	6	0,51	0,56	0,60	0,014	0,035	4	0,97	1,10	1,28			3	0,83	0,90	0,97			4	0,47	0,53	0,58		
Dd	LUM9	*L. verus*	8	0,34	0,55	0,65	0,040	0,113	5	0,86	0,93	1,08	0,039	0,087	6	0,83	0,97	1,12	0,052	0,126	5	0,39	0,61	0,71	0,061	0,136
Dd	LUM3	*L. penai*	8	0,50	0,58	0,68	0,020	0,058	7	0,86	1,08	1,27	0,063	0,168	7	0,85	0,92	0,99	0,019	0,050	7	0,45	0,53	0,62	0,024	0,064
Dd	VA3F	*L. penai*	7	0,48	0,55	0,61	0,019	0,050	7	0,84	0,98	1,12	0,047	0,124	6	0,97	1,01	1,04	0,011	0,028	7	0,44	0,57	0,73	0,034	0,090
Dd	VA1A	*L. penai*	25	0,43	0,56	0,65	0,013	0,067	17	0,71	1,05	1,32	0,041	0,167	14	0,83	0,98	1,19	0,026	0,098	17	0,42	0,55	0,89	0,026	0,107
Dc	VA3B	*L. penai*	26	0,37	0,54	0,69	0,013	0,068	25	0,77	1,03	1,35	0,029	0,147	24	0,84	0,95	1,10	0,013	0,062	24	0,40	0,54	0,64	0,014	0,070
Dc	VR5	*L. penai*	23	0,43	0,55	0,65	0,011	0,055	20	0,77	1,01	1,23	0,027	0,122	13	0,89	0,96	1,01	0,009	0,034	18	0,45	0,55	0,66	0,013	0,057
Db	COL-D	*L. penai*	10	0,50	0,58	0,66	0,016	0,049	9	0,96	1,14	1,38	0,041	0,123	7	0,89	0,99	1,14	0,035	0,091	9	0,43	0,51	0,65	0,024	0,072
Da	FTE3	*L. penai*	7	0,51	0,55	0,59	0,011	0,030	7	0,91	1,00	1,09	0,023	0,061	5	0,99	1,05	1,09	0,019	0,042	7	0,50	0,55	0,63	0,016	0,042
Da	FTE2	*L. penai*	6	0,45	0,56	0,63	0,031	0,076	6	1,02	1,07	1,14	0,022	0,055	6	0,81	0,96	1,14	0,045	0,110	6	0,40	0,53	0,62	0,039	0,095
Da	OR9	*L. penai*	10	0,32	0,56	0,69	0,039	0,124	8	0,56	0,98	1,46	0,101	0,286	6	0,87	0,99	1,09	0,035	0,086	8	0,47	0,59	0,69	0,026	0,075
Da	VR2B	*L. penai*	0						0						0						0					
C	VR2A	*L. penai*	4	0,48	0,56	0,66			4	0,98	1,17	1,28			3	0,89	0,94	0,99			4	0,40	0,48	0,52		
C	OR8	*L. penai*	6	0,48	0,55	0,63	0,024	0,058	6	0,94	1,03	1,12	0,030	0,072	6	0,88	0,98	1,09	0,029	0,071	6	0,48	0,54	0,64	0,028	0,069
C	VR1A	*L. penai*	10	0,41	0,51	0,59	0,018	0,056	9	0,66	0,95	1,12	0,046	0,139	7	0,88	0,99	1,13	0,030	0,079	9	0,44	0,56	0,85	0,040	0,121
C	VR4BB	*L. penai*	13	0,43	0,51	0,62	0,014	0,051	11	0,67	0,84	0,94	0,027	0,090	10	0,87	1,01	1,18	0,027	0,086	10	0,46	0,60	0,76	0,024	0,076
C	VR4A	*L. penai*	14	0,33	0,50	0,67	0,023	0,084	11	0,69	1,00	1,24	0,060	0,199	10	0,90	0,97	1,07	0,018	0,056	11	0,43	0,54	0,64	0,023	0,075
C	SR3	*L. penai*	25	0,42	0,54	0,65	0,011	0,053	23	0,75	0,98	1,16	0,022	0,107	20	0,81	0,94	1,08	0,016	0,070	22	0,44	0,56	0,76	0,014	0,068
B	VL2A	*L. penai*	33	0,41	0,54	0,66	0,010	0,058	29	0,66	1,01	1,35	0,030	0,160	24	0,88	0,97	1,08	0,012	0,058	28	0,45	0,54	0,70	0,012	0,065
B	SAM	*L. penai*	76	0,45	0,55	0,67	0,006	0,055	67	0,75	1,00	1,25	0,015	0,120	63	0,83	0,96	1,13	0,008	0,063	67	0,39	0,55	0,78	0,009	0,075
B	OR2	*L. penai*	49	0,30	0,53	0,68	0,012	0,084	47	0,70	0,97	1,22	0,020	0,137	39	0,80	0,95	1,13	0,012	0,075	46	0,35	0,55	0,79	0,012	0,081
A	SR4A	*L. penai*	15	0,37	0,55	0,66	0,018	0,071	14	0,71	0,95	1,21	0,036	0,137	12	0,80	1,00	1,14	0,030	0,103	14	0,37	0,58	0,78	0,028	0,103
	Vieux-C.	*L. penai*	9	0,50	0,61	0,73	0,025	0,075	4	0,92	1,05	1,13	0,052	0,103	4	0,95	0,99	1,01	0,013	0,026	4	0,52	0,58	0,70	0,040	0,081

2B: 1) P^3 size measurements (L, W, Wmh, Wdh) of *L. penai* and *L. verus*

P3/ (excl. juveniles)			Length (mm)						Width (mm)						Width mh (mm)						Width dh (mm)					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	SOL	*L. verus*	11	1,21	1,38	1,49	0,024	0,080	4	2,30	2,69	2,95	0,137	0,274	10	1,44	1,78	2,14	0,063	0,199	7	1,58	2,04	2,31	0,108	0,287
G3	TOR3B	*L. verus*	3	1,24	1,35	1,42			2	2,31		2,71			3	1,38	1,77	1,97			3	1,55	1,94	2,27		
G3	TOR3A	*L. verus*	0						0						0						0					
G3	TOR1	*L. verus*	9	1,14	1,4022	1,53	0,049	0,146	5	2,41	2,846	3,12	0,124	0,276	6	1,23	1,96	2,32	0,162	0,397	6	1,53	2,21	2,61	0,155	0,381
G2	BOR	*L. verus*	4	1,29	1,33	1,38			1		3,08				3	2,06	2,19	2,33			2	2,42		2,44		
G1	VT1B	*L. verus*	5	1,18	1,37	1,52	0,055	0,122	3	2,69	2,89	3,17			5	1,68	1,84	2,08	0,072	0,160	4	1,89	2,15	2,45		
G1	VT1A	*L. verus*	7	1,18	1,36	1,43	0,037	0,097	2	3,06		3,10			5	1,72	1,95	2,39	0,122	0,274	4	2,05	2,31	2,79		
G1	LP5B	*L. verus*	11	1,23	1,40	1,53	0,028	0,093	6	2,12	2,76	3,33	0,207	0,507	14	1,67	1,97	2,34	0,057	0,213	13	1,84	2,20	2,65	0,070	0,253
F	ARM7	*L. verus*	15	1,20	1,38	1,48	0,023	0,088	2	2,56		2,73			14	1,68	1,90	2,15	0,043	0,161	8	1,91	2,14	2,41	0,071	0,200
F	VT2C	*L. verus*	40	1,15	1,40	1,61	0,015	0,097	14	2,28	2,82	3,35	0,091	0,341	24	1,32	1,86	2,44	0,059	0,289	17	1,60	2,09	2,72	0,080	0,331
F	LUM22	*L. verus*	5	1,32	1,42	1,52	0,033	0,074	1		3,02				3	1,50	1,90	2,31			3	1,66	2,16	2,62		
E	LP4BA	*L. verus*	9	1,16	1,31	1,43	0,027	0,082	5	2,48	2,87	3,36	0,142	0,317	8	1,50	1,78	2,00	0,060	0,170	8	1,80	2,05	2,28	0,055	0,154
E	LP4A	*L. verus*	31	1,13	1,37	1,55	0,018	0,098	17	2,37	2,83	3,09	0,050	0,205	27	1,44	1,80	2,21	0,040	0,210	24	1,62	2,06	2,58	0,048	0,236
E	LUM12	*L. verus*	9	1,08	1,26	1,38	0,033	0,100	5	2,25	2,73	3,02	0,143	0,320	7	1,32	1,65	1,85	0,070	0,185	6	1,61	1,94	2,14	0,083	0,205
Dd	LUM10	*L. verus*	11	1,13	1,29	1,51	0,034	0,112	5	2,39	2,84	3,46	0,185	0,413	8	1,25	1,71	2,34	0,112	0,317	6	1,48	1,99	2,70	0,162	0,396
Dd	LUM9	*L. verus*	7	1,21	1,32	1,57	0,047	0,124	5	2,13	2,48	2,81	0,135	0,302	6	1,47	1,76	1,97	0,083	0,203	5	1,82	2,04	2,21	0,077	0,173
Dd	LUM3	*L. penai*	15	1,18	1,27	1,47	0,022	0,085	12	2,25	2,62	3,20	0,072	0,248	14	1,47	1,67	1,95	0,042	0,159	14	1,74	1,88	2,13	0,036	0,133
Dd	VA3F	*L. penai*	12	1,09	1,22	1,28	0,014	0,050	6	2,26	2,48	2,71	0,079	0,194	10	1,23	1,63	2,01	0,085	0,268	9	1,39	1,80	2,27	0,094	0,283
Dd	VA1A	*L. penai*	33	1,14	1,36	1,57	0,015	0,089	20	2,21	2,55	2,95	0,049	0,217	33	1,30	1,67	2,03	0,034	0,197	30	1,53	1,91	2,32	0,038	0,210
Dc	VA3B	*L. penai*	44	0,98	1,22	1,36	0,012	0,077	31	2,16	2,43	2,98	0,032	0,180	39	1,03	1,57	2,23	0,038	0,239	40	1,26	1,81	2,36	0,040	0,254
Dc	VR5	*L. penai*	27	1,08	1,22	1,38	0,014	0,073	11	1,95	2,32	2,65	0,066	0,219	26	1,19	1,61	1,93	0,034	0,175	20	1,49	1,86	2,16	0,039	0,175
Db	COL-D	*L. penai*	7	1,28	1,35	1,43	0,022	0,057	2	2,60		2,65			8	1,60	1,78	1,99	0,047	0,134	7	1,72	1,96	2,19	0,068	0,181
Da	FTE3	*L. penai*	5	1,19	1,26	1,32	0,024	0,053	3	2,36	2,45	2,59			6	1,23	1,60	1,88	0,089	0,219	5	1,48	1,93	2,36	0,156	0,350
Da	FTE2	*L. penai*	9	1,11	1,22	1,34	0,026	0,079	5	2,06	2,34	2,60	0,107	0,238	8	1,16	1,55	1,78	0,076	0,216	8	1,27	1,74	2,00	0,089	0,252
Da	OR9	*L. penai*	6	1,17	1,28	1,35	0,026	0,065	0						3	1,64	1,69	1,75			2	1,98		2,00		
Da	VR2B	*L. penai*	0						0						0						0					
Cb	VR2A	*L. penai*	6	1,23	1,36	1,67	0,067	0,165	4	2,09	2,31	2,48			5	1,34	1,56	1,81	0,095	0,212	3	1,56	1,68	1,86		
Cb	OR8	*L. penai*	6	1,12	1,28	1,39	0,043	0,107	3	2,28	2,37	2,47			6	1,43	1,58	1,73	0,056	0,137	5	1,58	1,78	2,01	0,081	0,181
Cb	VR1A	*L. penai*	13	1,10	1,27	1,50	0,029	0,104	6	1,84	2,51	3,03	0,159	0,389	12	1,25	1,59	1,78	0,057	0,199	11	1,37	1,82	2,15	0,072	0,240
Cb	VR4BB	*L. penai*	15	1,03	1,23	1,34	0,023	0,088	5	2,18	2,42	2,71	0,092	0,207	8	1,14	1,54	1,89	0,076	0,215	8	1,47	1,77	2,15	0,078	0,220
Cb	VR4A	*L. penai*	24	1,07	1,20	1,30	0,012	0,061	8	2,14	2,37	2,56	0,043	0,122	23	1,04	1,58	2,00	0,048	0,229	17	1,33	1,80	2,21	0,055	0,229
Ca	SR3	*L. penai*	21	1,08	1,22	1,38	0,015	0,068	9	2,01	2,31	2,57	0,067	0,201	19	1,06	1,53	2,07	0,050	0,220	18	1,24	1,74	2,22	0,054	0,230
B	VL2A	*L. penai*	45	1,06	1,25	1,41	0,013	0,087	24	2,18	2,56	3,17	0,050	0,245	45	1,21	1,67	2,25	0,034	0,231	40	1,43	1,88	2,40	0,035	0,222
B	SAM	*L. penai*	63	1,11	1,29	1,46	0,009	0,072	37	2,27	2,61	2,87	0,027	0,162	59	1,29	1,71	2,08	0,025	0,188	53	1,54	1,94	2,36	0,028	0,205
B	OR2	*L. penai*	64	1,12	1,28	1,45	0,010	0,079	27	2,17	2,56	3,19	0,047	0,247	51	1,10	1,66	2,61	0,041	0,293	48	1,23	1,90	2,85	0,045	0,312
A	SR4A	*L. penai*	14	1,20	1,27	1,42	0,018	0,069	6	2,19	2,40	2,60	0,060	0,147	16	1,39	1,64	2,05	0,041	0,165	14	1,64	1,85	2,21	0,043	0,161
	Vieux-C.	*L. penai*	4	1,14	1,26	1,30			4	2,23	2,47	2,57			4	1,48	1,53	1,60			3	1,88	1,89	1,91		

2B: 2) P^3 size measurements (Lpl, L/W, Wmh/L, Wmh/W) of *L. penai* and *L. verus*. Juvenile specimens are excluded.

P3/ (excl. juveniles)			Length pl (mm)						Length / Width						Width mh / Length						Width mh / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	SOL	*L. verus*	8	0,70	0,85	0,98	0,035	0,098	4	0,47	0,52	0,62			10	1,01	1,30	1,53	0,053	0,167	3	0,63	0,66	0,71		
G3	TOR3B	*L. verus*	3	0,82	0,88	0,93			2	0,52		0,54			3	1,11	1,30	1,42			2	0,60		0,72		
G3	TOR3A	*L. verus*	0						0						0						0					
G3	TOR1	*L. verus*	8	0,84	0,93	1,01	0,026	0,073	5	0,44	0,49	0,51	0,014	0,031	6	1,03	1,36	1,54	0,076	0,187	4	0,51	0,65	0,79		
G2	BOR	*L. verus*	4	0,74	0,82	0,86			1		0,44				3	1,60	1,68	1,81			1		0,71			
G1	VT1B	*L. verus*	3	0,86	0,88	0,92			3	0,48	0,49	0,51			5	1,24	1,35	1,42	0,031	0,068	3	0,61	0,65	0,70		
G1	VT1A	*L. verus*	4	0,70	0,78	0,84			2	0,45		0,46			4	1,21	1,41	1,73			2	0,55		0,78		
G1	LP5B	*L. verus*	11	0,78	0,88	1,05	0,022	0,074	6	0,44	0,51	0,61	0,029	0,071	7	1,24	1,47	1,72	0,066	0,175	4	0,55	0,66	0,75		
F	ARM7	*L. verus*	12	0,78	0,86	1,04	0,021	0,074	2	0,49		0,52			13	1,19	1,37	1,56	0,028	0,101	2	0,68		0,70		
F	VT2C	*L. verus*	34	0,53	0,86	1,11	0,018	0,105	14	0,41	0,51	0,67	0,017	0,065	23	0,88	1,31	1,68	0,044	0,210	12	0,54	0,64	0,76	0,019	0,067
F	LUM22	*L. verus*	6	0,66	0,84	0,93	0,038	0,093	1		0,48				3	1,14	1,36	1,59			1		0,76			
E	LP4BA	*L. verus*	10	0,74	0,85	0,99	0,023	0,072	5	0,41	0,45	0,47	0,011	0,024	8	1,17	1,34	1,49	0,041	0,117	5	0,54	0,63	0,68	0,027	0,060
E	LP4A	*L. verus*	26	0,66	0,87	1,03	0,017	0,087	17	0,42	0,48	0,53	0,009	0,036	26	0,98	1,31	1,60	0,026	0,134	15	0,52	0,62	0,77	0,021	0,082
E	LUM12	*L. verus*	7	0,68	0,77	0,86	0,027	0,071	4	0,44	0,48	0,53			6	1,02	1,32	1,57	0,081	0,198	4	0,51	0,62	0,77		
Dd	LUM10	*L. verus*	12	0,60	0,76	0,98	0,028	0,095	5	0,41	0,46	0,50	0,015	0,033	8	1,02	1,28	1,64	0,072	0,202	4	0,49	0,60	0,68		
Dd	LUM9	*L. verus*	7	0,67	0,79	0,95	0,034	0,089	4	0,46	0,50	0,56			6	1,20	1,33	1,47	0,044	0,108	4	0,61	0,68	0,73		
Dd	LUM3	*L. penai*	15	0,54	0,79	0,94	0,027	0,104	12	0,43	0,49	0,59	0,012	0,042	11	1,21	1,36	1,60	0,039	0,129	9	0,59	0,66	0,74	0,018	0,053
Dd	VA3F	*L. penai*	9	0,63	0,74	0,88	0,027	0,082	6	0,45	0,49	0,56	0,021	0,051	10	0,98	1,32	1,68	0,069	0,219	5	0,54	0,58	0,68	0,025	0,055
Dd	VA1A	*L. penai*	30	0,70	0,84	1,02	0,016	0,087	20	0,46	0,54	0,65	0,012	0,052	32	0,89	1,24	1,52	0,025	0,141	20	0,49	0,67	0,77	0,018	0,078
Dc	VA3B	*L. penai*	39	0,57	0,75	0,95	0,013	0,078	30	0,43	0,51	0,62	0,008	0,044	38	0,92	1,29	1,76	0,030	0,185	27	0,56	0,64	0,80	0,012	0,064
Dc	VR5	*L. penai*	23	0,56	0,71	0,93	0,018	0,086	9	0,47	0,51	0,58	0,013	0,040	22	1,03	1,32	1,51	0,032	0,149	10	0,59	0,70	0,80	0,019	0,060
Db	COL-D	*L. penai*	5	0,81	0,85	0,89	0,013	0,029	2	0,49		0,54			7	1,15	1,30	1,42	0,039	0,102	2	0,68		0,71		
Da	FTE3	*L. penai*	3	0,75	0,78	0,80			2	0,52		0,55			4	0,93	1,28	1,58			2	0,51		0,72		
Da	FTE2	*L. penai*	8	0,68	0,78	0,88	0,024	0,067	4	0,50	0,51	0,52			8	1,04	1,26	1,42	0,052	0,146	4	0,68	0,70	0,75		
Da	OR9	*L. penai*	4	0,00	0,60	0,96			0						3	1,21	1,30	1,39			0					
Da	VR2B	*L. penai*	0						0						0						0					
Cb	VR2A	*L. penai*	6	0,70	0,86	1,17	0,068	0,166	4	0,50	0,55	0,63			5	1,05	1,14	1,29	0,042	0,094	3	0,56	0,59	0,62		
Cb	OR8	*L. penai*	6	0,61	0,76	0,95	0,045	0,111	3	0,55	0,56	0,56			5	1,05	1,27	1,48	0,073	0,164	2	0,70		0,76		
Cb	VR1A	*L. penai*	11	0,68	0,81	1,08	0,035	0,116	6	0,44	0,52	0,60	0,026	0,063	12	1,01	1,25	1,43	0,045	0,155	6	0,58	0,66	0,70	0,019	0,046
Cb	VR4BB	*L. penai*	11	0,62	0,73	0,85	0,020	0,066	4	0,43	0,51	0,57			7	0,86	1,22	1,48	0,080	0,212	2	0,59		0,61		
Cb	VR4A	*L. penai*	16	0,64	0,72	0,78	0,013	0,053	8	0,47	0,51	0,57	0,012	0,033	21	0,83	1,33	1,74	0,044	0,203	7	0,55	0,63	0,76	0,028	0,074
Ca	SR3	*L. penai*	15	0,60	0,73	0,85	0,023	0,087	9	0,47	0,53	0,62	0,015	0,046	19	0,98	1,25	1,58	0,035	0,155	9	0,53	0,65	0,76	0,024	0,073
B	VL2A	*L. penai*	40	0,58	0,75	0,98	0,016	0,101	22	0,42	0,49	0,57	0,007	0,033	40	0,98	1,32	1,74	0,027	0,168	22	0,52	0,62	0,78	0,014	0,065
B	SAM	*L. penai*	43	0,60	0,75	0,88	0,010	0,068	36	0,44	0,49	0,55	0,006	0,035	56	1,00	1,35	1,63	0,021	0,155	34	0,55	0,66	0,79	0,010	0,060
B	OR2	*L. penai*	45	0,58	0,77	0,91	0,013	0,086	27	0,45	0,50	0,57	0,006	0,032	50	0,93	1,30	2,04	0,029	0,206	25	0,47	0,61	0,77	0,015	0,073
A	SR4A	*L. penai*	10	0,55	0,73	0,86	0,028	0,089	5	0,49	0,54	0,57	0,013	0,030	13	1,10	1,31	1,71	0,041	0,147	4	0,60	0,69	0,74		
	Vieux-C.	*L. penai*	3	0,75	0,83	0,92			4	0,50	0,51	0,51			2	1,19		1,24			2	0,60		0,63		

2C: P^2 size measurements (L, W, Wdh, Lpl, L/W) of *L. penai* and *L. verus*. Juvenile specimens are excluded. The isolated mesial accessory cusp is not included in the measurement when present.

P2/ (excl. juveniles)			Length (mm)						Width (mm)						Width dh (mm)						Length pl (mm)						Length / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	SOL	*L. verus*	6	0,79	0,88	0,98	0,025	0,060	6	1,54	1,71	1,79	0,038	0,092	7	0,20	0,27	0,38	0,024	0,063	5	0,75	0,83	0,88	0,024	0,053	5	0,47	0,52	0,57	0,019	0,042
G3	TOR3B	*L. verus*	12	0,83	0,93	1,05	0,017	0,059	13	1,73	1,84	1,92	0,018	0,066	12	0,24	0,33	0,46	0,019	0,067	13	0,65	0,82	0,95	0,029	0,103	12	0,44	0,50	0,56	0,010	0,036
G3	TOR3A	*L. verus*	0						0						0						0						0					
G3	TOR1	*L. verus*	0						0						0						0						0					
G2	BOR	*L. verus*	4	0,75	0,91	1,02			4	1,78	1,85	1,95			4	0,30	0,33	0,40			5	0,67	0,80	0,91	0,039	0,088	4	0,42	0,49	0,55		
G1	VT1B	*L. verus*	1		1,14				2	1,73		1,91			2	0,20		0,6			2	0,73		1,09			1		0,66			
G1	VT1A	*L. verus*	8	0,91	1,00	1,10	0,024	0,067	9	1,62	1,96	2,21	0,067	0,201	7	0,30	0,41	0,55	0,038	0,101	9	0,67	0,86	1,05	0,043	0,129	7	0,46	0,50	0,57	0,014	0,038
G1	LP5B	*L. verus*	6	0,87	0,95	1,04	0,024	0,059	5	1,65	1,82	2,02	0,080	0,178	5	0,25	0,36	0,41	0,031	0,069	6	0,82	0,87	1,00	0,027	0,066	5	0,47	0,51	0,55	0,016	0,036
F	ARM7	*L. verus*	12	0,76	0,93	1,04	0,025	0,087	9	1,64	1,80	1,94	0,035	0,105	12	0,21	0,39	0,58	0,031	0,109	14	0,67	0,85	0,95	0,023	0,087	8	0,46	0,52	0,61	0,019	0,053
F	VT2C	*L. verus*	12	0,79	0,98	1,17	0,038	0,133	12	1,58	1,88	2,25	0,052	0,179	12	0,20	0,37	0,57	0,029	0,100	12	0,70	0,85	1,05	0,028	0,097	12	0,44	0,52	0,63	0,016	0,054
F	LUM22	*L. verus*	2	0,98		1,17			2	1,90		1,94			2	0,34		0,34			1		0,84				2	0,52		0,60		
E	LP4BA	*L. verus*	2	0,90		0,99			4	1,58	1,74	1,91			5	0,21	0,32	0,40	0,034	0,076	4	0,66	0,75	0,81	0,032	0,064	2	0,48		0,52		
E	LP4A	*L. verus*	13	0,78	0,90	1,08	0,023	0,084	10	1,70	1,88	2,18	0,052	0,163	11	0,27	0,38	0,49	0,017	0,057	13	0,69	0,83	0,95	0,023	0,082	10	0,43	0,49	0,63	0,019	0,061
E	LUM12	*L. verus*	0						1		1,94				1		0,41				0						0					
Dd	LUM10	*L. verus*	1		0,81				1		1,61				2	0,38		0,51			3	0,50	0,65	0,73	0,077	0,133	0					
Dd	LUM9	*L. verus*	5	0,80	0,85	0,90	0,019	0,042	6	1,53	1,80	2,08	0,072	0,177	8	0,18	0,30	0,40	0,030	0,086	6	0,70	0,78	0,90	0,033	0,081	5	0,42	0,48	0,52	0,018	0,041
Dd	LUM3	*L. penai*	5	0,76	0,85	1,08	0,060	0,135	8	1,43	1,56	1,68	0,029	0,082	6	0,21	0,35	0,58	0,052	0,126	4	0,67	0,77	0,93	0,058	0,117	5	0,47	0,55	0,71	0,042	0,093
Dd	VA3F	*L. penai*	10	0,72	0,82	0,91	0,019	0,060	11	1,37	1,64	1,95	0,051	0,170	11	0,28	0,38	0,47	0,022	0,071	9	0,64	0,75	0,88	0,029	0,086	9	0,40	0,50	0,62	0,024	0,071
Dd	VA1A	*L. penai*	8	0,78	0,87	1,07	0,033	0,094	8	1,32	1,64	2,01	0,073	0,205	9	0,26	0,35	0,50	0,028	0,084	10	0,68	0,78	0,89	0,023	0,074	6	0,49	0,52	0,56	0,010	0,024
Dc	VA3B	*L. penai*	14	0,68	0,79	0,86	0,013	0,050	12	1,46	1,65	1,84	0,034	0,119	13	0,23	0,42	0,56	0,027	0,099	14	0,59	0,73	0,86	0,020	0,074	11	0,43	0,48	0,55	0,012	0,040
Dc	VR5	*L. penai*	9	0,69	0,83	0,89	0,024	0,071	5	1,58	1,82	2,00	0,068	0,151	8	0,30	0,42	0,72	0,049	0,139	9	0,60	0,72	0,84	0,027	0,080	5	0,42	0,46	0,49	0,012	0,027
Db	COL-D	*L. penai*	0						0						0						0						0					
Da	FTE3	*L. penai*	5	0,69	0,78	0,92	0,038	0,086	5	1,27	1,54	1,73	0,090	0,201	5	0,30	0,40	0,49	0,038	0,085	4	0,51	0,67	0,80			5	0,46	0,51	0,60	0,026	0,057
Da	FTE2	*L. penai*	2	0,84		0,84			2	1,48	1,55	1,62	0,070	0,099	2	0,41		0,41			2	0,63		0,64			2	0,52		0,57		
Da	OR9	*L. penai*	6	0,66	0,84	0,97	0,042	0,103	4	1,22	1,55	1,90			5	0,32	0,41	0,50	0,039	0,087	7	0,62	0,76	0,88	0,031	0,082	4	0,45	0,52	0,56		
Da	VR2B	*L. penai*	2	0,89		0,93			2	1,61		1,69			2	0,41		0,69			2	0,67		0,72			2	0,53		0,58		
Cb	VR2A	*L. penai*	1		1,05				1		1,75				1		0,51				1		0,94				1		0,60			
Cb	OR8	*L. penai*	9	0,80	0,87	0,97	0,020	0,060	8	1,59	1,77	2,03	0,053	0,150	8	0,30	0,41	0,46	0,020	0,056	8	0,73	0,82	0,96	0,028	0,080	8	0,43	0,49	0,55	0,015	0,044
Cb	VR1A	*L. penai*	9	0,73	0,82	0,92	0,022	0,067	8	1,57	1,64	1,72	0,020	0,057	9	0,23	0,40	0,64	0,048	0,144	9	0,68	0,75	0,82	0,016	0,048	8	0,44	0,49	0,58	0,016	0,046
Cb	VR4BB	*L. penai*	12	0,66	0,78	1,02	0,030	0,102	9	1,40	1,60	1,75	0,040	0,121	11	0,26	0,39	0,47	0,019	0,064	11	0,53	0,69	0,86	0,030	0,099	9	0,43	0,49	0,62	0,018	0,053
Cb	VR4A	*L. penai*	4	0,74	0,80	0,87			6	1,52	1,60	1,75	0,032	0,078	6	0,34	0,42	0,51	0,028	0,067	4	0,67	0,71	0,74			4	0,42	0,50	0,57		
Ca	SR3	*L. penai*	21	0,69	0,81	1,00	0,019	0,086	17	1,33	1,54	1,80	0,035	0,145	17	0,25	0,40	0,51	0,017	0,069	18	0,58	0,70	0,88	0,020	0,086	16	0,44	0,52	0,61	0,013	0,052
B	VL2A	*L. penai*	23	0,69	0,85	0,97	0,015	0,071	22	1,35	1,63	1,94	0,033	0,153	27	0,27	0,42	0,58	0,016	0,084	24	0,62	0,73	0,89	0,016	0,076	20	0,44	0,53	0,65	0,012	0,054
B	SAM	*L. penai*	66	0,60	0,86	1,16	0,010	0,085	60	1,30	1,66	1,93	0,015	0,117	62	0,26	0,45	1,02	0,014	0,111	62	0,55	0,70	0,83	0,008	0,066	57	0,41	0,52	0,67	0,007	0,051
B	OR2	*L. penai*	31	0,69	0,86	1,08	0,014	0,080	28	1,36	1,72	2,07	0,032	0,170	30	0,27	0,44	0,77	0,020	0,111	28	0,57	0,70	0,81	0,012	0,064	28	0,36	0,50	0,62	0,010	0,053
A	SR4A	*L. penai*	6	0,72	0,83	0,89	0,025	0,062	4	1,52	1,61	1,72			6	0,30	0,42	0,59	0,051	0,126	3	0,64	0,67	0,72			4	0,48	0,53	0,59		

2D: 1) P_3 size measurements (L, W, Lme, Lpce, Wpm) of *P. lopezmartinezae* and *P. tobieni*

P/3 (excl. juveniles)			Length (mm)						Width (mm)						Length m-e (mm)						Length pc-e (mm)						Width p-m (mm)					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. tobieni*	4	1,39	1,42	1,44			5	1,49	1,67	1,76	0,047	0,105	8	0,84	0,99	1,12	0,029	0,082	8	0,91	1,02	1,17	0,026	0,074	7	1,00	1,07	1,15	0,024	0,064
H	NOM1	*P. tobieni*	0						0						0						0						0					
G3	SOL	*P. tobieni*	15	1,33	1,44	1,60	0,024	0,092	20	1,42	1,59	1,84	0,028	0,125	35	0,77	0,99	1,13	0,013	0,074	36	0,89	1,06	1,18	0,011	0,066	34	0,82	1,07	1,25	0,016	0,094
G3	PJE2	*P. tobieni*	0						0						0						0						0					
G3	TOR3B	*P. tobieni*	28	1,20	1,38	1,59	0,018	0,096	27	1,24	1,57	1,79	0,026	0,135	29	0,87	0,98	1,11	0,012	0,065	28	0,90	1,01	1,13	0,012	0,065	28	0,82	1,04	1,43	0,024	0,129
G3	TOR3A	*P. tobieni*	17	1,28	1,44	1,54	0,016	0,067	16	1,34	1,59	1,76	0,031	0,126	19	0,79	0,99	1,08	0,016	0,071	20	0,85	1,07	1,28	0,020	0,090	18	0,67	1,07	1,28	0,032	0,136
G3	TOR1	*P. tobieni*	3	1,36	1,40	1,43			3	1,46	1,60	1,71			3	0,97	0,99	1,01			3	0,99	1,03	1,06			3	1,03	1,05	1,07		
G2	MAN	*P. tobieni*	3	1,22	1,28	1,41			3	1,27	1,38	1,60			4	0,78	0,91	1,05			4	0,88	0,95	1,08			3	0,78	0,90	1,04		
G1	VT1A	*Prolagus* ex. interc.	2	1,32		1,35			2	1,39		1,40			2	0,89		0,95			2	0,95		1,01			2	0,97		0,99		
F	VT2C	*Prolagus* ex. interc.	0						0						0						0						0					
E	LP4BA	*Prolagus* ex. interc.	0						0						0						0						0					
Dd	VA3F	*Prolagus* ex. interc.	0						0						0						0						0					
Dc	VR5	*Prolagus* ex. interc.	2	1,37		1,45			1		1,38				2	0,91		0,91			2	0,92		1,00			2	0,88		0,96		
Db	COL-D	*Prolagus* ex. interc.	0						0						0						0						0					
C	VR1A	*P. lopezmartinezae*	0						0						1		0,85				1		0,95				1		0,93			
C	VR4BB	*P. lopezmartinezae*	0						0						0						0						0					
C	SR3	*P. lopezmartinezae*	2	1,39		1,59			1		1,43				2	0,96		0,96			2	0,87		0,94			2	0,95		0,97		
B	VL2A	*P. lopezmartinezae*	2	1,38		1,44			1		1,39				2	0,84		0,98			2	1,00		1,00			2	1,00		1,04		
B	SAM	*P. lopezmartinezae*	20	1,22	1,40	1,56	0,019	0,083	20	1,14	1,38	1,52	0,024	0,108	26	0,91	0,99	1,13	0,010	0,052	27	0,91	1,01	1,15	0,012	0,064	22	0,77	0,93	1,08	0,016	0,077
B	OR2	*P. lopezmartinezae*	1		1,49				1		1,43				1		0,96				2	0,84		1,00			1		0,97			
A	SR4A	*P. lopezmartinezae*	1		1,40				5	1,38	1,47	1,55	0,030	0,067	7	0,95	1,05	1,13	0,025	0,066	7	1,01	1,08	1,15	0,020	0,054	7	0,94	1,00	1,06	0,016	0,043

2D: 2) P_3 size measurements (La, Wa, L/W, La/Wa) of *P. lopezmartinezae* and *P. tobieni*. Juvenile specimens are excluded.

P/3 (excl. juveniles)			Length a (mm)						Width a (mm)						Length / Width						Length a / Width a					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. tobieni*	4	0,35	0,39	0,46			4	0,89	0,96	1,08			3	0,80	0,83	0,84			4	0,32	0,41	0,47		
H	NOM1	*P. tobieni*	0						0						0						0					
G3	SOL	*P. tobieni*	16	0,29	0,38	0,47	0,013	0,051	16	0,50	0,64	0,83	0,024	0,095	12	0,81	0,89	0,95	0,013	0,044	16	0,44	0,60	0,71	0,019	0,077
G3	PJE2	*P. tobieni*	0						0						0						0					
G3	TOR3B	*P. tobieni*	28	0,24	0,36	0,53	0,014	0,072	29	0,44	0,64	0,83	0,020	0,107	26	0,75	0,89	1,12	0,016	0,082	28	0,40	0,57	0,84	0,021	0,112
G3	TOR3A	*P. tobieni*	18	0,31	0,38	0,47	0,011	0,047	18	0,52	0,67	0,84	0,023	0,098	15	0,81	0,90	1,01	0,016	0,061	18	0,46	0,58	0,65	0,014	0,059
G3	TOR1	*P. tobieni*	3	0,34	0,37	0,41			3	0,60	0,62	0,66			3	0,84	0,88	0,93			3	0,56	0,60	0,68		
G2	MAN	*P. tobieni*	3	0,30	0,34	0,39			4	0,42	0,56	0,67			3	0,88	0,93	0,96			3	0,60	0,67	0,81		
G1	VT1A	*Prolagus* ex. interc.	2	0,32		0,38			2	0,48		0,54			2	0,95		0,96			2	0,59		0,79		
F	VT2C	*Prolagus* ex. interc.	0						0						0						0					
E	LP4BA	*Prolagus* ex. interc.	0						0						0						0					
Dd	VA3F	*Prolagus* ex. interc.	0						0						0						0					
Dc	VR5	*Prolagus* ex. interc.	2	0,42		0,46			1		0,49				1		0,99				1		0,94			
Db	COL-D	*Prolagus* ex. interc.	0						0						0						0					
C	VR1A	*P. lopezmartinezae*	0						0						0						0					
C	VR4BB	*P. lopezmartinezae*	0						0						0						0					
C	SR3	*P. lopezmartinezae*	2	0,41		0,61			2	0,58		0,68			1		0,97				2	0,71		0,90		
B	VL2A	*P. lopezmartinezae*	2	0,44		0,45			2	0,52		0,56			1		0,99				2	0,80		0,85		
B	SAM	*P. lopezmartinezae*	20	0,29	0,40	0,50	0,012	0,052	20	0,35	0,53	0,62	0,018	0,079	15	0,95	1,02	1,14	0,014	0,054	20	0,63	0,76	1,23	0,029	0,128
B	OR2	*P. lopezmartinezae*	1		0,50				1		0,50				1		1,04				1		1,00			
A	SR4A	*P. lopezmartinezae*	2	0,39		0,42			2	0,47		0,54			1		0,90				2	0,72		0,89		

2E: 1) P^3 size measurements (L, W, Wmh, Wdh) of *P. lopezmartinezae* and *P. tobieni*;

P3/ (excl. juveniles)			Length (mm)						Width (mm)						Width mh (mm)						Width dh (mm)					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. tobieni*	3	1,31	1,37	1,44			2	2,07		2,29			3	1,54	1,62	1,72			2	1,77		1,99		
H	NOM1	*P. tobieni*	1	1,54	1,54	1,54			0						1		1,83				1		2,03			
G3	SOL	*P. tobieni*	21	1,31	1,42	1,65	0,017	0,078	17	1,90	2,12	2,41	0,036	0,147	18	1,26	1,50	1,74	0,034	0,146	17	1,45	1,69	1,96	0,035	0,145
G3	PJE2	*P. tobieni*	1		1,43				1		2,45				1		1,61				1		1,83			
G3	TOR3B	*P. tobieni*	14	1,17	1,39	1,53	0,028	0,104	10	1,95	2,23	2,54	0,064	0,203	11	1,34	1,51	1,66	0,033	0,109	10	1,49	1,70	1,91	0,043	0,135
G3	TOR3A	*P. tobieni*	20	1,19	1,38	1,51	0,019	0,086	15	1,96	2,21	2,47	0,040	0,156	19	1,22	1,60	1,91	0,042	0,184	18	1,38	1,78	2,13	0,048	0,202
G3	TOR1	*P. tobieni*	1		1,51				0						0						0					
G2	MAN	*P. tobieni*	3	1,18	1,33	1,46			2	1,95		2,08			3	1,21	1,38	1,60			3	1,36	1,55	1,77		
G1	VT1A	*Prolagus* ex. interc.	2	1,23		1,24			2	1,98		2,12			2	1,32		1,38			2	1,51		1,56		
F	VT2C	*Prolagus* ex. interc.	2	1,26		1,50			0						2	1,43		1,60			1		1,61			
E	LP4BA	*Prolagus* ex. interc.	0						0						1		1,22				1		1,30			
Dd	VA3F	*Prolagus* ex. interc.	1		1,26				0						1		1,26				0					
Dc	VR5	*Prolagus* ex. interc.	1		1,55				0						0						0					
Db	COL-D	*Prolagus* ex. interc.	1		1,47				0						1		1,47				0					
C	VR1A	*P. lopezmartinezae*	1		1,20				0						0						0					
C	VR4BB	*P. lopezmartinezae*	1		1,30				1		2,13				1		1,27				1		1,45			
C	SR3	*P. lopezmartinezae*	1		1,28				1		2,33				1		1,45				1		1,55			
B	VL2A	*P. lopezmartinezae*	2	1,19		1,48			1		2,08				1		1,51				1		1,58			
B	SAM	*P. lopezmartinezae*	20	1,16	1,32	1,48	0,019	0,085	16	1,92	2,16	2,44	0,043	0,170	19	0,92	1,33	1,63	0,038	0,167	19	1,18	1,48	1,65	0,026	0,115
B	OR2	*P. lopezmartinezae*	10	1,19	1,34	1,43	0,025	0,078	9	1,86	2,14	2,53	0,073	0,218	10	1,13	1,35	1,52	0,048	0,151	10	1,25	1,51	1,84	0,056	0,177
A	SR4A	*P. lopezmartinezae*	4	1,39	1,43	1,53			2	2,18		2,49			5	1,26	1,38	1,48	0,040	0,089	4	1,54	1,58	1,64		

2E: 2) P^3 size measurements (Lpl, L/W, Wmh/L, Wmh/W) of *P. lopezmartinezae* and *P. tobieni*. Juvenile specimens are excluded.

P3/ (excl. juveniles)			Length pl (mm)						Length / Width						Width mh / Length						Width mh / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. tobieni*	3	0,71	0,82	0,90			2	0,63		0,66			3	1,16	1,18	1,19			2	0,75		0,77		
H	NOM1	*P. tobieni*	1		0,90				0						1		1,19				0					
G3	SOL	*P. tobieni*	21	0,63	0,79	0,94	0,018	0,080	16	0,55	0,68	0,78	0,015	0,059	17	0,88	1,06	1,33	0,030	0,124	14	0,56	0,72	0,85	0,024	0,089
G3	PJE2	*P. tobieni*	1		0,72				1		0,58				1		1,13				1		0,66			
G3	TOR3B	*P. tobieni*	15	0,62	0,76	0,86	0,017	0,065	10	0,58	0,63	0,74	0,014	0,045	10	0,92	1,09	1,24	0,032	0,101	8	0,61	0,68	0,75	0,016	0,045
G3	TOR3A	*P. tobieni*	21	0,59	0,73	0,94	0,018	0,081	15	0,58	0,63	0,69	0,009	0,036	18	1,00	1,15	1,36	0,025	0,104	15	0,60	0,72	0,85	0,019	0,075
G3	TOR1	*P. tobieni*	1		0,88				0						0						0					
G2	MAN	*P. tobieni*	3	0,60	0,72	0,84			2	0,61		0,65			3	0,98	1,03	1,10			2	0,62		0,64		
G1	VT1A	*Prolagus* ex. interc.	2	0,64		0,78			2	0,58		0,62			2	1,06		1,12			2	0,62		0,70		
F	VT2C	*Prolagus* ex. interc.	2	0,72		0,95			0						2	1,07		1,13			0					
E	LP4BA	*Prolagus* ex. interc.	1		0,61				0						0						0					
Dd	VA3F	*Prolagus* ex. interc.	1		0,73				0						1		1,00				0					
Dc	VR5	*Prolagus* ex. interc.	2	0,84		1,04			0						0						0					
Db	COL-D	*Prolagus* ex. interc.	1		0,91				0						1		1,00				0					
C	VR1A	*P. lopezmartinezae*	0						0						0						0					
C	VR4BB	*P. lopezmartinezae*	1		0,71				1		0,61				1		0,98				1		0,60			
C	SR3	*P. lopezmartinezae*	1		0,88				1		0,55				1		1,13				1		0,62			
B	VL2A	*P. lopezmartinezae*	2	0,83		0,97			1		0,71				1		1,02				1		0,73			
B	SAM	*P. lopezmartinezae*	20	0,58	0,82	0,96	0,020	0,089	16	0,56	0,62	0,69	0,012	0,047	19	0,69	1,01	1,41	0,034	0,149	16	0,46	0,61	0,69	0,015	0,060
B	OR2	*P. lopezmartinezae*	11	0,71	0,80	0,97	0,022	0,073	9	0,55	0,63	0,76	0,022	0,066	10	0,80	1,01	1,20	0,037	0,118	9	0,57	0,63	0,73	0,016	0,049
A	SR4A	*P. lopezmartinezae*	5	0,80	0,87	0,96	0,026	0,058	2	0,61		0,64			4	0,88	0,95	1,06			2	0,54		0,68		

2F: P^2 size measurements (L, W, Wdh, Lpl, L/W) of *P. lopezmartinezae* and *P. tobieni*. Juvenile specimens are excluded. The isolated mesial accessory cusp is not included in the measurement when present.

P2/ (excl. juveniles)			Length (mm)						Width (mm)						Width dh (mm)						Length pl (mm)						Length / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. tobieni*	4	0,74	0,79	0,88			4	1,63	1,75	1,98			4	0,41	0,48	0,55			4	0,62	0,71	0,66			4	0,38	0,45	0,51		
H	NOM1	*P. tobieni*	0						0						0						0						0					
G3	SOL	*P. tobieni*	21	0,67	0,82	0,95	0,019	0,088	15	1,51	1,71	1,91	0,032	0,124	21	0,34	0,63	0,77	0,021	0,096	20	0,50	0,64	0,82	0,017	0,075	15	0,42	0,49	0,58	0,012	0,047
G3	PJE2	*P. tobieni*	1		0,82				1		1,52				1		0,53				1		0,68				1		0,54			
G3	TOR3B	*P. tobieni*	20	0,54	0,76	0,95	0,020	0,090	18	1,53	1,73	2,02	0,036	0,155	19	0,34	0,56	0,81	0,028	0,120	20	0,44	0,64	0,80	0,019	0,087	18	0,35	0,43	0,51	0,011	0,046
G3	TOR3A	*P. tobieni*	24	0,57	0,77	0,92	0,019	0,091	20	1,43	1,67	1,89	0,029	0,129	20	0,28	0,61	0,80	0,032	0,143	23	0,49	0,59	0,76	0,011	0,055	20	0,39	0,47	0,54	0,010	0,043
G3	TOR1	*P. tobieni*	0						0						0						0						0					
G2	MAN	*P. tobieni*	0						0						0						0						0					
G1	VT1A	*Prolagus* ex. interc.	0						0						0						0						0					
F	VT2C	*Prolagus* ex. interc.	0						0						0						0						0					
E	LP4BA	*Prolagus* ex. interc.	0						0						0						0						0					
Dd	VA3F	*Prolagus* ex. interc.	1		0,78				1		1,76				1		0,61				1		0,69				1		0,44			
Dc	VR5	*Prolagus* ex. interc.	0						0						0						0						0					
Db	COL-D	*Prolagus* ex. interc.	0						0						0						0						0					
C	VR1A	*P. lopezmartinezae*	0						0						0						0						0					
C	VR4BB	*P. lopezmartinezae*	0						0						0						0						0					
C	SR3	*P. lopezmartinezae*	0						0						0						0						0					
B	VL2A	*P. lopezmartinezae*	2	0,92		0,94			1		1,48				1		0,71				2	0,45		0,66			1		0,64			
B	SAM	*P. lopezmartinezae*	14	0,66	0,78	0,93	0,026	0,098	12	1,30	1,46	1,64	0,026	0,090	12	0,37	0,60	0,79	0,037	0,127	12	0,49	0,56	0,66	0,017	0,060	12	0,45	0,53	0,65	0,017	0,059
B	OR2	*P. lopezmartinezae*	5	0,53	0,72	1,02	0,082	0,184	4	1,02	1,34	1,59			5	0,40	0,52	0,68	0,049	0,109	5	0,40	0,56	0,65	0,046	0,103	4	0,49	0,58	0,64		
A	SR4A	*P. lopezmartinezae*	4	0,71	0,78	0,82			3	1,47	1,53	1,63			4	0,63	0,69	0,72			4	0,46	0,62	0,81			3	0,44	0,51	0,55		

CHAPTER 3

Systematics of immigrant species of *Prolagus* (Ochotonidae, Lagomorpha, Mammalia) from the late early and middle Miocene of north-eastern Central Spain

Kees Hordijk & Albert J. van der Meulen

3.1 Abstract

Pikas are a common component in the Miocene small-mammal record of Spain, but have remained rather elusive in comparison to the rodents. The immigration and evolution of two morphologically very similar pika lineages in Spain, which include *Prolagus oeningensis* (König, 1825) and *Prolagus major* López, 1977, are described and reviewed on the basis of extensive new material from the rich small mammal record from the Daroca-Villafeliche area in the Calatayud-Montalbán Basin from the time interval between the late early Miocene and the early late Miocene (17-10 Ma). The immigration and subsequent evolutionary development of the two lineages provide new information for small-mammal biostratigraphy and for the phylogeny of Miocene *Prolagus* Pomel, 1853.

The arrival of a new species in Iberian mammal zone Cb, *Prolagus vargasensis* n. sp., coincides with the immigration and evolution of several key rodent species in the area. *P. vargasensis* n. sp. adds to the regional diversity of the Ochotonidae Thomas, 1897 on the Iberian Peninsula, which already includes two other pika lineages in that time interval. This new species significantly extends the stratigraphic range in the Calatayud-Montalbán record of the common morphological group of species that also includes *P. oeningensis*, and it is considered to represent a Spanish endemic species in spite of its immigration into the basin. It is demonstrated that *P. major* has not evolved from *P. oeningensis* directly, but rather appears to have already evolved from *P. vargasensis* n. sp. at the time of the permanent settlement of *P. oeningensis* in the area.

3.2 Introduction

The Spanish small-mammal record of the middle Miocene is characterized by the presence of four pika lineages with hypselodont teeth (López-Martínez, 1989). Two of these have already been present during part of the early Miocene (López-Martínez, 1984; Chapter 2). The other two lineages, which include the widespread species *Prolagus oeningensis* (König, 1825) and the Spanish endemic *Prolagus major* López-Martínez, 1977, appear later in the fossil record and are the subject of this study. These highly similar lineages represent a distinctly different morphological group with respect to the earlier ones that include *Lagopsis penai* (Royo, 1928), *L. verus* (Hensel, 1856), *Prolagus lopezmartinezae* n. sp., Chapter 2 and *P. tobieni* López, 1977.

Table 3.1: The listing of the analyzed assemblages. A: Locality names and abbreviations, repository, age estimates from Daams *et al.* (1999a) and van Dam *et al.* (2006), and the total number of P^2, P^3 and P_3 specimens of the studied lineages. In case of two repository institutions, the first holds the original or largest collection. B: Total number of P^3, P_3, and deciduous teeth of all Ochotonidae and the number of species present in the assemblages. The references indicate earlier publications of part of the assemblages: 1. de Bruijn & van Meurs (1967); 2. López-Martínez (1977); 3. López-Martínez (1989). Reference between brackets indicates a different assemblage from the same locality. Footnotes: * included for comparative purposes, but additional material of *P. major* has been included in the analysis; ** from outside the Aragonian type area, in the vicinity of the Armantes section (Krijgsman *et al.*, 1994); *** scant material, the taxon is identified by other teeth than the P^3 or P_3; **** comparative material stored at IVAU. López-Martínez (1974) used comparative material from the same localities which is stored at the Centre des Sciences de la Terre of the Université Claude Bernard Lyon 1. Vieux-Collonges a mixed MN 4-5 assemblage, Sansan is the reference locality for MN 6 and La Grive M for MN 7/8 (de Bruijn *et al.*, 1992). Numerical age estimates for Sansan are ~13.75 Ma (Daams *et al.* 1999b), ~13.6 Ma (Kälin & Engesser, 2001) and ~14.1 Ma (Kälin & Kempf, 2009). Costeur *et al.* (2007) list a compilation of rough age estimates including for the fissure fillings of Vieux-Collonges (~16.0 Ma) and La Grive M (~12.3 Ma).

A

Locality name	Locality code	Repository	MN zone correlation (after Daams et al., 1999)	Iberian local zone (after Daams et al., 1999)	Age (Daams et al., 1999)	Age (van Dam et al., 2006)	***P. vargasensis - P. major***			***P. oeningensis***		
							P2	P3	p3	P2	P3	p3
Carrilanga 1	CAR1	NCBN	9	H	10,50	11,57				110	133	167
Nombrevilla 1	NOM1	IVAU	9	H	11,00	10,76				13	9	8
Solera	SOL	NCBN	7/8	G3	11,75	12,01				33	60	91
Paje 2	PJE2	MNCN	7/8	G3	12,17	12,20				7	10	8
Paje 1	PJE1	MNCN	7/8	G3	12,30	12,34				2	7	16
Toril 3B	TOR3B	MNCN	7/8	G3	12,59	12,11				4	8	5
Toril 3A	TOR3A	MNCN	7/8	G3	12,60	12,12				1	4	10
Toril 1	TOR1	NCBN	7/8	G3	12,62	12,14	0	0	2	2	8	11
Borjas	BOR	NCBN	6	G2	13,20	13,26				7	6	17
Manchones*	MAN	IVAU	6	G2	13,25	13,31	5	1	3		167	171
Valalto 1B	VT1B	NCBN-MNCN	6	G1	13,30	13,36	1		7			3
Valalto 1A	VT1A	MNCN	6	G1	13,35	13,41	4	1	3	2	2	4
Las Planas 5B	LP5B	NCBN-MNCN	6	G1	13,47	13,56	5	6	6	4	14	4
Armantes 7**	ARM7	IVAU	6	F			7	4	7			
Valalto 2C	VT2C	NCBN	6	F	13,68	13,74	6	5	4			
Las Umbrias 22	LUM22	MNCN	6	F	13,73	13,76	3	7	4			
Las Planas 4BA	LP4BA	MNCN	5	E				5	9			
Las Planas 4A	LP4A	IVAU-NCBN	5	E	13,96	13,98	1	2	1			
Las Umbrias 12	LUM12	MNCN	5	E	14,01	14,03					1	3
Las Umbrias 10	LUM10	MNCN	5	Dd	14,07	14,09						2
Las Umbrias 9	LUM9	MNCN	5	Dd	14,16	14,18	3	1				
Las Umbrias 3	LUM3	MNCN	5	Dd	14,37	14,37			1			
Vargas 5	VR5	MNCN	5	Dc	15,32	15,32						
Fuente Sierra 3	FTE3	MNCN	5	Da	15,92	15,88	1		3			
Fuente Sierra 2	FTE2	MNCN	5	Da	15,93	15,89	3	7	5			
Olmo Redondo 9	OR9	NCBN	5	Da	15,95	15,91	1	1	2			
Vargas 2B	VR2B	MNCN	5	Da	15,96	15,92	1	1				
Vargas 2A	VR2A	MNCN	4	Cb	15,98	15,94		1				
Olmo Redondo 8	OR8	NCBN	4	Cb	15,99	15,95		1	1			
Vargas 1A	VR1A	NCBN	4	Cb	16,14	16,11	1	4	7			
Vargas 4BB	VR4BB	MNCN	4	Cb	16,15	16,12	4	3	5			
Vargas 4A	VR4A	MNCN	4	Cb	16,18	16,15	3	6	3			
La Grive M	GM	IVAU	7/8							11	11	13
Sansan	SA	IVAU	6							5	9	18
Vieux-Collonges	VC	IVAU	4-5								5	21

B

P. vargasensis n. sp. - *P. major*	*P. oeningensis*	# P3/ and P/3 of other ochotonids	# ochotonid species present	# deciduous ochotonid teeth	Assemblages in prior publications
P3p3	P3p3	P3p3			
0	300	13	2	10	
0	17	1	2	3	1, 3
0	151	111	3	31	
0	18	1	2	13	
0	23	0	1	6	
0	13	71	3	42	
0	14	50	3	22	
2	19	22	4	5	
0	23	12	2	2	
4	338	489	4	48	1, 2, 3
7	3	11	3	4	
4	6	28	4	19	
12	18	48	3	23	
11	0	49	2	5	1, 2, 3
9	0	91	3	6	
11	0	17	2	4	
14	0	23	3	7	
3	0	63	2	22	1, (3)
0	4	27	2	17	
0	2	19	2	4	
1	0	26	2	3	
1	0	47	2	2	
0.5***	0	87	3	3	
3	0	18	2	3	
12	0	17	2	5	
3	0	27	2	1	
2	0	0,5	2	0	
1	0	15	2	3	
2	0	18	2	6	
11	0	30	3	7	
8	0	45	3	4	
9	0	53	2	2	

The rich magnetostratigraphically dated record in the study area provides a good opportunity to establish the timing of immigration relatively precisely and to establish the evolutionary stages and the biostratigraphy of these two lineages in detail.

Our objective is to outline the taxonomy and immigration history of the *P. oeningensis* and *P. major* lineages in Spain by providing new and updated species descriptions based on extensive new material from the Calatayud-Montalbán Basin. For this purpose, a selection of 32 localities is used comprising representative material from Iberian local biozones C to H (MN4-MN9). The studied material also includes known and new material from four previously published assemblages (de Bruijn & van Meurs, 1967; López-Martínez, 1977, 1989).

The resulting overview sheds new light on the phylogenetic affinity between *P. oeningensis* and *P. major* and the Miocene immigration history of *Prolagus* Pomel, 1853 in Spain. The evolutionary history of these immigrant lineages and its implications are discussed elaborately in Chapter 4 along with that of the two resident ochotonid lineages.

3.3 Material and methods

3.3.1 Institutional abbreviations

The material studied is stored in the research collections of the following institutes.
IVAU: Instituut voor Aardwetenschappen Utrecht (Institute of Earth Sciences Utrecht), Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands.
MNCN: Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences), Department of Paleobiology, Madrid, Spain.
NCBN: Netherlands Centre for Biodiversity Naturalis (National Museum of Natural History Naturalis), Leiden, the Netherlands.

3.3.2 Sample treatment

The sediment containing the fossil material has been screen washed in the field using the basic sieve setup described in Daams & Freudenthal (1988b) and with some improvements that have been implemented since. The residue was treated with acetic acid and wet sieved in the laboratory to remove the remaining carbonate matrix. The vertebrate fossil material was sorted manually from the siliciclastic residue aided by a binocular.

3.3.3 Material

The P_3, P^2 and P^3 are markedly the most distinctive elements for the pika lineages under consideration and are, the P_3 in particular, usually diagnostic to the species level. The remaining upper cheek teeth (P^4-M^2) and lower cheek teeth are of lesser importance for taxonomy and are therefore not studied in detail. Relevant information is provided in the descriptions of the species.

Deciduous teeth are relatively well represented in the available assemblages. However, these teeth have not been analyzed due to the fact that four different pika lineages are present in the studied area and time interval. It is currently not possible to taxonomically identify these elements with any reasonable degree of certainty and this remains to be solved in a future study. The total number of deciduous teeth present in the assemblages is indicated in Table 3.1, as are the repositories and numbers of diagnostic ochotonid specimens present in the analyzed assemblages. New ochotonid material is described from all 32 assemblages, 28 of which new entirely. Material from four assemblages included in this study, which are indicated in Table 3.1, has been published

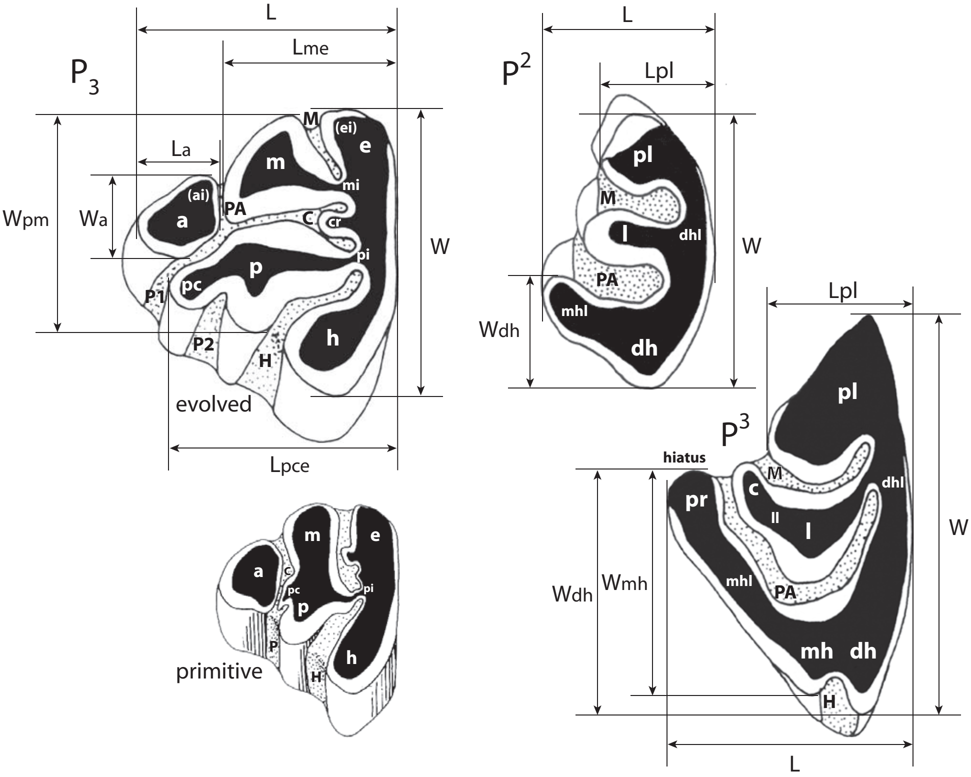


Figure 3.1: Nomenclature and size measurements for ochotonid teeth. The nomenclature generally follows the descriptive terminology of López-Martínez (1974, 1989), with some modifications (Chapter 2). Tooth cusps and lophs (white letters). a: anteroconid; p: protoconid; m: metaconid; h: hypoconid; e: entoconid; pc: protoconulid; cr: crochet; al: anterolophid; ml: metalophid; mi: metaisthmid; ai: anteroisthmid; ei: entoisthmid; pi: protoisthmid; l: lagicone; ll: lagiloph; c: centrocone; pr: precone; pl: postlobus; mh: mesial hypercone; dh: distal hypercone; mhl: mesial hyperloph; dhl: distal hyperloph. Inflexions (black letters). A: anteroflexid; PA: paraflexus/-id; P: protoflexid (1 & 2); M: mesoflexus/-id; H: hypoflexus/-id; C: centroflexid. Fossettes represent closed equivalents of inflexions. Tooth size measurements. L: length; W: width; La: a length; Wa: a width; Lme: m-e length; Lpce: pc-e length; Wdh: pr-dh width; Wmh: pr-mh width. Tooth drawings are modified after López-Martínez (1988) and Álvarez Sierra *et al.* (1991).

previously (de Bruijn & van Meurs, 1967; López-Martínez, 1977, 1989). These assemblages have been completed with additional previously unstudied material from the original samples. The *Prolagus oeningensis* material from Manchones is used as comparative material only, since it has been extensively studied in previous publications. In analogy to López-Martínez (1974), *Prolagus* material from Sansan, La Grive M and Vieux-Collonges is used as a comparative reference. The assemblages studied by López-Martínez (1974) are stored at the Centre des Sciences de la Terre of the Université Claude Bernard Lyon 1, France. The comparative material from the same localities used in this study is stored at the IVAU.

3.3.4 Measurement technique

Tooth size measurements have been taken using a Reflex Microscope. A series of size measures has been defined for each of the diagnostic elements (i.e. P_3, P^2 and P^3) in order to capture changes in size and shape, and to include damaged specimens that miss a particular part of their original structure (Fig. 3.1). Tooth size measures are calculated from distances between measured coordinates. All coordinates for a specimen are measured in a single run to ensure that the length and width measures are at right angles and to ensure that all measures correspond to exactly the same orientation of the specimen.

The tables showing measurements and morphological counts only include fully erupted teeth of young adults and older individuals. Teeth of unworn or slightly worn juvenile specimens are excluded, because these show a strong deviation from the general morphology and size.

Grayscale picture images are compiled from stacked images using a Leica MZ 16 FA stereomicroscope with a Leica DFC 420 C digital camera.

3.3.5 Nomenclature

The nomenclature of lagomorph tooth morphology employed here (Fig. 3.1) follows Chapter 2, which is a slightly modified version of the descriptive terminology introduced by López-Martínez (1974, 1989) and applied by Angelone (2007).

The deep centroflexid in the P_3 that is present in most middle Miocene and all younger Neogene *Prolagus* species is a structure that has formed as a result of mosaic evolution from the merger of the original primitive centroflexid (Figure 3.1) that extends between the protoconid and metaconid, with the distal part of the mesoflexid (López-Martínez, 1997). Despite its dual origin, we will refer to it as a deep centroflexid.

Molarization is a general evolutionary trend and condition that is observed in Miocene European ochotonids. Molarization in deciduous teeth is more advanced than in adult teeth. The shapes of the P_4 and P^4 are basically identical to that of the molars. The P_3 does not show molarization, while such a trend, although largely incomplete, is present in the P^3. A triangular shaped P^3 is less molarized compared to a more trapezoid P^3, which is related to the orientation and length of the mesial hyperloph and differs between genera. Its mesial hyperloph is lengthened and extends past the lagicone toward the labial side. Similar to the P^3, the P^2 may show lengthening of the mesial hyperloph over geological time. The shape of a derived P^2 more closely resembles that of the D^2, which is generally more similar to the P^3.

The loss or reduction of labial enamel inflexions and fossettes in upper cheek teeth is another general evolutionary trend that is separate from the process of molarization. These structures are present in both molars and premolars of primitive ochotonids.

3.4 Systematic paleontology

The abbreviations used in the listing of synonymy generally follow Matthews (1973): v indicates material studied by the author; (v) designates material documented by good and expressive drawings or photos; vp denotes material studied by the author of which a part belongs to the species under consideration; the publication date in italics indicates that the taxon is only mentioned without further description or illustration; a point. marks an assignment with high confidence;? indicates a distinct degree of uncertainty in the assignment; an asterisk * denotes the first description of a taxon to which the assignment of the specimens refer.

ORDER LAGOMORPHA BRANDT, 1855
FAMILY OCHOTONIDAE THOMAS, 1897
GENUS *PROLAGUS* POMEL, 1853

* 1853 Prolagus POMEL, 1853: 43, in Pomel
. 1856 Myolagus HENSEL, 1856: 695, in Hensel
(v). 1899 Prolagus POMEL, 1853: 449, in Major
(v). 1974 Prolagus POMEL, 1853: 38, in López-Martínez
(v). 1975 Prolagus POMEL, 1853: 851, in López-Martínez & Thaler
(v). 1975 Prolagus POMEL, 1853: 143, in Tobien
(v). 1979 Prolagus POMEL, 1853: 113-114, in Ringeade
(v). 1989 Prolagus POMEL, 1853: 110, in López-Martínez

TYPE SPECIES

Lagomys sansaniensis LARTET 1851, from Sansan (Gers, France). Major (1899) included the species *Lagomys sansaniensis* in *Anoema oeningensis* KÖNIG, 1825 from Öhningen (Upper Freshwater Molasse, Baden-Württemberg, Germany) and included *Anoema oeningensis* in the genus *Prolagus*.

AGE

MN6 (Sansan), MN7/8 (Öhningen), Middle Miocene.

ORIGINAL DIAGNOSIS

Pomel (1853: 43, *in* Hensel, 1856: 701-702).

PREVIOUS EMENDED DIAGNOSES

Tobien (1975: 143), López-Martínez & Thaler (1975: 851), Ringeade (1979: 113-114), Chapter 2.

EMENDED DIAGNOSIS

Chapter 2: Tooth formula: (2, 0, 3, 2)/(1, 0, 2, 2). Ochotonids of small to large size. Adult teeth are hypsodont and rootless. The anteroconid in the P_3 is isolated in the vast majority of specimens, but an occasional connection to the protoconid or metaconid is possible. A protoconulid may be absent, incipient or well developed. The centroflexid in P_3 can be absent, shallow or deep. The trigonid and talonid of the P_4 and M_1 form two lobes of similar width. A third lobe, the hypoconulid, is always and exclusively present in M_2, and is partly or completely isolated from the hypoconid-entoconid lobe. The M_3 is always absent. The P^2 has a distinct meso- and paraflexus and the mesial hyperloph can be very short to well developed. The P^3 has a well developed paraflexus and mesoflexus and a shallow and relatively narrow hypoflexus may be present. The P^4 is molariform and usually includes one or more rudimentary enamel fossettes. Enamel fossettes in the M^1-M^2 may be present or absent and may reduce or become lost with wear. The reduction of fossettes in P^4-M^2 is more progressive towards the posterior, while the depth of the hypoflexus increases.

REMARKS

The diagnosis followed here (Chapter 2) combines several diagnostic features that were partly omitted in each of the previous ones and which specifies a range of possible morphologies. However, it should be noted that this diagnosis is entirely based on the dentition. For osteological features and cranial anatomy we refer to Dawson (1969) and López-Martínez (1985, 1989).

Prolagus vargasensis n. sp.

v. *1967 Prolagus* sp.: 210, from Armantes 3, *in* de Bruijn
v. 1967 *Prolagus oeningensis* (König, 1825): 129, from Las Planas 4A, *in* De Bruijn & van Meurs
v. *1977 Prolagus* sp.: 51, from Armantes 3, *in* Daams *et al.*
v. *1977 Prolagus oeningensis* (König, 1825): 49 & 53, from Las Planas 4A, *in* Daams *et al.*
1989 *Prolagus oeningensis* (König, 1825): 116, from Las Planas 4A, *in* López-Martínez
1989 *Prolagus major* López-Martínez, 1977: 125, from Las Planas 4B, *in* López-Martínez.
2008 *Prolagus* cf. *major* López-Martínez, 1977: 400, from Melero-20, *in* Murelaga *et al.*

Type Locality

Vargas 1A, Calatayud-Montalbán Basin, Spain.

Age

Iberian local zone Cb, MN 4, Early Aragonian, late Early Miocene.

Holotype

P_3: RGM433852 (NCBN) (Plate 3.1, fig. 4)

Paratypes

Associated diagnostic elements from Vargas 1A (NCBN): 6 P_3 (RGM433853 – RGM433858); 4 P^3 (RGM433874 – RGM433877); 1 P^2 (RGM433889).

Stratigraphic Range

Local zone Cb to F (MN4-MN6); late Early to early Late Aragonian; late Early Miocene to Middle Miocene.

Derivatio Nominis

This species is named after the Rambla de Vargas; the valley in which its first appearance in the basin is recorded.

Diagnosis

A *Prolagus* of medium size and robust appearance. The protoconulid in the P_3 is well developed and a deep centroflexid is always present. The presence and development of a crochet at the posterior apex of the centroflexid is variable. It can be absent, incipient or well developed. The anteroconid is generally rounded and slightly smaller or of similar size compared to the metaconid. The P^3 has a long lagiloph and a well developed para- and mesoflexus. A weak indentation between the lagicone and lagiloph is commonly present in the paraflexus, but may be absent. The P^2 has a posteriorly oriented para- and mesoflexus. Its mesial hyperloph represents its greatest length, variably being short or showing a tendency for lengthing. The P^4 has a para- and mesofossette. The M^1 has a narrow J-shaped parafossette.

Differential Diagnosis

The P_3 of *Prolagus praevasconiensis* Ringeade, 1979, *Prolagus vasconiensis* Viret, 1930 (*in* Roman & Viret, 1930), *Prolagus fortis* López-Martínez & Sesé, 1991 (*in* Alvarez Sierra *et al.*, 1991), *Prolagus lopezmartinezae* and *Prolagus tobieni* López, 1977 (*in* López-Martínez *et al.*, 1977) differ from *P. vargasensis* in having a protoconid-metaconid connection and a poorly developed or absent protoconulid.

The P_3 of *Prolagus aguilari* López-Martínez, 1997 and *Prolagus schnaitheimensis* Tobien, 1975 have a larger and wider anteroconid and lack a consistently deep centroflexid. *Ptychoprolagus forsthartensis* Tobien, 1975, which is a direct descendant of the latter species, differs from *P. vargasensis* in having crenulated enamel in the meso- and paraflexusses and fossettes of the P^3-M^2.

The P_3 of *P. vargasensis* is on average larger than that of *Prolagus oeningensis* (König, 1825) and shows distinctly more variation in the presence and development of the crochet. *Prolagus major* López, 1977 is larger and more robust. *Prolagus crusafonti* López, 1975 is smaller and more gracile compared to *P. vargasensis*.

The species from the late Miocene to Holocene time interval, *Prolagus sardus* (Wagner, 1829), *Prolagus calpensis* Major, 1905, *Prolagus bilobus* Heller, 1936, *Prolagus michauxi* López 1975, *Prolagus ibericus* López, 1975, *Prolagus figaro figaro* López, 1975, *Prolagus figaro depereti* López, 1975, *Prolagus imperialis* Mazza, 1987, *Prolagus apricenicus* Mazza, 1987, *Prolagus sorbinii* Masini, 1989, *Prolagus caucasicus* Averianov & Tesakov, 1998 and *Prolagus italicus* Angelone, 2008 generally differ from *P. vargasensis* in having a more strongly modified anteroconid shape in the P_3 that strongly deviates from a more primitive smooth (sub)-round to somewhat compressed shape. *Prolagus osmolskae* Fostowicz-Frelik, 2010 is distinctly larger than *P. vargasensis*. With the exception of *P. ibericus*, the mesial hyperloph in the P^2 of these late Neogene forms is usually more developed.

Material And Measurements

The material analysed is given in Table 3.1. Quantified morphological features are shown in Table 3.2 & 3.3. Scatter diagrams of tooth sizes are shown in Figs. 3.2-3.4. Summarized measurements are listed in Appendices 3.A1-2, 3.B1-2 and 3.C. Photographed specimens are shown in Plates 3.1-3.2.

Description

P^2 (Plate 3.2): The mesoflexus and paraflexus are well developed and generally point in a posterior direction. The apex of the paraflexus can be slightly bent toward the labial side in some specimens, such as the specimen from VR1A. The hypercone is large and well developed. The mesial hyperloph is rather slender and short, but represents the greatest length of the tooth. Its tip tends to point in a slightly labial direction. In some cases the mesial hyperloph is somewhat lengthened. The postlobus is well developed and is more bulgy in comparison to the mesial hyperloph and the lagicone.

P^3 (Plate 3.2): The tooth generally has a triangular shape. The mesial hyperloph extends to almost two thirds of the tooth width, which is approximately equal to the tooth length (Figs. 3.3E & 3.3F; App. 3.B2). A distinct precone is lacking. The lagiloph is long and usually reaches the labial exterior outline of the tooth. In some cases, the lagiloph is slightly shorter and does not reach the outline. On a few occasions, the anterior tip of the postlobus beares a notch due to the presence of a small and shallow inflexion of which it is unclear whether it represents a remnant metaflexus. An indentation in the enamel between the lagicone and lagiloph is commonly present, which can be weak or rather pronounced. In some specimens, the lagicone-lagiloph connection is smooth. A shallow but distinct hypoflexus is present, dividing the lingual side of the hypercone in a mesial and distal hypercone, respectively.

P^4-M^1 (Plate 3.2): The material is very scanty. The P^4 bears both a mesoflexus and paraflexus. The mesoflexus is small and can be round, oval or more or less bean shaped, while the paraflexus is relatively long and narrow and has a U-shape. The anterior arm of the latter flexus may be slightly longer than the posterior arm. A damaged M^1 from LP4BA lacks a mesoflexus and contains a fairly large but narrow J-shaped paraflexus.

P_3 (Plate 3.1): The P_3 has a relatively robust appearence and a triangular shaped occlusal surface. Its antero-labial side is slightly longer in comparison to its antero-lingual side. The anteroconid is generally rounded. In some cases it is slightly compressed anteriorly. The postero-lingual side of the anteroconid is a bit squeezed in some specimens, which results in a more tapered, angular corner, although the generally rounded anteroconid shape is retained. In the upper part of its stratigraphic range, an anteroisthmid connecting the metaconid with the anteroconid is present in three specimens, while this feature is absent in the older assemblages (Table 3.2). The metaconid tends to be slightly larger in the younger assemblages (e.g. LUM22) in comparison to the older ones (e.g. VR1A). The entoconid and hypoconid are well developed and their dentine fields are confluent. The entoconid approaches a rectangular shape with its long edges lying in a transversal direction. The hypoconid is more rounded and ellipsoid in shape. Its long axis is oriented in an antero-labial to postero-lingual direction. The protoconulid is large and well developed, but not very elongate. The position of the metaisthmus is slightly anterior in comparison to that of the protoisthmus. The centroflexid is deep in all available specimens. The presence and development of a crochet is variable. In six specimens, the metaisthmid is absent, resulting in an isolated metaconid (Table 3.2). The enamel walls of the centroflexid are usually smooth, but a specimen from LP4BA and from LUM22 show some small structures. The mesoflexid is variable in shape, but is usually straight and in a transversal direction. Its apex can show minor complexities in the form of a very small posterior extension. In others the mesoflexid can be pointing in slightly more posterior direction. The hypoflexid is deep and bears an indentation positioned between the protoconid and the protoisthmus. This indentation separates a transversal or slightly posteriorly oriented transversal labial part of the hypoflexid from the deeper part of the hypoflexid that is oriented in a more posterior direction. Its apex terminates at the protoisthmid opposite to the apex of the centroflexid.

P_4-M_1: The teeth consist of two separate lobes of approximately similar width and are fused together by crown cement. The posterior walls of the lobes have thick enamel. The trigonid has a rhomboid shape. The talonid is more compressed and somewhat wedge shaped; its labial side is thicker and attaches to the trigonid. The position of the talonid is slightly more labial than that of the trigonid. The crown of the P_4 is a more or less straight column. That of the M_1 is slightly curved posteriorly. These tooth elements are non-diagnostic at the genus level and are morphologically indistinguishable from those of other contemporaneous hypselodont European ochotonids of roughly similar size, such as other *Prolagus* species and *Lagopsis*.

M_2 (Plate 3.1): Like in all other *Prolagus*, the M_2 is three-lobed. The hypoconulid is fully developed and isolated from the talonid along the total height of the crown. Its posterior enamel wall is flattened, although its occlussal surface is somewhat oval shaped.

REMARKS

We have reassigned two *Prolagus* specimens from Las Planas 4A (IVAU) that have previously been assigned to *P. oeningensis* (see synonymy list), together with previously undescribed material from the same assemblage (IVAU & NCBN), to *P. vargasensis* on the basis of their size (Table 3.1; Fig. 3.2-3.4). This conclusion is in agreement with the observation of López-Martínez (1977) who noted that a single *Prolagus* specimen from Las Planas 4B (collection Instituto Lucas Mallada, Spain) is intermediate in size and morphology between *P. oeningensis* and *P. major* and suggested that it could be distinguished taxonomically. López-Martínez (1989), however, includes this specimen in *P. major*.

Our new extensive new material from a series of localities clearly supports López-Martínez's (1977) suggestion and we hypothesize that the specimen from Las Planas 4B (ILM) is likely from *P. vargasensis*. We have not studied this particular specimen. The assemblage from Las Planas

4B stored at the IVAU unfortunately only contains *Lagopsis verus* (Hensel, 1856). Since the ages of Las Planas 4A and 4B are very close, we consider the observation of López-Martínez (1977) in the Las Planas 4B material to be indirectly confirmed by our Las Planas 4A material. Furthermore, *P. vargasensis* is present in Las Planas 4BA (Table 3.1), which has been sampled close to the approximate position of Las Planas 4B.

Figures 3.2-3.4 and Appendices 3.A-C show that the size, the length measures in particular, of the *Prolagus* from Vargas 1A and the additional assemblages in the Villafeliche area included in *P. vargasensis* is larger than that of *P. oeningensis* from Sansan and La Grive M (comparative material IVAU). *P.* cf. *oeningensis* from Vieux-Collonges (comparative material IVAU), which is roughly time equivalent with the oldest known *P. vargasensis*, is smaller as well. The sizes reported for *P. oeningensis* from Mühlbach 1 & 2 (MN5, Austria) (Boon-Kristkoiz, 2003; Harzhauser *et al.*, 2003) are also smaller than those of *P. vargasensis*.

The observed size difference with *P. oeningensis* provides the main basis for *P. vargasensis*, because the generally high morphological resemblance between these species does not allow for a clear distinction at the species level. Despite this morphological resemblance, *P. vargasensis* does show characteristic features that differ from *P. oeningensis* (*sensu stricto*). The crochet is markedly less consistently present in the P_3 of *P. vargasensis*. The mesial hyperloph in the P^2 of *P. vargasensis* tends to be slightly longer or better developed in part of the material.

The isolated metaconid observed in some P_3 of *P. vargasensis* has also been observed in *P.* cf. *oeningensis* from Vieux-Collonges (Table 3.2) and Sant Mamet (López-Martínez, 1989) and in *P. oeningensis* (*sensu lato*) from other localities in the late early Miocene of western Central Europe (Huin, 1979; Prieto *et al.*, 2009). The common presence of this morphology is associated with a more primitive evolutionary stage in the evolution of the deep centroflexid in *Prolagus* (Bulot, 1988; López-Martínez, 1997).

Similarly, the variability in the presence and development of a crochet in the centroflexid of *P. vargasensis* has been observed in relatively primitive assemblages of *P. oeningensis* (*sensu lato*) as well, such as *P.* cf. *oeningensis* from Vieux-Collonges (Table 3.2) and *P. oeningensis* (*sensu lato*) from Hüllistein (Kälin, 1993). However, this variability has also been associated with the late Miocene species *Prolagus crusafonti*, which is considered an evolutionary descendent of *P. oeningensis* (López-Martínez, 1988, 1989).

Moreover, all P_3 specimens from the youngest assemblages that are assigned to *P. vargasensis*, i.e. Las Planas 4BA, Las Umbrías 22 and Valalto 2C, respectively, have a distinct crochet present (Table 3.2). This apparent invariability may be realistic, but may also be the result of coincidence and sample size. Therefore, the presence or absence of the crochet in the P_3 can be considered as a significant feature in the evolution of *Prolagus*, but needs to be considered with care.

Murelaga *et al.* (2008) have found a slightly damaged P_3 specimen in the assemblage from Melero-20 (Ebro Basin), which they have tentatively assigned to *Prolagus* cf. *major*. The reported length of 1.88 mm and our scaled size estimates based on the available drawing indicate that this specimen fits very nicely in the size range of *P. vargasensis*. On the basis of its identical morphology and size we provisionally include this specimen in *P. vargasensis*. This is in agreement with the correlation of the Melero-20 assemblage to zone E on the basis of rodents.

De Bruijn (1967) and Daams *et al.* (1977) have not reported the presence of a *Prolagus* next to *Lagopsis penai* in their species lists of the small mammals from Torralba 1 (IVAU). However, this assemblage includes two specimens of *P. vargasensis* (1 P_3, Plate 3.8, & 1 P^3).

Cuevas Gonzales (2005) reports the presence of *Prolagus* cf. *oeningensis* at the localities of Somosaguas Norte and Somosaguas Sur, which is indicated as the first known occurrence of

Table 3.2: Counted morphologies in the P_3 of *P. vargasensis* and *P. major*. Juvenile specimens are excluded. Asterisk footnotes: * denotes the type assemblage of the species; ** damaged, observed in lower part of the crown.

p/3					Anteroconid				Anteroflexid			Protoconulid			Centroflexid			Crochet			Connections							Relative size		
MN zone	local zone	Locality	Species	Ntotal (excl. juveniles)	(sub)round	ellipsoid	flattened/broad/triangular	diamond shaped	distinct with cement	distinct inflexion	absent/weak/incipient inflexion	absent	incipient/small	developed	absent	incipient/superficial	deep	absent	incipient/small	developed	metaconid isolated	anterolophid	metalophid	protoisthmid present	protoisthmid absent	metaisthmid	anteroisthmid	anteroconid < metaconid	anteroconid = metaconid	anteroconid > metaconid
7/8	G3	TOR1	*P. major*	2			2				2			2			2	1	1		1			2		1		2		
6	G2	MAN*	*P. major*	3		2	1				3			3			3	2		1				3		3		1	2	
6	G1	VT1B	*P. major*	7	2	5					7			7			7			7				7		7	1	6	1	
6	G1	VT1A	*P. major*	3	2						2			2			3			3				3		3	2	2		
6	G1	LP5B	*P. major*	6	1	5					6			6			6			6				6		6	1	2	3	
6	F	ARM7	*P. major*	7		4					5			7			7			7		1		7		7		2	2	
6	F	VT2C	*P. vargasensis*	4	1	1		1			3			4			4			4				4		4	2	1	1	1
6	F	LUM22	*P. vargasensis*	4	2						2			4			4			4	1			4		3		1	1	
5	E	LP4BA	*P. vargasensis*	9	3			2	1		6			8			9			9				9		9	1	3	2	
5	E	LP4A	*P. vargasensis*	1	1						1			1			1			1				1		1			1	
5	Dd	LUM9	*P. vargasensis*	0																										
5	Dd	LUM3	*P. vargasensis*	1	1**						1			1			1	1						1		1			1**	
5	Dc	VR5	*P. vargasensis*	0																										
5	Da	FTE3	*P. vargasensis*	3	1						1			3			3	1		2	1			3		2			1	
5	Da	FTE2	*P. vargasensis*	4	1	1					2			4			4	1		3	1			4		3		2		
5	Da	OR9	*P. vargasensis*	2										2			2	1	1		2			2						
5	Da	VR2B	*P. vargasensis*	0																										
4	C	VR2A	*P. vargasensis*	0																										
4	C	OR8	*P. vargasensis*	1	1						1			1			1	1						1		1			1	
4	C	VR1A*	*P. vargasensis*	7	4	1					5			7			7	1	5	1	1			7		6		3	2	
4	C	VR4BB	*P. vargasensis*	5	1						1			5			5	5						5		5				
4	C	VR4A	*P. vargasensis*	3	2						2			3			3	2	1					3		3			2	

Table 3.3: Counted morphologies in the P^3 and P^2 of *P. vargasensis* and *P. major*. Juvenile specimens are excluded.

P3/					Mesoflexus			Precone		Lagilophe			**P2/**	Hypoflexus			
MN zone	local zone	Locality	Species	Ntotal (excl. juveniles)	absent	incipient	developed	indistinct (mhl = pr)	distinct (precone thicker than mhl)	long	short	absent (only lagicone)	Ntotal (excl. juveniles)	absent	incipient/superficial	distinct	with cement
7/8	G3	TOR1	*P. major*	0									0				
6	G2	MAN	*P. major*	1			1	1		1			5	5			
6	G1	VT1B	*P. major*	0									1	1			
6	G1	VT1A	*P. major*	1				1		1			4	1	1		
6	G1	LP5B	*P. major*	6			6	6		6			5	4			
6	F	ARM7	*P. major*	4			4	4		4			7	6			
6	F	VT2C	*P. vargasensis*	5			5	3		4	1		6	4			
6	F	LUM22	*P. vargasensis*	7			7	4		7			4	3			
5	E	LP4BA	*P. vargasensis*	5			5	2		5			0				
5	E	LP4A	*P. vargasensis*	2			2	2		2			1	1			
5	Dd	LUM9	*P. vargasensis*	0									3	2			
5	Dd	LUM3	*P. vargasensis*	0									0				
5	Dc	VR5	*P. vargasensis*	0													
5	Da	FTE3	*P. vargasensis*	0									1	1			
5	Da	FTE2	*P. vargasensis*	7			7	7		7			2	2			
5	Da	OR9	*P. vargasensis*	0									1				
5	Da	VR2B	*P. vargasensis*	0									1				
4	C	VR2A	*P. vargasensis*	1			1	1		1			0				
4	C	OR8	*P. vargasensis*	1			1	1		1			0				
4	C	VR1A	*P. vargasensis*	4			3	4		2	2		1				
4	C	VR4BB	*P. vargasensis*	3			3	2		3			4	2			
4	C	VR4A	*P. vargasensis*	6			6	5		4	2		3	3			

Prolagus in the Madrid Basin, Spain. Unfortunately, drawings and sizes are not provided, which prohibits any taxonomic verification. However, the correlation of these faunas to zone E suggest the possibility that these specimens may be referable to *P. vargasensis*, while the original assignment to *P. oeningensis* is possible as well.

Prolagus major López-Martínez, 1977

v. *1967 Prolagus* sp.: 211, from Armantes 7, *in* de Bruijn

v. 1967 *Prolagus sardus* (Wagner, 1829): 133, from Manchones & Arroyo 6, *in* de Bruijn & van Meurs

v. 1967 *Prolagus bilobus* Heller, 1936: 133, from Armantes 7 & Manchones, *in* de Bruijn & van Meurs

v.* 1977 *Prolagus major* López, 1977: 16, from Manchones, Arroyo del Val 6 and Armantes 7, *in* López-Martínez

v. *1977 Prolagus sardus* (Wagner, 1829): 49, from Arroyo del Val 6, *in* Daams *et al.*

v. *1977 Prolagus bilobus* Heller, 1936: 49 & 51, from Manchones 1, *in* Daams *et al.*

1986 Prolagus major López, 1977: 203, fig. 3, from Valladolid 1, Simancas 2, Torremormojón 6A & 6B, *in* López-Martínez *et al.*

v. 1989 *Prolagus major* López, 1977: 125, from Manchones, Arroyo del Val 6 and Armantes 7, *in* López-Martínez

? 1990 *Prolagus* cf. *oeningensis* (König, 1825): 442, from Lupiana, *in* Sesé *et al.*

v. *2005 Prolagus major* López, 1977: 23, from Manchones, *in* Angelone

Type Locality

Manchones, Calatayud-Montalbán Basin, Spain.

Age

Local zone G2, MN 6, Late Aragonian.

Holotype

P_3, MAN-6501 (former cat.no. MAN-1251) (Plate 3.3, fig. 10).

Stratigraphic Range

Local zone F to G3, MN6 – MN7/8, Late Aragonian, late Middle Miocene.

Original Diagnosis

López-Martínez (1989): "*Prolagus* de gran talla, P_3 semejante al de *P. oeningensis*, crochet en la mitad de los individuos de la población, anterocónido pequeño y redondeado. P^2 primitivo, hipercono prominente, M^1 y M^2 sin fosetas."

Emended Diagnosis

Prolagus of large size. Its P_3 has a deep centroflexid in which a crochet is variably present. Its anteroconid approaches an ellipsoid shape that usually is a bit squeezed on the postero-lingual side resulting in a somewhat tapered, angular corner. The P^2 has a wide meso- and paraflexus, and a short to distinctly elongated mesial hyperloph. The paraflexus and mesoflexus in the P^3 are deep and curved. Its centrocone reaches the labial exterior outline of the tooth. The P^4 has a parafossette and a mesofossette, the M^1 has a parafossette.

Differential Diagnosis

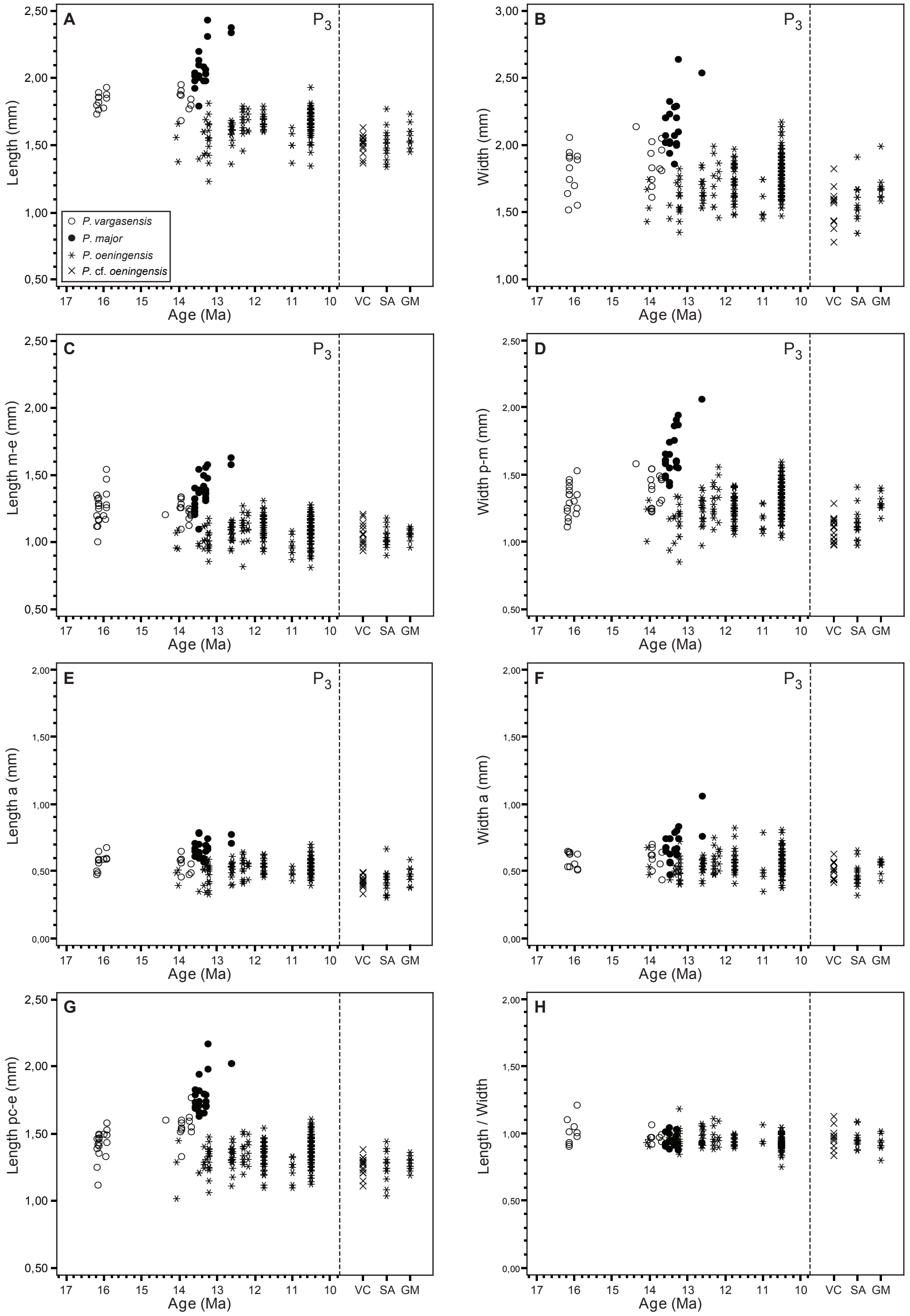
Prolagus major differs from *P. vargasensis*, *P. oeningensis* and *P. crusafonti* by its larger size. Its anteroconid is more ellipsoid and tapered postero-lingually compared to that of *P. vargasensis*. The presence of the crochet is more variable in the P_3 of *P. major* in comparison to *P. oeningensis* (*sensu stricto*).

P. praevasconiensis, *P. vasconiensis*, *P. fortis*, *P. aguilari*, *P. schnaitheimensis*, *P. lopezmartinezae* and *P. tobieni* differ from *P. major* in always or commonly lacking a deep centroflexid the P_3 and their protoconulid in the P_3 is distinctly less developed in comparison to the well developed protoconulid in *P. major*. *Ptychoprolagus forsthartensis* differs from *P. major* in the frequent presence of a metalophid and an entoisthmid in the P_3, and in having crenulated enamel in the meso- and paraflexusses and fossettes of the P^3-M^2.

The species from the late Miocene to Holocene, *P. sardus*, *P. calpensis*, *P. bilobus*, *P. michauxi*, *P. figaro figaro*, *P. figaro depereti*, *P. imperialis*, *P. apricenicus*, *P. sorbinii*, *P. caucasicus* and *P. italicus* generally differ from *P. major* in having a more strongly modified anteroconid shape in the P_3 and, with the exception of *P. ibericus*, in having a more developed mesial hyperloph in the P^2. The P^3 of *P. osmolskae* is slightly larger and its enamel thickness is differentiated more strongly than in *P. major*.

Material And Measurements

The material analyzed is shown in Table 3.1. Quantified morphological features are shown in Table 3.2 & 3.3. Scatter diagrams of tooth sizes are shown in Figs. 3.2-3.4. Summarized measurements

A
B
C
D
E
F
G
H
P_3
Length (mm)
Width (mm)
Length m-e (mm)
Width p-m (mm)
Length a (mm)
Width a (mm)
Length pc-e (mm)
Length / Width
Age (Ma)
17
16
15
14
13
12
11
10
VC
SA
GM
0,00
0,50
1,00
1,50
2,00
2,50
3,00
P. vargasensis
P. major
P. oeningensis
P. cf. oeningensis

← *Figure 3.2:* Scatter plots for the P_3 of *P. vargasensis*, *P. major* and *P. oeningensis*. A: Length (L); B: Width (W); C: Length metaconid-entoconid (Lme); D: Width protoconid-metaconid (Wp-m); E: Length anteroconid (La); F: Width anteroconid (Wa); G: Length protoconulid-entoconid (Lpc-e); and H: Length/Width (L/W). Juvenile specimens are excluded.

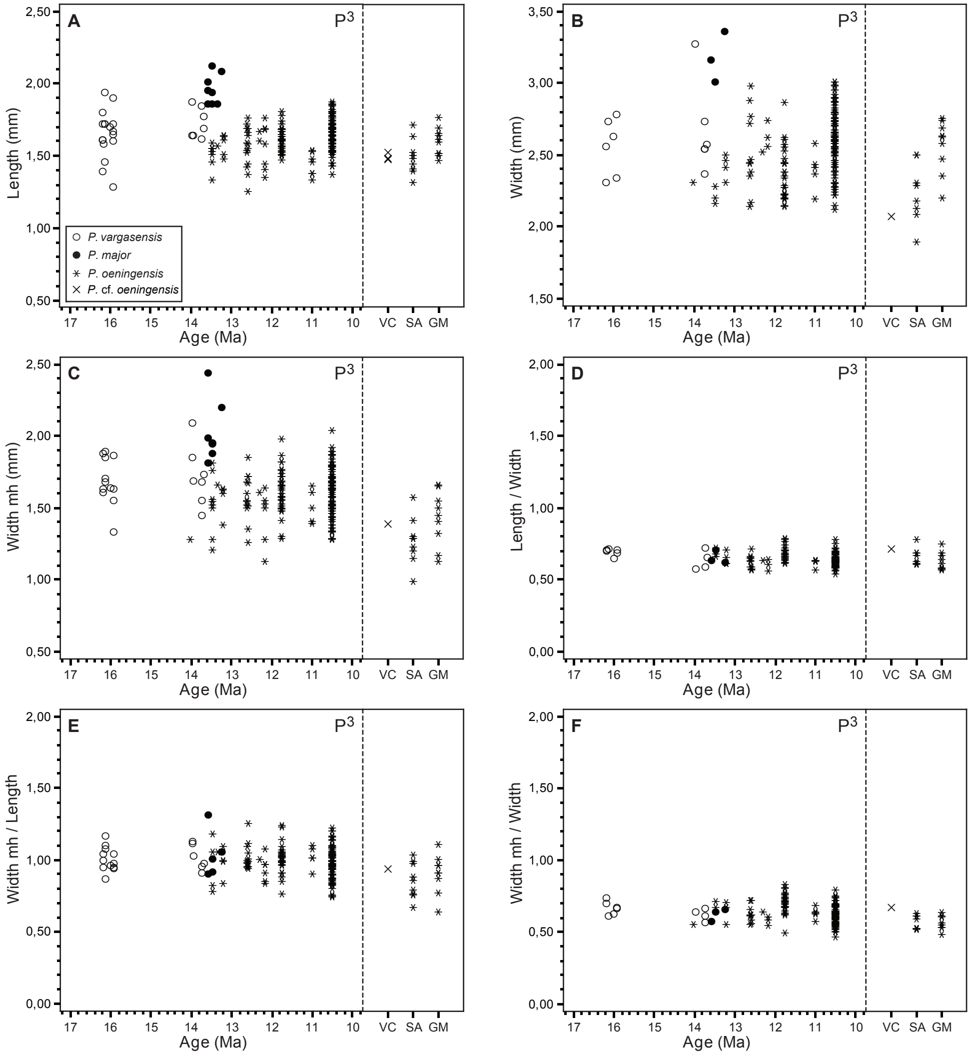


Figure 3.3: Scatter plots for the P^3 of *P. vargasensis* n. sp., *P. major* and *P. oeningensis*. A: Length (L); B: Width (W); C: Width mesial hyperloph (Wmh); D: Length/Width (L/W); E: Width mesial hyperloph/Length (Wmh/L); and F: Width mesial hyperloph/Width (Wmh/W). Juvenile specimens are excluded.

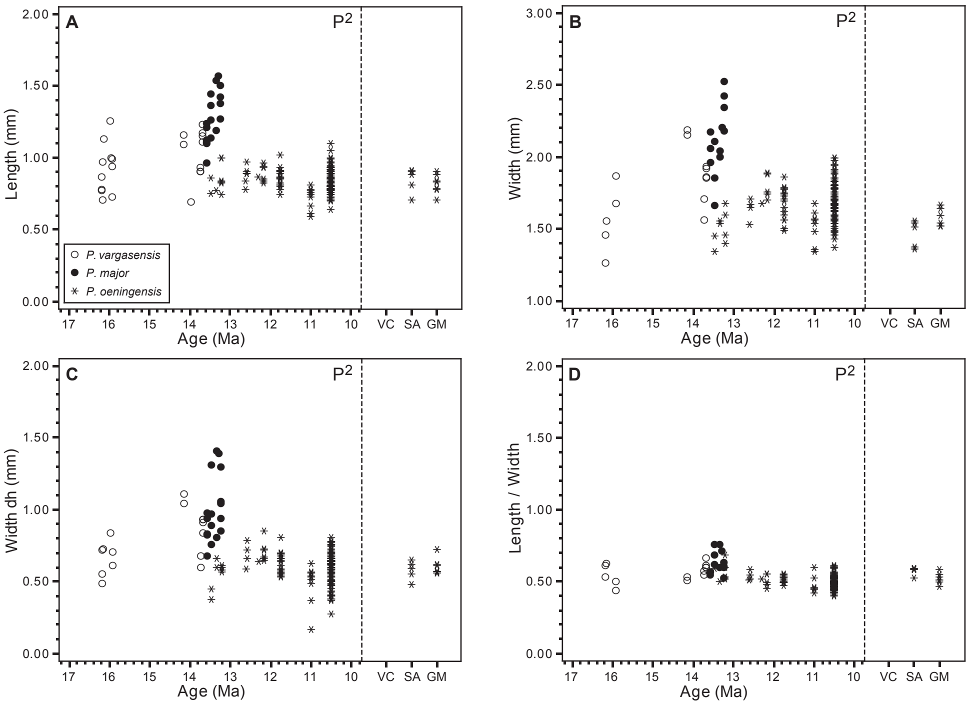


Figure 3.4: Scatter plots for the P^2 of *P. vargasensis* n. sp., *P. major* and *P. oeningensis*. A: Length (L); B: Width (W); C: Width distal hyperloph (Wdh); and D: Length/Width (L/W). Juvenile specimens are excluded.

are listed in Appendices 3.A1-2, 3.B1-2 and 3.C. Photographed specimens are shown in Plates 3.3-3.4.

DESCRIPTION

P^2 (Plate 3.4): The hypercone, lagicone and postlobus are well developed. The hypercone and mesial hyperloph represent the longest length of the occlusal surface in all specimens. The postlobus has the shortest length. The length of the mesial hyperloph is variable. The specimens from ARM7 all have a relatively short mesial hyperloph that does not enclose the paraflexus, but their apices tend to point in a slightly lingual direction. This morphology is also present in two specimens from MAN. In three specimens from MAN the paraflexus is enclosed by the mesial hyperloph. A long mesial hyperloph that reaches over the lagicone is present in a specimen from VT1A and from VT1B. The lagicone of two specimens from MAN and one from ARM7 show a shallow mesial groove or undulation. The mesoflexus and paraflexus are deep, straight, and relatively wide and point in a posterior direction. In a few specimens the paraflexus shows a small extension or a little curvature of the apex toward the labial side at in the base of the lagicone.

P^3 (Plate 3.4): The material is limited and often damaged, in particular the postlobus and the endpoint of the mesial hyperloph, which does not show a distinct thickened precone. The occlusal surface of the tooth has a triangular shape. The paraflexus and mesoflexus are deep and curved. The small accessory cusp present in the posterior part of the paraflexus of the only P^3 from MAN is not present in the rest of the available material. The mesial hyperloph, on which a distinct precone is lacking, extends to almost two thirds of the tooth width, which is approximately equal to the tooth length (Figs. 3.4E & 3.4F; App. 3.B2). The lagiloph is long and its centrocone reaches the labial exterior outline of the tooth in all available specimens. An indentation in the enamel between the lagicone and lagiloph is commonly present, which can be weak or rather pronounced. In two specimens from LP5B the lagicone-lagiloph connection is smooth. A shallow but distinct hypoflexus is present that divides the hypercone. The mesial hypercone is well developed, showing no sign of reduction.

P^4 (Plate 3.4): The material is very scanty. The P^4 from ARM7 and from MAN have both a mesoflexus and paraflexus. The mesoflexus is small and more or less bean shaped, while the paraflexus is relatively long and narrow and has an asymmetrical U-shape.

P_3 (Plate 3.3): The P_3 is large and robust. The outline of the occlussal surface is triangular, of which the labial side is longer than the lingual side. The anteroconid is generally ellipsoid, but approaches a somewhat triangular-like shape in some cases, because the postero-lingual side is squeezed and tapers into a distinct corner. The anteroconid in the youngest assemblage (TOR1) is large and triangular shaped. The well developed protoconulid is bent labially only slightly in most cases and points in a mainly anterior direction. The anteroconid is placed slightly more toward the lingual side of the tooth, due to this configuration. Four specimens have an anteroisthmid connecting the anteroconid with the metaconid (Table 3.2). The metaconid is large and quite angular. The entoconid and hypoconid are well developed in a more or less rectangular and in a rounded ellipsoid shape, respectively. The confluency of their dentine fields is narrowed because of a deep centroflexid and hypoflexid that reach close to the posterior wall of the tooth. The position of the metaisthmus is slightly anterior in comparison to that of the protoisthmus. The centroflexid is deep in all available specimens. A crochet is present in the stratigraphically older assemblages, while in the younger ones, this feature is variable and might be absent, as is the case in the holotype (Plate 3.3, fig. 10). In one specimen from TOR1 the metaisthmid is absent, resulting in an isolated metaconid (Table 3.2). The enamel of the metaconid wall of the centroflexid is usually smooth, but shows some undulations in specimens from various localities (Plate 3.3, figs. 4, 11-13). The mesoflexid is variable in shape, being short and wide to relatively narrow and longer. In the latter case, the mesoflexid is slightly bent to the posterior, while in the former it is pointing in a transversal direction. The mesoflexid may have minor complexities such as a small anterior extension into the metaconid. The hypoflexid is deep. Its apex terminates at the protoisthmid opposite to the centroflexid. In most specimens the hypoflexid is bent just posterior of the protoconid, its apex pointing in more posterior direction. In some cases a second apex-like indentation is present posterior to the protoconid. In one specimen from ARM7 the hypoflexid is straight.

Remarks

The large teeth of *P. major* are quite rare in the available assemblages, hampering an optimal view of the variation in morphology and size. However, the available material fits the type material from Manchones and the material from Armantes 7 well and significantly adds to the knowledge on the morphological variation of this species. The most notable new information that has come to light with the new material is the improved view of the morphology of the P_3 and the P^2. Furthermore, comparison with the material from Arroyo del Val 6 (Plate 3.8) that had been included with the original description of the species, has revealed that the M^1 has a distinct narrow J-shaped parafossette, which could not be verified in the new material due to a lack of M^1 specimens. These new observations based on the new and the comparative material have necessitated emendation of the original diagnosis.

P. major is the largest ochotonid present in the succession from the Daroca-Villafeliche area. However, the size of the smaller specimens of *P. major* does overlap with that of the larger ones of *P. vargasensis*. The morphologically similar *P. oeningensis* is always distinctly smaller. Apart from size, the morphology of *P. major* suggests a very close relationship with *P. vargasensis*. The youngest assemblages of the latter share a number of characteristics in common with *P. major*, such as the robust appearance and the occasional presence of the anteroisthmid in the P_3. *P. oeningensis* on the other hand, is very similar to the former two species, but to a slightly lesser degree.

Overall, the features characterizing *P. major* represent a more advanced stage in evolution in comparison to those present in *P. vargasensis*. The shape of the anteroconid is more derived in *P. major*. It has a generally ellipsoid shape with a tendency toward a larger and more triangular shape, while *P. vargasensis* generally has the rounded, more primitive shape of the anteroconid, although the early stages of the more derived morphology are already visible. The morphology of the P^2 of these two species is very similar, but the long mesial hyperloph present in the P^2 of several *P. major* specimens indicates a more advanced stage of evolution as well.

The lengthening of the mesial hyperloph in the P^2 is an example of advancing molarization. Previously, this particular feature has been observed in late Miocene and Pliocene species such as *P. michauxi*, in Italian island species of *Prolagus* and on very rare occasions in *P. crusafonti* (López-Martínez & Thaler, 1975; López-Martínez, 1989; Angelone, 2005). A tendency for mesial hyperloph lengthening has also been observed in the late early Miocene *Ptychoprolagus forsthartensis* from Germany (Ziegler & Fahlbusch, 1986; Angelone, 2005). Molarization of the P^2 has therefore occurred several times in separate lineages in the genus *Prolagus* (in this case including the closely related *Ptychoprolagus*). *P. major* represents a middle Miocene example of P^2 molarization.

Sesé *et al.* (1990) assigned a few specimens from Lupiana (Madrid Basin, Spain) to *Prolagus* cf. *oeningensis* and reported a P_3-length of 2.03 mm. This size is distinctly larger than that of *P. oeningensis* from the Calatayud-Montalbán Basin and also larger than that of our comparative material from Sansan and La Grive M (Fig. 3.2). The dimensions of *P. major* appear to fit the size of the Lupiana material better, suggesting that it can be included in the latter species.

The presence of *P. major* in Torremormojón 6A & 6B in the Duero Basin has been observed by López-Martínez *et al.* (1986). The age of these MN 7/8 localities localities can be correlated to C5r.2r in the early late Miocene (Krijgsman *et al.* 1996) and represents the youngest known occurrence of this species. The *P. major* material from the Calatayud-Montalbán Basin has not been compared with that from Torremormojón.

PROLAGUS OENINGENSIS (KÖNIG, 1825)

* 1825 *Anoema œningensis* KÖNIG, 1825: from Œningen, *in* König.
1845 *Lagomys meyeri* V. TSCHUDI: 7, from Oeningen, *in* von Meyer
. 1851 *Lagomys sansaniensis* LARTET, 1851: 51, from Sansan, *in* Lartet
. *1853 Lagomys Prolagus sansaniensis* LARTET, 1851: 43, from Sansan, *in* Pomel
1856 *Myolagus meyeri* (V. TSCHUDI): 699, from Oeningen, *in* Hensel
. 1899 *Prolagus œningensis* (KÖNIG, 1825): 450, from Œningen, Sansan, Steinheim, La- Grive-Saint-Alban, *in* Major

v. 1967 *Prolagus oeningensis* (König, 1825): 129, from Arroyo del Val 6, Manchones & Nombrevilla, *in* de Bruijn & van Meurs
. 1972 *Prolagus oeningensis* (König, 1825): 305, from Anwil, La Grive & Sansan, *in* Engesser
. 1974 *Prolagus oeningensis* (König, 1825): 47, from Sansan & Oeningen, *in* López-Martínez
1977 Prolagus oeningensis (König, 1825): 60, from Escobosa I, *in* López-Martínez *et al.*
v. *1977 Prolagus oeningensis* (König, 1825): 49 & 53, from Arroyo del Val 6 & Manchones, *in* Daams *et al.*
v(v). 1989 *Prolagus oeningensis* (König, 1825): 116, from Manchones, Arroyo del Val 6 & Escobosa, *in* López-Martínez
v. 1989 *Prolagus crusafonti* López, 1975: 127, from Nombrevilla, López-Martínez.
1993 *Prolagus oeningensis* (König, 1825): 140, from Vermes 1 and 2, Sansan, Le Locle Sous le Stand, Anwil and Nebelbergweg, *in* Kälin
2001 *Prolagus oeningensis* (König, 1825): 51, from Nebelbergweg, *in* Kälin & Engesser
2003 *Prolagus oeningensis* (König, 1825): 64, from Çandır, *in* de Bruijn *et al.*
v. *2007 Prolagus crusafonti* López, 1975: 417, from Nombrevilla, *in* Angelone
. 2009 *Prolagus* aff. *oeningensis* (König, 1825): 68, from Sandelzhausen, *in* Angelone
. 2009 *Prolagus oeningensis* (König, 1825): 83, from Escobosa de Calatañazor, *in* Angelone & Sesé.
2009 *Prolagus oeningensis* (König, 1825): 252, from Oggenhausen 2, *in* Böttcher *et al.*

Type Locality
Oeningen (Öhningen), Upper Freshwater Molasse (Obere Süßwassermolasse), Germany.

Age
MN 7/8
late Middle Miocene.

Local Stratigraphic Range
Local zone Dd to H; MN5-MN9; Middle Miocene to early Late Miocene.

Previous Emended Diagnosis
López-Martínez (1974): "*Prolagus* de petite taille, à dents plus élargies que *P. vasconiensis*. La P_3 a un crochet dans plus de 80% des individus de la population. Elle est plus large que longue. Les M_1 conservent l'hiatus mésial. Aux dents supérieures, les lagilophes sont longs et séparés des lagicônes gonflés par une échancrure. L'hiatus de email est présent sur au moins 95% des individus de la population. Aux molaires supérieures, les fossettes sont élargies en "J"."

Emended Diagnosis
López-Martínez (1989): "*Prolagus* de pequeña talla, de dientes inferiores más ensanchados que *P. vasconiensis*. P_3 tiene un "crochet" en más del 80% de la poblation, y es más ancho que largo. M_1 conserva el hiatus mesial. En los dientes superiores, los lagilofos son largos, y separados de los lagiconos gruesos por una escotadura. El hiatus del esmalte está presente al menos en un 95% de los P^3 de la población. En los molares superiores, las fosetas están ensanchadas en "J"."

Material And Measurements
The material analysed is shown in Table 3.1. Quantified morphological features are shown in Table 3.2 & 3.3. Scatter diagrams of tooth sizes are shown in Figs. 3.2-3.4. Summarized measurements are listed in Appendices 3.D1-2, 3.E1-2 and 3.F. Photographed specimens are shown in Plates 3.5-3.6.

DESCRIPTION

P^2 (Plate 3.6): No specimens are preserved from LUM10 and LUM12. The P^2 morphology is basic, having a well developed and straight paraflexus and mesoflexus that point in a posterior direction. Generally, these inflexions have approximately similar depths, but occasionally, the paraflexus is slightly shallower. The posterior end of the paraflexus occasionally tends to be broader and somewhat flattened in comparison to the more rounded mesoflexus. The paraflexus can be slightly extended labially on rare occasions. The well developed hypercone approaches a triangular shape. The mesial hyperloph is short, but represents the largest length of the tooth. A specimen from LP5B has an isolated round accessory cusp anterior to the paraflexus. The postlobus is short and usually slightly more bulgy in comparison to the lagicone. A hypoflexus is commonly absent, but regularly a shallow inflexion is present, two of which, from BOR and CAR1 respectively, contain some cement (Table 3.5).

P^3 (Plate 3.6): The P^3 has a triangular shape. Its mesial hyperloph reaches to roughly two thirds of the tooth width, although there is notable variation. The width of the mesial hyperloph is comparable with the tooth length (Figs. 3.3E & 3.3F; App. 3.E2). A well-defined precone is generally lacking, but on some occasions the endpoint of the mesial hyperloph is thickened (Table 3.5). The long lagiloph generally reaches the labial outline of the tooth. The enamel of the postlobus is smooth in the mesoflexus. However, thirteen specimens from CAR1 show a distinct notch in the postlobus at the tooth outline, which is also present in some specimens from other assemblages such as SOL (Plate 3.6, fig. 6-7). The mesoflexus is deep and curved in all specimens. An indentation in the enamel between the lagicone and lagiloph is commonly present in the paraflexus. A shallow but distinct hypoflexus is present. The distal hypercone is slightly larger and extends more prominently form the tooth outline than the mesial hypercone.

P^4-M^2 (Plate 3.6): The P^4 is molariform. Its mesoflexus is small and V-shaped, but may also approach an oval shape, while the distinctly longer paraflexus is narrow and J-shaped. In one of the two maxillae from PJE2 and in a partial maxilla from CAR1 part of the palate is preserved, which bear a small round premolar foramen directly lingual to the mesial hypercone of the P^4. The mesoflexus in the M^1 may be a small oval or is lacking. The paraflexus is I- or J-shaped. The M^2 may bear a small round or oval paraflexus or may be absent, both of which occur in the maxillae from CAR1. The hypoflexus in the P^4 does not reach to the middle of the tooth width, while that in the M^1 and M^2 reaches distinctly past the tooth midpoint.

P_3 (Plate 3.5): The P_3 has a somewhat labially skewed triangular occlusal surface. Its antero-labial side is slightly longer in comparison to its antero-lingual side. The anteroconid is generally rounded, but a variety of shapes is present in the available material. These are most commonly (sub)-circular and oval shapes, but some anteroconids have a diamond shape or approach a more triangular, anteriorly compressed form (Table 3.4). This broad range of variation is observed in the very large collection from Manchones, but is represented in the smaller assemblages as well. The occlusal surface of the anteroconid is generally smaller than that of the metaconid, but these are commonly of similar size too (Table 3.4). In some cases the anteroconid is slightly larger than the metaconid. However, the one from LUM10 is a relatively young specimen in which the metaconid is relatively small and one from BOR is an aberrant specimen, which has an unusually large anteroconid containing an inflexion on its posterior side. A well developed protoconulid extends from the protoconid in an antero-labial direction. The metaconid is well developed and is never isolated (Table 3.4). It commonly approaches a quasi square shape. The entoconid and hypoconid are well developed. Their dentine fields are confluent, but may occasionally be distinctly narrowed by the hypoflexid and, in rare cases, the centroflexid. The assemblage from NOM1 contains both

Table 3.4: Counted morphologies in the P_3 of *P. oeningensis*. Juvenile specimens are excluded. See description in text for additional remarks.

p/3					Anteroconid				Anteroflexid			Protoconulid			Centroflexid			Crochet			Connections							Relative size		
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	(sub)round	ellipsoid	flattened/broad/triangular	diamond shaped	distinct with cement	distinct inflexion	absent/weak/incipient inflexion	absent	incipient/small	developed	absent	incipient/superficial	deep	absent	incipient/small	developed	metaconid isolated	anterolophid	metalophid	protoisthmid present	protoisthmid absent	metaisthmid	anteroisthmid	anteroconid < metaconid	anteroconid = metaconid	anteroconid > metaconid
9	H	CAR1	*P. oeningensis*	165	35	43	3	7		2	88			165		2	163	2	3	160		2	2	165		165	16	57	30	2
9	H	NOM1	*P. oeningensis*	8	2	2		1			5			8			8			8				8		8			3	1
7/8	G3	SOL	*P. oeningensis*	87	9	11	1	4			27			87			87	1	1	85		1		87		86	1	10	10	4
7/8	G3	PJE2	*P. oeningensis*	6	3	3					6			6			6			6				6		6	1	3	2	
7/8	G3	PJE1	*P. oeningensis*	14	4	5		4	1		12			14			14			14				14		14		8	4	
7/8	G3	TOR3B	*P. oeningensis*	4		4					4			4			4			4				4		4		1	1	2
7/8	G3	TOR3A	*P. oeningensis*	8		3		2			5			8			8			8				8		8		1	3	1
7/8	G3	TOR1	*P. oeningensis*	11	4	3		1			8			11			11			11				11		11	2	5	2	
6	G2	BOR	*P. oeningensis*	17	3	5	3	3	1		14			17			17		1	15				17		15		7	3	2
6	G1	VT1B	*P. oeningensis*	3	2	1					3			3			3			3				3		3	1	3		
6	G1	VT1A	*P. oeningensis*	4	1	2					3			4			4			4				4		4		3		
6	G1	LP5B	*P. oeningensis*	3		1					1			3			3			3				3		3		1		
5	E	LUM12	*P. oeningensis*	2	1						1			2			2			2				2		2	1	1		
5	Dd	LUM10	*P. oeningensis*	2		1		1			2			2			2			2				2		2		1		1
7/8		LGM	*P. oenigensis*	10	4	1	3	2			10			10			10			10				10		10		9	1	
6		SANS	*P. oenigensis*	17	9	2	2	2			15			17			17	1	2	14	1			17		16		9	2	
4-5		VICO	*P.* cf. *oeningensis*	19	9	4		2			15			19			19	3	5	11	6			19		13		15		

Table 3.5: Counted morphologies in the P^3 and P^2 of *P. oeningensis*. Juvenile specimens are excluded.

P3/					Mesoflexus			Precone		Lagilophe			**P2/**	Hypoflexus			
MN zone (after Daams et al. (1999)	local zone	Locality	Species	Ntotal (excl. juveniles)	absent	incipient	developed	indistinct (mhl = pr)	distinct (precone thicker than mhl)	long	short	absent (only lagicone)	Ntotal (excl. juveniles)	absent	incipient/superficial	distinct	with cement
9	H	CAR1	*P. oeningensis*	132			132	106	4	132			109	93	10		1
9	H	NOM1	*P. oeningensis*	9			9	6		9			13	9	3		
7/8	G3	SOL	*P. oeningensis*	60			60	36	4	60			32	25			
7/8	G3	PJE2	*P. oeningensis*	9			9	6	1	9			7	3	3		
7/8	G3	PJE1	*P. oeningensis*	5			5	1	1	4	1		1		1		
7/8	G3	TOR3B	*P. oeningensis*	7			7	7		7			4	4			
7/8	G3	TOR3A	*P. oeningensis*	3			3	3		4			1	1			
7/8	G3	TOR1	*P. oeningensis*	6			6	5	1	6			2	1			
6	G2	BOR	*P. oeningensis*	6			6	4	1	6			7	3	1		1
6	G1	VT1B	*P. oeningensis*	0									0				
6	G1	VT1A	*P. oeningensis*	2			2	2		2			2	1	1		
6	G1	LP5B	*P. oeningensis*	12			12	9	1	12			3	1	2		
5	E	LUM12	*P. oeningensis*	1			1	1		1			0				
5	Dd	LUM10	*P. oeningensis*	0									0				
7/8		LGM	*P. oenigensis*	11			11	9	1	11			7	7			
6		SANS	*P. oenigensis*	9			9	8	1	9			5	5			
4-5		VICO	*P.* cf. *oeningensis*	5			5	4		5			0				

specimens with good confluence and specimens in which confluence is almost lost. The entoconid approaches a rectangular shape, having its long edges in a transversal direction, while the hypoconid is more ellipsoid shaped and oriented antero-labially. An anteroisthmid is occasionally present in various assemblages (Table 3.4). In the large assemblage from CAR1, however, almost 10% have this feature, which is not the case in the large assemblages from MAN and SOL. The protoconid and metaconid are connected in two specimens from CAR1, while also having a metaisthmid. One specimen from PJE2 has an entoisthmid present. The metaisthmus is positioned slightly anterior to that of the protoisthmus. Accept for two specimens from CAR1 having a distinct anteroflexid, this feature is generally absent (Table 3.4), although that from NOM1 contains two specimens with a very shallow antero-labial inflexion. The centroflexid is deep in all but two specimens from CAR1. A well developed crochet is dominantly present in all assemblages. Only a few specimens from BOR, SOL and CAR1 have a small incipient crochet and one specimen from SOL and two from CAR1 lack a crochet. The crochet is generally positioned somewhat postero-lingually at the posterior tip of the centroflexus, but can also be placed in a more central posterior position. The enamel walls of the centroflexid are without additional structures. The shape of the mesoflexid is variable. It is commonly straight and relatively wide and predominantly lies in a transversal direction. In others the mesoflexid may be pointing in slightly more posterior direction and can be deeper and narrower as well. The hypoflexid is deep. Its labial wall is generally straight, while its lingual side shows marked variation. An indentation just posterior to the protoconid is commonly present in the material, which may be either a distinct small inflexion, or a less sharply developed undulation.

P_4-M_1: The teeth consist of two separate lobes with thick posterior walls of approximately similar width and are fused together by crown cement. The trigonid has a rhomboid shape. The talonid is more compressed and somewhat wedge shaped; its labial side is thicker and attaches to the trigonid. The M_1 is slightly curved posteriorly, while the P_4 is straighter.

M_2: Like in all other *Prolagus*, the M_2 is three-lobed with a fully developed hypoconulid that is isolated from the talonid, and having a somewhat flattened posterior enamel wall.

Remarks

López-Martínez (1974) reproduced the drawing of a specimen from the “Seyfried’schen Sammlung” published by von Meyer (1845), as the holotype of *P. oeningensis*. Von Meyer (1845) described the presence of a three-lobed M_2 and the absence of an alveolus for the M_3 in a mandible of the same species from the “Lavater’schen Sammlung”. Von Meyer (1845) further mentions that the specimen from Öhningen that was originally described by König (1825) and studied by Cuvier is housed at the British Museum. It appears therefore that the specimen from the Seyfried collection described by von Meyer (1845) is possibly not the holotype of *P. oeningensis* described by König (1825). However, these specimens do appear to represent the same species from the same locality. In addition to the material described by von Meyer and König, a similar slab of rock, presumably collected roughly around the same time in history, with an impression of a complete and mostly articulated skeleton from Öhningen with some bones preserved in the impression that has been assigned to *P. oeningensis*, is present in the collection of the Teylers Museum (Haarlem, the Netherlands; John de Vos, personal communication), which we have not studied in detail.

The fossils available and used for the 19th century descriptions do not involve assemblages of isolated teeth, but rather (impressions of) skeletons and have therefore not been focused on details of the dentition. We do not have a representative tooth assemblage from the type locality at our disposal. For practical purposes and in accordance with the practice of Major (1899) and López-

Martínez (1974, 1989), who have used material from Sansan and La Grive as a representative substitute for the type material from Öhningen, we used assemblages of isolated teeth from Sansan and La Grive M for comparison (Plates 3.7-3.8). Major (1899) included the *Prolagus* from Öhningen and Sansan in a single species. Sansan, the reference locality for MN 6, is the type locality of the genus *Prolagus*. La Grive M is the reference locality for MN 7/8, to which the locality of Öhningen has been correlated (de Bruijn *et al.*, 1992).

The size and morphology of the *P. oeningensis* material from Spain highly resembles *P. oeningensis* from Sansan and La Grive M in the comparative assemblages (Table 3.4 & 3.5, Figs. 3.2-3.4). The *P.* cf. *oeningensis* assemblage from Vieux-Collonges (Plates 3.7-3.8), on the other hand, shows several differences and is considered more primitive on the basis of its commonly isolated metaconid, the anteroconid that is always smaller than the metaconid and the variable presence and development of the crochet in the P_3. The relative anteroconid-metaconid size shows variation in the studied section. Although the anteroconid is most frequently slightly smaller than the metaconid, it is also commonly of equal size and, in a few cases, slightly larger than the metaconid. Moreover, the crochet is dominantly present and well developed in these *P. oeningensis* assemblages as well, which is in agreement with the observations of López-Martínez (1988). The shape of the anteroconid in *P. oeningensis* shows distinct variation and is not limited to the stereotype round shape.

López-Martínez (1989) documented a shallow groove in the anteroconid of some P_3 in a different assemblage from Nombrevilla (coll. Instituto Paleontología Sabadell). A weak inflexion in the anteroconid is present also in two P_3's from Nombrevilla in our collection. This feature is better developed in two specimens from Carrilanga.

The sizable assemblage from Carrilanga is also characterized by a high percentage (~10%) of P_3 specimens bearing an anteroisthmid. Such a structure is generally not common in *P. oeningensis*, but has been reported from other assemblages as well, such as *P. oeninensis* from Nebelbergweg (MN9, Switzerland) (Kälin, 1993; Kälin & Engesser, 2001). Similarly, an anteroisthmid is shown in a number of species of *Prolagus*. López-Martínez (1989) depicted a *P. ibericus* specimen with an anteroisthmid. *P. vargasensis* and *P. major* can have this feature as well (Plate 3.1 & 3.3). An anteroisthmid is also present in a specimen of the closely related *Piezodus tomerdingensis* Tobien, 1975 from Chaveroches (France) (Tobien, 1975). Thus the occasional presence of the anteroisthmid therefore occurs in various species over a long time interval. However, it is yet unknown whether the relatively high percentage of this morphology in the assemblage from Carrilanga has any stratigraphic or ecological significance. A regular occurrence of this type of morphology may suggest a possible relation with increased or specialized food processing efficiency, in which the long metaconid-anteroconid loph may perhaps provide a more effective grinding surface for tougher food types, but could also be the result of coincidence.

The distinction between the P^2 of *P. tobieni* and *P. oeningensis* is usually straightforward on the basis of their generally different morphology. However, their morphological variation does show some overlap and their size significantly overlaps (Chapter 2). The number of specimens in assemblages in which these two species are sympatric may therefore be slightly over- or underestimated.

The size and position of the premolar foramen present in maxillae of *P. oeningensis* material from the Calatayud-Montalbán Basin is identical to that from La Grive M in the comparative assemblage and the *P. oeningensis* material shown by Angelone & Sesé (2009). Its position is posterior with respect to that in *P. tobieni* (Angelone & Sesé, 2009) and *Lagopsis verus* (Chapter 2, Plate 2.4 & 2.9) in which this structure lies lingual to the P^3.

Several characteristics observed in morphological range of the homogeneous *P. oeningensis* assemblages from the Daroca-Villafeliche record are associated with *P. crusafonti*. López-Martínez & Thaler (1975: 854) have characterized *P. crusafonti*, among other less diagnostic features, as a relatively primitive species that is smaller than *P. oeningensis* and that has a P^2 with a shallow inflexion on the hypercone and has a P_3 of which the crochet is absent or strongly reduced in half of the assemblage. Its anteroconid in the P_3 is better developed than that of *P. oeningensis*, because its anteroconid and metaconid surfaces are generally of about equal size.

The assemblages from the study area contain several P^2 specimens that have a shallow or incipient hypoflexus. Part of the P_3 material represents specimens with an anteroconid that is of equal size or even slightly larger than the metaconid. The frequency of these morphologies represents a minority only and the reduction of the crochet is not evident in our material, which results in our assignment to *P. oeningensis*.

A comparable observation concerning the co-occurrence of the *oeningensis* and *crusafonti* morphotypes has also been made recently in the middle Miocene locality of Sandelzhausen (late MN5, Southern Germany). Angelone (2009) has reported the presence of *P. crusafonti* morphotypes in an otherwise homogeneous assemblage of *P. oeningensis*.

3.5 Results

The new material from the Calatayud-Montalbán Basin significantly changes and expands the previously known record of the Ochotonidae in the middle Miocene of Spain. The first appearances and stratigraphic ranges of *Prolagus vargasensis*, *Prolagus oeningensis* and *Prolagus major* provide new and better constrained tie-points for biostratigraphy.

P. vargasensis from Vargas 4A marks the first occurrence of a *Prolagus* with a deep centroflexid in the P_3 in the Calatayud-Montalbán Basin. The size of *P. vargasensis* remains unchanged throughout zones Cb to F (Figs. 3.2-3.4). The record of this species in zones Db to Dd is very scanty and it is largely absent in the record during this time interval. *P. vargasensis* reappears in zones E and F.

Contrary to size, the morphology of *P. vargasensis* shows some minor change throughout its stratigraphic range. In the P_3, the crochet tends to be more developed and consistently present in the youngest assemblages. The P_3 therefore tend to be more similar to *P. oeningensis* with respect to this feature than the older assemblages.

P. oeningensis makes a brief first appearance in the Calatayud-Montalbán Basin in the top of zone Dd and in the early part of zone E, in Las Umbrías 10 & 12, respectively. *P. vargasensis* is not present in these assemblages, while in the remainder of zone E and in zone F, *P. vargasensis* is present and *P. oeningensis* remains absent.

P. major appears in the top of zone F. It morphologically resembles both *P. vargasensis* and *P. oeningensis*, but shows most detailed similarity with the former. The size difference between *P. major* and *P. vargasensis* is distinctly smaller than that between the former and *P. oeningensis*. In addition to its large size, *P. major* shows signs of molarization of the P^2 in which the mesial hyperloph is occasionally lengthened.

The stratigraphic ranges of *P. vargasensis* and *P. major* are non-overlapping. The stratigraphic range of *P. oeningensis*, on the other hand, overlaps with both of these species. However, *P. vargasensis* has not been found associated with *P. oeningensis* in any assemblage, while *P. major* and *P. oeningensis* are occasionally sympatric in zones G1 to G3.

Armantes 7 represents the oldest known record of *P. major* in the region. It is approximately coeval with or just pre-dates the re-entry and long-term settlement of the *P. oeningensis* lineage in the area, which reappears in the record in Las Planas 5B, zone G1. Toril 1 (zone G3) represents the last known occurrence of *P. major* in the study area. *P. oeningensis* consistently continues its presence in the area into zone H. There is no apparent evolutionary trend in the morphology and size of its teeth from its first appearance and continuing throughout zone H.

3.6 Discussion and conclusions

3.6.1 Biostratigraphy

The Neogene mammalian fossil record of the Iberian Peninsula is sampled intensively and has been shown to be fairly complete (Alba *et al.*, 2001). The presence of *Prolagus vargasensis* in the Aragonian has nevertheless remained shrouded in previous studies due to the distinctly lower availability of localities in previous decades, the rarity of this species in mammal assemblages, and its superficial resemblance to *P. oeningensis*.

P. vargasensis represents a third distinctly recognizable ochotonid lineage next to that of *Lagopsis penai* and *Prolagus lopezmartinezae* in the Spanish fossil record as early as the late early Miocene. Species with the derived, deep centroflexid in the P_3 as present in *P. vargasensis* are currently unknown from older or approximately time-equivalent intervals of the Spanish geological record. The first appearance of *P. vargasensis* in Vargas 4A in the study area in local zone Cb is therefore interpreted as an immigration event. Secondly, *P. vargasensis* is currently only known from Spanish localities. Although its precise origin is as yet unestablished, we consider *P. vargasensis* an endemic species from the moment of its arrival in the Calatayud-Montalbán Basin.

The entry of *P. vargasensis* in the Calatayud-Daroca area coincides with that of *Democricetodon franconicus* Fahlbusch, 1966, *Eumyarion* Thaler, 1966 and the first occurrence of the chronospecies *Democricetodon moralesi* van der Meulen, Peláez-Campomanes & Daams, 2003 (Daams & Freudenthal, 1988; van der Meulen *et al.*, 2003, in review). *P. vargasensis* therefore provides a new useful biostratigraphic marker complementary to these rodent species and adds additional weight to the significance of the small mammal immigration phase within zone C.

P. vargasensis and *P. major* are stratigraphically superposed, while the range of *P. oeningensis* overlaps with that of both species. Combination of the present evidence of size, morphology and superposition strongly suggests anagenetic evolution of *P. vargasensis* to *P. major* in the top of zone F. The new data indicate that a direct phylogenetic connection between *P. oeningensis* and *P. major*, as has been originally hypothesized by López-Martínez (1977, 1989) on the basis of the P_3 specimen of intermediate size from Las Planas 4B in zone E, is significantly less likely.

The relative stratigraphic position of Valalto 2C and Armantes 7, which are both zone F localities based on their rodent composition, is not precisely known. The *Prolagus* assemblages from Valalto 2C and Armantes 7 have been assigned to *P. vargasensis* and *P. major*, respectively, on the basis of tooth size. Under the assumption that our interpretation of the anagenetic relationship between *P. vargasensis* and *P. major* is correct, than Valalto 2C can be considered to be older than Armantes 7.

The last occurrence of *P. major* in the Calatayud-Montalbán Basin has been recorded in Toril 1 (base zone G3), but this is not its last known occurrence. López-Martínez *et al.* (1986) have reported this species from younger localities at the end of zone G3 in the Duero Basin, which have been dated to C5r.2r in the early late Miocene by Krijgsman *et al.* (1996). The presently known stratigraphic range of *P. major* therefore extends from the end of zone F to the end of zone G3 and this species is therefore a potentially useful biostratigraphic marker for the late Aragonian.

The presence of *P.* cf. *oeningensis*, a primitive representative of the *P. oeningensis* lineage, in the slightly younger locality of Sant Mamet that is overlain by transgressive marine sediments and has been correlated to the lower part of C5Br (Vallès Penedès Basin, early middle Aragonian), indicates that this lineage has been able to invade Spain prior to the Langhian transgression that submerged the Vallès-Penedès Basin (López-Martínez, 1989; Garcés Crespo, 1995). It has however not been found in time equivalent localities in the Calatayud-Montalbán Basin.

The first appearance of *P. oeningensis* (*sensu stricto*) in the Calatayud-Montalbán Basin has been recorded at the end of zone Dd, which significantly postdates its presence in more northern parts of Western Europe. Its subsequent occurrence is in the early part of zone E. At both instances in the Dd-E boundary interval *P. oeningensis* was represented by very few specimens. Due to its scarcity in this time interval in the study basin, its use as a biostratigraphic marker is limited. In the interval spanning the remainder of zone E and in zone F *P. oeningensis* has not been found in the study area. Despite its general rarity and temporary absence in zones E-F, its first occurrence in Dd does provide potentially useful information for biostratigraphic correlation purposes.

P. oeningensis reappears in the Calatayud-Montalbán record at the base of zone G1 and is consistently present throughout the section. Its inferred range continues to at least zone H (early MN9), which is in agreement with the occurrence of *P. oeningensis* in the MN9 assemblage from Nebelbergweg in Switzerland (Kälin & Engesser, 2001).

The morphological variability present in *P. oeningensis* affirms the view that *P. crusafonti* is most closely related to the former (López-Martínez, 1988). López-Martínez (1988) noted that, although these species succeed each other in time, populations of intermediate age that either contain an association of the two forms or a transitional form have not been found.

The material described here strongly suggests the anagenetic evolution of *P. crusafonti* from *P. oeningensis*. Morphotypes typically associated with *P. crusafonti* are present within the normal variation of *P. oeningensis*. The timing of this evolutionary transition could however not be constrained in the studied succession and time interval. On the basis of the present data, the transition to *P. crusafonti* occurred in a, probably only slightly, younger interval in the early late Miocene.

3.6.2 Spatio-temporal variation of *P. oeningensis*

López-Martínez (1974) initially proposed to include *P. oeningensis* from Sansan and Öhningen (e.g. La Grive) in different subspecies, *P. o. sansaniensis* and *P. o. oeningensis* respectively, primarily on the basis of a difference in size. López-Martínez (1989) later refrained from applying this subdivision, but indicated that the homogeneity of middle Miocene *Prolagus* assemblages with *oeningensis*-like morphology in Europe remains to be investigated. The sizes (Figs. 3.2-3.4) and the morphology of the comparative material used in this study (Table 3.4-3.5, Plates 3.7 & 3.8) show that there is no apparent difference between *P. oeningensis* from Sansan and from La Grive M that would allow distinction at the subspecies level.

The morphology of all *P. oeningensis* assemblages from Spain fits well with the diagnosis of López-Martínez (1989). This appears to be more difficult for some older assemblages in western central Europe that have been assigned to this species. Kälin (1993) includes the *Prolagus* assemblages from Hüllistein and Vermes 1 & 2 (Switzerland) in *P. oeningensis*, but these assemblages, which are all significantly older than the *P. oeningensis* assemblages from the Daroca-Villafeliche area, do not meet the minimum requirement of 80% presence of a distinct crochet in the P_3 that is given in the diagnosis of López-Martínez (1989). Hüllistein has only nine P_3 specimens in which just one has a crochet (11%). Vermes 1 has nine of which six have a crochet (67%) and Vermes 2 has 18 of which 12 have a crochet (67%) (Kälin, 1993). Considering these small numbers, it appears that sample size might be an important factor responsible for this apparent misfit.

A binomial test (after Davis, 2002) in which the probability of finding a specimen with a crochet is set at 80% following the minimum requirement in the diagnosis, reveals that the composition of the assemblages from Vermes 1 & 2 cannot be significantly excluded from a representative *P. oeningensis* assemblage ($p = 0.164$ and 0.071, respectively), while the composition from Hüllistein ($p = 1.84*10^{-5}$) is unlikely to be the result of a random sampling of *P. oeningensis*. This indicates that the latter assemblage significantly differs from the minimum crochet frequency requirement in the diagnosis of *P. oeningensis*.

The *Prolagus* from Hüllistein, which can be dated to around ~16 Ma (Kempf *et al.*, 1997), is evidently more primitive than *P. oeningensis* (*sensu stricto*) and is more similar to the stage of evolution of *P. vargasensis* around the same age in having a complete centroflexid, but lacking the frequent presence of a crochet. An emendation of the diagnosis of *P. oeningensis* would be required in order to include assemblages such as from Hüllistein.

A similar issue arises with assemblages that are characterized by specific morphotypes in the evolution of *P. oeningensis* from *P. vasconiensis*. López-Martínez (1997) has shown that the evolution of the deep centroflexid in the P_3 is characterized by mosaic evolution of a suite of characters and is not the result of topological change by gradual deepening of the shallow centroflexid, as has been demonstrated in *Prolagus aguilari* from Beaulieu (early Miocene, France), which represents a lineage separate from *P. oeningensis*.

Bulot (1988) designated the "artenensis" morphotype, a P_3 characterized by the isolation of the metaconid, i.e. the metalophid and metaisthmid are absent, after correspondence with Huin on the assemblage from Artenay (France) in which this morphology is very common. According to Bulot (1988), Huin viewed this morphology as intermediate between *P. vasconiensis* and *P. oeningensis* and considered the assemblage as a possible new species.

Although this new species has never been described, López-Martínez (1997) retained the morphotype name and defined the distinctly less common "beaulieu" morphotype, which is another transitional mosaic morphotype characterized by the presence of both a metaisthmid and metalophid.

Transitional mosaic morphotypes can occur throughout a long time interval, but are most common during the late early Miocene. Assemblages are generally assigned to *P. oeningensis* in this lineage, although usually with a cf. (or aff.) designation. The artenensis morphotype is also present in a few *P. vargasensis* specimens in zone Da (isolated metaconid; Table 3.2), while the "beaulieu" morphotype is observed in the *P. oeningensis* assemblage from Carrilanga 1 (metalophid and metaisthmid; Table 3.4).

Assemblages containing these transitional mosaic morphotypes are known, among others, from Vieux-Collonges, La Romieu and Béon 2 in France (Mein, 1958; Huin, 1979; Bulot *et al.*, 2009), Sant Mamet in the Vallès-Penedès Basin in northeastern Spain (López-Martínez, 1989), Benken and Hüllistein in Switzerland (Bolliger, 1992), Mokrá in the Czech Republic (Sabol *et al.*, 2007) and Untereichen-Altenstadt 540m in Germany (Prieto *et al.*, 2009). Ziegler & Fahlbusch (1986) list transitional assemblages from several MN4 localities in Germany, but have not provided enough information that would allow a detailed verification.

Huin (1979) reports that 36 of the 100 P_3 from La Romieu have an isolated metaconid and 61 have a metaisthmid only, thus implying that the remaining three have a metalophid present assuming that the material is not damaged. The morphological range and frequency of this assemblage is quite different from that of *P. oeningensis* from La Grive M and Sansan, which appears to be the case for the other localities as well.

Beside the variability in the presence of the crochet in early *P. oeningensis* from various localities, the transitional assemblages between *P. vasconiensis* and *P. oeningensis* also suggest that a revision of the early history of the latter lineage is appropriate, either to include or exclude them in the diagnosis. The region of the origin and evolution of the lineage leading to *P. oeningensis* is most likely western central Europe. Except the rare occurrences in the Vallès-Penedès Basin, this lineage is absent in the Spanish fossil record during the time interval for which a revision is relevant, which is roughly between 17.5 and 15.5 Ma. A revision of the *P. oeningensis* lineage in this particular time interval should be based on material from the region of its origin. In the absence of a proper fossil record of this lineage in Spain during this particular time interval, we refrain from emending the existing diagnosis.

Apart from the taxonomic obscurity in the early phase of the stratigraphic range of *P. oeningensis*, there is ample room for discussion on the taxonomic interpretation and definition in the late phase of the range of *P. oeningensis* as well. Angelone (2009) assigns the *Prolagus* assemblage from Sandelzhausen (late MN 5, Southern Germany) that is sympatric with the ochotonids *Lagopsis penai* and "*Amphilagus*" sp., to a single species, *P.* aff. *oeningensis*, but suggests the possibility that both *P. oeningensis* and the otherwise late Miocene *P. crusafonti* may be present in this assemblage. Convergent evolution of this morphology has been provided as an alternative possibility.

The age of Sandelzhausen can be estimated at around 15.1 Ma based on the presence of two species of *Megacricetodon* FAHLBUSCH, 1964 (Abdul Aziz *et al.*, 2008; Wessels & Reumer, 2009) in combination with a normal polarity chron (Abdul Aziz *et al.*, 2008) that can be correlated to the magnetostratigraphically calibrated rodent biostratigraphy in Switzerland and chron C5Bn.2n, respectively (Kälin, 1997; Kempf *et al.*, 1997; Kälin & Kempf, 2009). This age is markedly older than any known occurrence of *P. oeningensis* (*sensu stricto*) in Spain and indicates that specimens with a morphotype that is generally associated with *crusafonti* are already present in populations of *P. oeningensis* in Central Europe relatively early, during the middle Miocene.

We agree with Angelone's (2009) decision to assign the assemblage from Sandelzhausen to one species. However, we consider the hypothesized possible presence of two *Prolagus* species in the Sandelzhausen fauna unlikely. The hypothesized heterogeneity of the *Prolagus* material from Sandelzhausen seems to be based on a rather typological approach to species assignment. Grouping morphological stereotypes or size extremes in an overall homogeneous but variable assemblage can possibly lead to over-splitting. The morphology of the bulk of the assemblage is likely to be somewhere between these morphotypes, which makes consistent identification and species assignment problematic. We prefer a more assemblage based approach for the taxonomy of fossil assemblages in which morphological variability within populations is taken into account. The *Prolagus* assemblage from Sandelzhausen fits the morphology of *P. oeningensis* well and it appears to be homogeneous, despite the morphological variability. This pattern does not require convergent evolution as an explanation for the presence of these morphotypes. Although we consider the presence of a *crusafonti*-morphotype a feature of interest, a convincing and consistent argument for distinguishing two species in this *Prolagus* assemblage is lacking, particularly when taking the large sample size available from Sandelzhausen into account.

López-Martínez (1984) and Chapter 2 describe examples of a similar type of morphological variability in the *Lagopsis* lineage. Both studies have shown that *Lagopsis* assemblages may include morphotypes that are characteristic of its ancestral or descendent chronospecies within the lineage, but represent assemblages of a single species only. At a certain stratigraphic level the relative frequency of the morphotypes shift, at which point the species assignment is changed to that of the other consistently dominant morphotype.

The current diagnoses of *P. oeningensis* and *P. crusafonti*, in López-Martínez (1989) and López-Martínez & Thaler (1975) respectively, are useful for the distinction of chronospecies, but are insufficient for the distinction of these species in case of sympatry. Although López-Martínez (1988) specified the distinguishing features of *P. oeningensis* and *P. crusafonti* in more detail, the defining features remain only useful in the temporal domain. The latter study highlighted the morphological variation present within assemblages of these species and has convincingly shown that the frequency and development of the crochet and the frequency of the relative anteroconid-metaconid size in the P_3 are their main diagnostic features. The sizes of *P. oeningensis* and *P. crusafonti* (López-Martínez & Thaler, 1975; López-Martínez, 1988, 1989) significantly overlap and therefore size cannot be used as an alternative or additional distinguishing characteristic.

Plates chapter 3

Plate 3.1

Prolagus vargasensis n. sp.
1. P_3 VR4A-L2A-01; Vargas 4A
2. P_3 inv. VR4A-L2A-06; Vargas 4A
3. P_3 inv. RGM-433857; Vargas 1A
4. P_3 RGM-433852; *holotype*; Vargas 1A
5. P_3 inv. RGM-433858; Vargas 1A
6. P_3 FTE2-1B-01; Fuente Sierra 2
7. P_3 inv. LUM3-2A-06; Las Umbrías 3
8. P_3 inv. RGM-434523; Las Planas 4A
9. P_3 inv. LP4BA-1B-08; Las Planas 4BA
10. P_3 LUM22-1B-01; Las Umbrías 22
11. P_3 LUM22-1B-02; Las Umbrías 22
12. P_3 inv. LUM22-1B-05; Las Umbrías 22
13. P_3 RGM-434341; Valalto 2C
14. P_3 inv. RGM-434342; Valalto 2C
15. P_3 inv. RGM-434343; Valalto 2C
16. M_2 RGM-unregistered; Vargas 1A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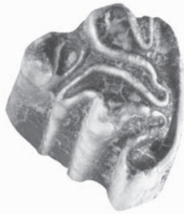
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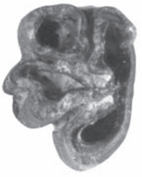
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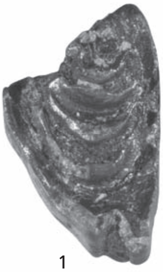
Plate 3.2

Prolagus vargasensis n. sp.
1. P^3 VR4A-L4B-01; Vargas 4A
2. P^3 inv. VR4A-L4B-07; Vargas 4A
3. P^3 RGM433874; Vargas 1A
4. P^3 inv. RGM-433875; Vargas 1A
5. P^3 inv. RGM-433877; Vargas 1A
6. P^3 FTE2-L3A-01; Fuente Sierra 2
7. P^3 inv. FTE2-L3A-06; Fuente Sierra 2
8. P^3 inv. FTE2-L3A-07; Fuente Sierra 2
9. P^3 inv. FTE2-L3A-09; Fuente Sierra 2
10. P_3 LP4A-LP-1381; Las Planas 4A
11. P^3 inv. RGM-434404; Valalto 2C
12. P^3 inv. RGM-434405; Valalto 2C
13. P^2 VR2B-L1A-08; Vargas 2B
14. P^2 RGM-433889; Vargas 1A
15. P^2 RGM-434424; Valalto 2C
16. P^2 inv. LUM9-L3B-03; Las Umbrías 3
17. P^2 RGM-434423; Valalto 2C
18. P^2 inv. RGM-434426; Valalto 2C
19. P^4 inv. VR4BB-L6B-01; Vargas 4BB
20. P^4 inv. LP4BA-L6B-02; Vargas 4BB
21. M^1 inv. LP4BA-L4B-01; Las Planas 4BA



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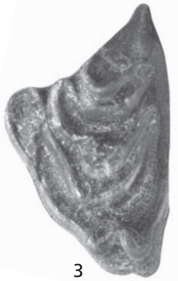

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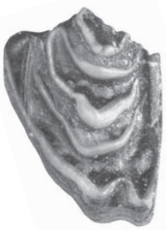

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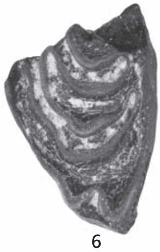

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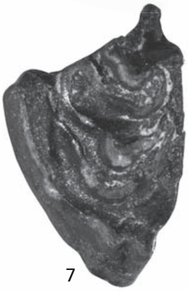

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Plate 3.3

Prolagus major
1. P_3 ARM7-58-851; Armantes 7
2. P_3 ARM7-58-853; Armantes 7
3. P_3 ARM7-58-854; Armantes 7
4. P_3 inv. ARM7-58-855; Armantes 7
5. P_3 RGM-434254; Las Planas 5B
6. P_3 RGM-434252; Las Planas 5B
7. P_3 inv. RGM-43425; Las Planas 5B
8. P_3 VT1A-L2B-01; Valalto 1A
9. P_3 RGM-434561; Valalto 1B
10. P_3 inv. MAN-6501; *holotype*; Manchones
11. P_3 inv. RGM-434565; Valalto 1B
12. P_3 RGM-434177; Toril 1
13. P_3 inv. RGM-434178; Toril 1


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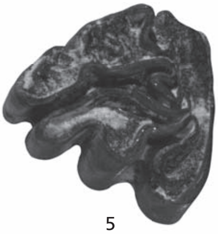
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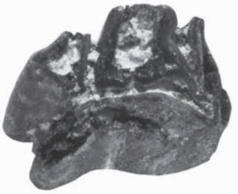
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Plate 3.4

Prolagus major

1. P^3 ARM7-58-881; Armantes 7
2. P^3 RGM-434276; Las Planas 5B
3. P^3 inv. RGM-434280; Las Planas 5B
4. P^3 inv. MAN-6502; Manchones
5. P^4 MAN-6503; Manchones
6. M^1 ARM7-2A-1220; Armantes 7
7. P^2 ARM7-58-896; Armantes 7
8. P^2 inv. ARM7-58-893; Armantes 7
9. P^2 RGM-434299; Las Planas 5B
10. P^2 inv. RGM-434301. Las Planas 5B
11. P^2 MAN-3377; Manchones
12. P^2 inv. MAN-6279B; Manchones
13. P^2 inv. MAN-6272A. Manchones
14. P^2 VT1A-L6A-02; Valalto 1A
15. P^2 inv. VT1B-L2A-05; Valalto 1B

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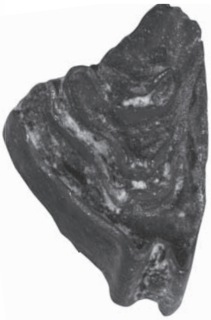

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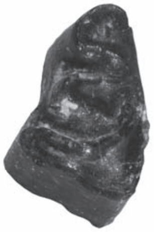

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Plate 3.5

Prolagus oeningensis
1. P_3 LUM10-L2B-01; Las Umbrías 10
2. P_3 LUM12-L1B-02; Las Umbrías 12
3. P_3 VT1A-L2A-01; Valalto 1A
4. P_3 inv. MAN-6182B; Manchones
5. P_3 RGM-434163; Toril 1
6. P_3 RGM-434166; Toril 1
7. P_3 TOR3B-L3B-02; Toril 3B
8. P_3 PJE2-L1A-02; Paje 2
9. P_3 PJE2-L1A-01; Paje 2
10. P_3 PJE2-L1A-03; Paje 2
11. P_3 inv. RGM-435414; Solera
12. P_3 inv. RGM-435395; Solera
13. P_3 RGM-435361; Solera
14. P_3 inv. NOM1-NO-324; Nombrevilla 1
15. P_3 inv. NOM1-NO-323; Nombrevilla 1
16. P_3 inv. NOM1-NO-321; Nombrevilla 1
17. P_3 RGM-433228; Carrilanga 1
18. P_3 RGM-433237; Carrilanga 1
19. P_3 RGM-433304; Carrilanga 1
20. P_3 RGM-433247; Carrilanga 1


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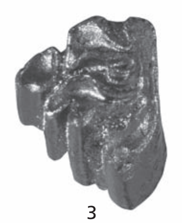
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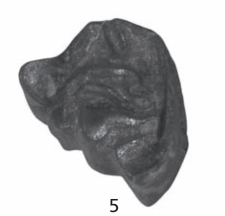
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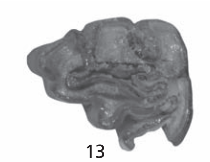
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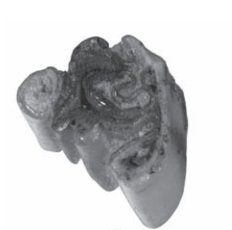
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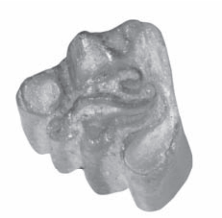
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Plate 3.6

Prolagus oeningensis.
1. P^3 LUM12-L3A-01; Las Umbrías 12
2. P^3 inv. RGM-434287; Las Planas 5B
3. P^3 TOR3B-L5B-05; Toril 3B
4. P^3 PJE2-L2A-03; Paje 2
5. P^3 PJE2-L3A-01; Paje 2
6. P^3 RGM-435534; Solera
7. P^3 inv. RGM-435561; Solera
8. P^3 NOM1-NO-331; Nombrevilla 1
9. P^3 RGM-433412; Carrilanga 1
10. P^3 NOM1-NO-337; Nombrevilla 1
11. P^2 inv. RGM-434307; Las Planas 5B
12. P^2 MAN-6262A; Manchones
13. P^2 RGM-435639; Solera
14. P^2 RGM-435642; Solera
15. P^2 inv. NOM1-2A-02; Nombrevilla 1
16. P^2 RGM-433539; Carrilanga 1
17. P^2 inv. TOR3B-L8A-05; Toril 3B
18. P^2 TOR3B-L7A-05; Toril 3B
19. P^4 LUM10-L2B-06; Las Umbrías 10
20. M^1 inv. LUM10-L2B-08; Las Umbrías 10
21. M^2 LUM10-L2B-10; Las Umbrías 10


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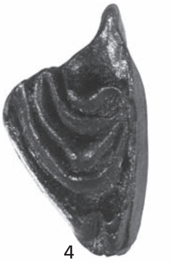
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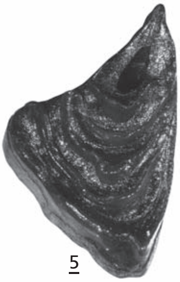
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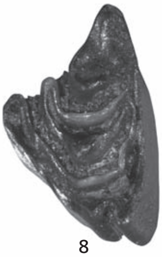
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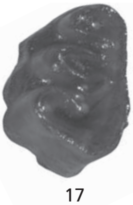
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Plate 3.7: Comparative material

Prolagus cf. *oeningensis*
1. P_3 VICO-1B-04; Vieux-Collonges
2. P_3 VICO-1B-02; Vieux-Collonges
3. P_3 VICO-1B-05; Vieux-Collonges
4. P_3 inv. VICO-2A-02; Vieux-Collonges

Prolagus oeningensis
5. P_3 SANS-1A-02; Sansan
6. P_3 SANS-1A-01; Sansan
7. P_3 inv. SANS-1B-01; Sansan
8. P_3 inv. SANS-1B-06; Sansan
9. P_3 inv. LGRM-1B-01; La Grive M
10. P_3 inv. LGRM-1B-03; La Grive M
11. P^4-M^2 LGRM-3B-04; La Grive M
12. P^4 inv. SANS-3A-06; Sansan
13. P^4 inv. SANS-3A-08; Sansan
14. M^1 SANS-3B-02; Sansan
15. M^2 inv. SANS-3B-09; Sansan


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Plate 3.8: Comparative material

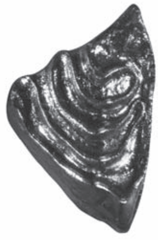
Prolagus oeningensis (France)
1. P^3 inv. SANS-2A-05; Sansan
2. P^3 inv. SANS-2A-06; Sansan
3. P^3 inv. SANS-2A-04; Sansan
4. P^3 inv. LGRM-2A-01; La Grive M
7. P^2 SANS-2B-01; Sansan
8. P^2 inv. SANS-2B-05; Sansan
9. P^2 LGR-2B-01; La Grive M

Prolagus cf. *oeningensis*
5. P^3 VICO-3A-07; Vieux-Collonges
6. P^3 inv. VICO-3B-01; Vieux-Collonges

Prolagus oeningensis (Spain)
10. P_3 AR-3060; Arroyo del Val 6
11. P_3 inv. AR-3056; Arroyo del Val 6
12. P_3 AR-3066; Arroyo del Val 6
13. P_3 inv. AR-3074; Arroyo del Val 6
14. P^3 inv. AR-3031; Arroyo del Val 6

Prolagus major
15. P_3 AR-3051; Arroyo del Val 6
16. P^4 inv. AR6-unregistered; Arroyo del Val 6
17. M^1 inv. AR6- unregistered; Arroyo del Val 6
19. P^2 AR6- unregistered; Arroyo del Val 6

Prolagus vargasensis n. sp.
18. P_3 inv. TRB1-18-12; Torralba 1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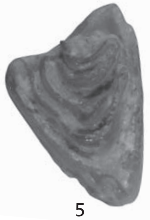
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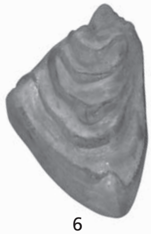
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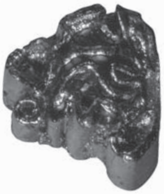
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Appendices chapter 3

3A: P_3 size measurements of *P. vargasensis* and *P. major.* 1) Length, Width, Length metaconid-entoconid, Length protoconulid-entoconid, Width protoconid-metaconid

P/3 (excl. juveniles)			Length (mm)						Width (mm)						Length m-e (mm)						Length pc-e (mm)						Width p-m (mm)					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
G3	TOR1	*P. major*	2	2,34		2,37			1		2,54				2	1,58		1,63			2	2,02		2,02			1		2,06			
G2	MAN	*P. major*	2	2,31		2,43			2	2,10		2,64			2	1,48		1,58			2	1,98		2,17			3	1,55	1,79	1,94		
G1	VT1B	*P. major*	3	1,98	2,02	2,06			4	2,00	2,13	2,29			6	1,31	1,39	1,56	0,037	0,090	6	1,70	1,73	1,79	0,014	0,035	5	1,56	1,65	1,91	0,065	0,145
G1	VT1A	*P. major*	2	1,98		2,08			3	1,86	2,07	2,28			2	1,42		1,50			2	1,65		1,80			2	1,75		1,86		
G1	LP5B	*P. major*	6	1,79	2,04	2,20	0,058	0,143	5	1,94	2,11	2,33	0,074	0,164	5	1,10	1,36	1,54	0,071	0,159	6	1,63	1,75	1,94	0,047	0,114	5	1,42	1,74	1,56	0,061	0,137
F	ARM7	*P. major*	4	1,92	1,99	2,04			5	2,02	2,10	2,20	0,041	0,092	7	1,21	1,29	1,40	0,024	0,064	5	1,69	1,75	1,83	0,027	0,060	6	1,48	1,57	1,65	0,028	0,069
F	VT2C	*P. vargasensis*	2	1,80		1,84			3	1,81	1,94	2,05			3	1,20	1,22	1,24			3	1,51	1,61	1,77			4	1,31	1,43	1,48		
F	LUM22	*P. vargasensis*	1		1,77				1		1,82				4	1,13	1,20	1,25			2	1,59		1,62			2	1,29		1,49		
E	LP4BA	*P. vargasensis*	4	1,68	1,85	1,95			5	1,61	1,78	2,03	0,072	0,161	6	1,10	1,28	1,34	0,037	0,091	6	1,33	1,52	1,60	0,040	0,097	8	1,22	1,35	1,54	0,049	0,137
E	LP4A	*P. vargasensis*	1		1,88				1		1,94				1		1,26				1		1,51				1		1,46			
Dd	LUM9	*P. vargasensis*	0						0						0						0						0					
Dd	LUM3	*P. vargasensis*	0						1		2,14				1		1,21				1		1,60				1		1,58			
Dc	VR5	*P. vargasensis*	0						0						0						0						0					
Da	FTE3	*P. vargasensis*	1		1,93				1		1,92				3	1,36	1,46	1,54			1		1,58				1		1,53			
Da	FTE2	*P. vargasensis*	2	1,85		1,88			2	1,55		1,89	0,170	0,240	2	1,26		1,28			3	1,43	1,48	1,53			2	1,25		1,35		
Da	OR9	*P. vargasensis*	0						0						1		1,17				1		1,33				1		1,21			
Da	VR2B	*P. vargasensis*	0						0						0						0						0					
C	VR2A	*P. vargasensis*	0						0						0						0						0					
C	OR8	*P. vargasensis*	1		1,78				1		1,70				1		1,20				1		1,50				1		1,30			
C	VR1A	*P. vargasensis*	5	1,76	1,84	1,89	0,022	0,050	6	1,74	1,90	2,06	0,044	0,109	7	1,16	1,25	1,33	0,024	0,064	7	1,35	1,44	1,50	0,020	0,052	7	1,29	1,38	1,46	0,022	0,059
C	VR4BB	*P. vargasensis*	0						1		1,52				3	1,00	1,15	1,32			2	1,12		1,42			2	1,15		1,18		
C	VR4A	*P. vargasensis*	2	1,73		1,80			1		1,64				3	1,12	1,22	1,35			3	1,25	1,37	1,46			3	1,11	1,20	1,25		

3A: 2) Length anteroconid, Width anteroconid, Length/Width, Length a/Width a. Juvenile specimens are excluded.

P/3 (excl. juveniles)			Length a (mm)						Width a (mm)						Length / Width						Length a / Width a					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
G3	TOR1	*P. major*	2	0,71		0,77			2	0,76		1,06			1		0,93				2	0,73		0,93		
G2	MAN	*P. major*	3	0,66	0,69	0,74			2	0,74		0,83			1		0,88				2	0,82		1,00		
G1	VT1B	*P. major*	3	0,57	0,64	0,69			5	0,62	0,67	0,80	0,034	0,075	3	0,92	0,98	1,03			3	0,90	1,00	1,11		
G1	VT1A	*P. major*	2	0,57		0,60			2	0,66		0,79			2	0,91		0,96			2	0,72		0,91		
G1	LP5B	*P. major*	6	0,60	0,69	0,79	0,033	0,080	6	0,47	0,62	0,74	0,044	0,107	5	0,88	0,96	1,04	0,027	0,060	6	0,95	1,14	1,41	0,078	0,191
F	ARM7	*P. major*	4	0,61	0,66	0,71			4	0,65	0,69	0,74			4	0,90	0,94	1,01			4	0,90	0,96	1,03		
F	VT2C	*P. vargasensis*	2	0,49		0,55			2	0,44		0,64			2	0,94		0,99			2	0,86		1,11		
F	LUM22	*P. vargasensis*	1		0,47				1		0,55				1		0,97				1		0,85			
E	LP4BA	*P. vargasensis*	5	0,46	0,57	0,65	0,031	0,070	5	0,50	0,62	0,70	0,036	0,079	3	0,92	0,98	1,07			5	0,80	0,93	1,05	0,045	0,100
E	LP4A	*P. vargasensis*	1		0,58				1		0,62				1		0,97				1		0,94			
Dd	LUM9	*P. vargasensis*	0						0						0						0					
Dd	LUM3	*P. vargasensis*	0						0						0						0					
Dc	VR5	*P. vargasensis*	0						0						0						0					
Da	FTE3	*P. vargasensis*	1		0,68				1		0,63				1		1,01				1		1,08			
Da	FTE2	*P. vargasensis*	2	0,59		0,60			2	0,51		0,52			2	0,98		1,21			2	1,15		1,16		
Da	OR9	*P. vargasensis*	0						0						0						0					
Da	VR2B	*P. vargasensis*	0						0						0						0					
C	VR2A	*P. vargasensis*	0						0						0						0					
C	OR8	*P. vargasensis*	1		0,59				1		0,55				1		1,05				1		1,07			
C	VR1A	*P. vargasensis*	5	0,56	0,59	0,65	0,015	0,034	4	0,53	0,61	0,64			4	0,90	0,94	1,02			4	0,88	0,96	1,11		
C	VR4BB	*P. vargasensis*	1		0,49				1		0,64				0						1		0,77			
C	VR4A	*P. vargasensis*	2	0,47		0,50			2	0,53		0,65			1		1,10				2	0,72		0,94		

3B: P^3 size measurements of *P. vargasensis* and *P. major.* 1) Length, Width, Width mesial hyperloph, Width distal hyperloph

P3/ (excl. juveniles)			Length (mm)						Width (mm)						Width mh (mm)						Width dh (mm)					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
G3	TOR1	*P. major*	0						0						0						0					
G2	MAN	*P. major*	1		2,08				1		3,36				1		2,20				1		2,33			
G1	VT1B	*P. major*	0						0						0						0					
G1	VT1A	*P. major*	1		1,86				0						0						0					
G1	LP5B	*P. major*	3	1,86	1,97	2,12			1		3,01				4	1,88	1,93	1,95			2	1,97		2,13		
F	ARM7	*P. major*	3	1,86	1,94	2,01			1		3,16				3	1,81	2,08	2,44			2	1,99		2,09		
F	VT2C	*P. vargasensis*	2	1,69		1,77			1		2,57				1		1,73				1		1,90			
F	LUM22	*P. vargasensis*	2	1,62		1,84			4	2,37	2,55	2,73			3	1,45	1,56	1,68			3	1,59	1,66	1,76		
E	LP4BA	*P. vargasensis*	1		1,64				0						1		1,69				1		1,73			
E	LP4A	*P. vargasensis*	2	1,64		1,87			1		3,27				2	1,85		2,09			1		2,28			
Dd	LUM9	*P. vargasensis*	0						0						0						0					
Dd	LUM3	*P. vargasensis*	0						0						0						0					
Dc	VR5	*P. vargasensis*	0						0						0						0					
Da	FTE3	*P. vargasensis*	0						0						0						0					
Da	FTE2	*P. vargasensis*	6	1,28	1,64	1,90	0,083	0,203	2	2,34		2,78			4	1,33	1,59	1,86			3	1,48	1,72	1,99		
Da	OR9	*P. vargasensis*	0						0						0						0					
Da	VR2B	*P. vargasensis*	0						0						0						0					
C	VR2A	*P. vargasensis*	0						0						0						0					
C	OR8	*P. vargasensis*	1		1,70				1		2,63				1		1,64				1		1,85			
C	VR1A	*P. vargasensis*	4	1,46	1,71	1,94			1		2,73				4	1,68	1,78	1,89			4	1,71	1,87	1,98		
C	VR4BB	*P. vargasensis*	1		1,58				0						0						0					
C	VR4A	*P. vargasensis*	5	1,39	1,63	1,80	0,069	0,154	2	2,31		2,56			3	1,61	1,71	1,88			2	1,76		1,95		

3B: 2) Length postlobus, Length/Width, Width mesial hyperloph/Length, Width mesial hyperloph/Width. Juvenile specimens are excluded.

P3/ (excl. juveniles)			Length pl (mm)						Length / Width						Width mh / Length						Width mh / Width					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
G3	TOR1	*P. major*	0						0						0						0					
G2	MAN	*P. major*	1		1,42				1		0,62				1		1,06				1		0,65			
G1	VT1B	*P. major*	0						0						0						0					
G1	VT1A	*P. major*	0						0						0						0					
G1	LP5B	*P. major*	4	0,92	1,08	1,22			1		0,70				2	0,92		1,01			1		0,64			
F	ARM7	*P. major*	3	1,08	1,11	1,16			1		0,64				2	0,90		1,31			1		0,57			
F	VT2C	*P. vargasensis*	4	0,79	1,04	1,37			1		0,66				1		0,98				0					
F	LUM22	*P. vargasensis*	4	0,89	0,96	1,06			2	0,59		0,72			2	0,91		0,96			3	0,57	0,61	0,66		
E	LP4BA	*P. vargasensis*	3	0,94	1,02	1,06			0						1		1,03				0					
E	LP4A	*P. vargasensis*	2	1,01		1,06			1		0,57				2	1,12		1,13			1		0,64			
Dd	LUM9	*P. vargasensis*	0						0						0						0					
Dd	LUM3	*P. vargasensis*	0						0						0						0					
Dc	VR5	*P. vargasensis*	0						0						0						0					
Da	FTE3	*P. vargasensis*	0						0						0						0					
Da	FTE2	*P. vargasensis*	6	0,78	0,93	1,14	0,051	0,124	2	0,68		0,71			4	0,94	0,98	1,04			2	0,66		0,67		
Da	OR9	*P. vargasensis*	0						0						0						0					
Da	VR2B	*P. vargasensis*	0						0						0						0					
C	VR2A	*P. vargasensis*	0						0						0						0					
C	OR8	*P. vargasensis*	1		0,93				1		0,65				1		0,96				1		0,62			
C	VR1A	*P. vargasensis*	4	0,96	1,00	1,05			1		0,71				4	0,87	1,05	1,16			1		0,62			
C	VR4BB	*P. vargasensis*	1		1,06				0						0						0					
C	VR4A	*P. vargasensis*	6	0,78	0,96	1,07	0,040	0,097	2	0,70		0,70			3	0,95	1,00	1,04			2	0,70		0,73		

3C: P^2 size measurements of *P. vargasensis* and *P. major.* Length, Width, Width distal hyperloph, Length postlobus, Length/Width. Juvenile specimens are excluded.

P2/ (excl. juveniles)			Length (mm)						Width (mm)						Width dh (mm)						Length pl (mm)						Length / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
G3	TOR1	*P. major*	0						0						0						0						0					
G2	MAN	*P. major*	4	1,27	1,39	1,50			4	2,18	2,37	2,52			5	0,85	1,04	1,30	0,076	0,169	4	0,93	1,03	1,14			4	0,52	0,59	0,63		
G1	VT1B	*P. major*	1		1,57				1		2,20				1		1,39				1		0,83				1		0,71			
G1	VT1A	*P. major*	2	1,19		1,54			2	2,00		2,04			2	0,81		1,41			3	0,85	0,89	0,95			2	0,60		0,75		
G1	LP5B	*P. major*	4	1,14	1,30	1,44			3	1,66	1,87	2,11			4	0,76	0,98	1,31			4	0,63	0,71	0,75			3	0,62	0,69	0,76		
F	ARM7	*P. major*	6	0,96	1,12	1,24	0,040	0,099	3	1,96	2,06	2,17			5	0,68	0,85	0,98	0,053	0,117	5	0,62	0,76	0,87	0,042	0,095	3	0,54	0,56	0,57		
F	VT2C	*P. vargasensis*	4	1,11	1,17	1,23			4	1,85	1,89	1,93			4	0,84	0,90	0,93			4	0,70	0,75	0,80			4	0,60	0,62	0,66		
F	LUM22	*P. vargasensis*	3	0,90	0,91	0,93			2	1,56		1,71			2	0,60		0,68			3	0,67	0,71	0,75			2	0,54		0,58		
E	LP4BA	*P. vargasensis*	0						0						0						0						0					
E	LP4A	*P. vargasensis*	1		0,69				0						0						1		0,69				0					
Dd	LUM9	*P. vargasensis*	2	1,09		1,16			2	2,15		2,19			2	1,04		1,11			3	0,91	0,93	0,98			2	0,51	0,52	0,53		
Dd	LUM3	*P. vargasensis*	0						0						0						0											
Dc	VR5	*P. vargasensis*	0						0						0						0											
Da	FTE3	*P. vargasensis*	1		0,73				1		1,68				1		0,61				1		0,61				1		0,43			
Da	FTE2	*P. vargasensis*	2	0,94		0,99			1		1,87				1		0,71				2	0,69		0,81			1		0,50			
Da	OR9	*P. vargasensis*	1		1,00				0						0						1		1,00				0					
Da	VR2B	*P. vargasensis*	1		1,25				0						1		0,84				1		0,64				0					
C	VR2A	*P. vargasensis*	0						0						0						0						0					
C	OR8	*P. vargasensis*	0						0						0						0						0					
C	VR1A	*P. vargasensis*	1		1,13				0						0						1		0,73				0					
C	VR4BB	*P. vargasensis*	2	0,71		0,97			1		1,55				1		0,73				2	0,66		0,68			1		0,63			
C	VR4A	*P. vargasensis*	3	0,77	0,81	0,87			2	1,26		1,46			3	0,49	0,59	0,72			3	0,65	0,73	0,78			2	0,53	0,57	0,61		

3D: P_3 size measurements of *P. oeningensis*. 1) Length, Width, Length metaconid-entoconid, Length protoconulid-entoconid, Width protoconid-metaconid

P/3 (excl. juveniles)			Length (mm)						Width (mm)						Length m-e (mm)						Length pc-e (mm)						Width p-m (mm)					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. oeningensis*	86	1,35	1,67	1,93	0,009	0,086	124	1,47	1,79	2,17	0,012	0,139	149	0,81	1,10	1,28	0,007	0,084	141	1,13	1,39	1,61	0,008	0,090	148	1,03	1,33	1,59	0,009	0,110
H	NOM1	*P. oeningensis*	5	1,37	1,52	1,63	0,045	0,100	6	1,45	1,59	1,74	0,054	0,132	8	0,87	0,97	1,08	0,025	0,072	8	1,10	1,23	1,33	0,030	0,085	8	1,06	1,16	1,29	0,031	0,088
G3	SOL	*P. oeningensis*	19	1,60	1,68	1,79	0,012	0,050	36	1,48	1,73	1,97	0,022	0,130	48	0,93	1,13	1,31	0,011	0,078	49	1,10	1,36	1,54	0,013	0,091	63	1,05	1,26	1,42	0,012	0,094
G3	PJE2	*P. oeningensis*	5	1,60	1,68	1,77	0,033	0,074	4	1,46	1,72	1,87			6	1,01	1,13	1,22	0,032	0,077	6	1,26	1,38	1,50	0,036	0,089	5	1,14	1,38	1,56	0,073	0,163
G3	PJE1	*P. oeningensis*	11	1,46	1,68	1,79	0,030	0,099	7	1,54	1,73	1,99	0,069	0,181	13	0,82	1,11	1,27	0,030	0,110	10	1,20	1,36	1,51	0,031	0,099	11	1,09	1,28	1,44	0,033	0,109
G3	TOR3B	*P. oeningensis*	4	1,50	1,61	1,67			4	1,57	1,61	1,65			4	1,02	1,05	1,11			4	1,18	1,31	1,43			4	1,12	1,17	1,25		
G3	TOR3A	*P. oeningensis*	4	1,54	1,61	1,67			5	1,63	1,66	1,73	0,020	0,045	7	1,01	1,10	1,16	0,023	0,060	8	1,24	1,34	1,46	0,024	0,067	6	1,18	1,26	1,38	0,033	0,080
G3	TOR1	*P. oeningensis*	8	1,36	1,60	1,68	0,036	0,102	6	1,53	1,70	1,85	0,057	0,140	10	0,94	1,06	1,15	0,023	0,072	9	1,11	1,30	1,39	0,027	0,082	8	0,97	1,24	1,40	0,048	0,137
G2	BOR	*P. oeningensis*	13	1,23	1,56	1,81	0,043	0,155	13	1,35	1,60	1,82	0,038	0,137	15	0,86	1,02	1,18	0,021	0,081	15	1,06	1,31	1,48	0,029	0,110	12	0,85	1,15	1,33	0,037	0,128
G1	VT1B	*P. oeningensis*	2	1,44		1,69			1		1,72				2	1,02		1,13			1		1,31				1		1,34			
G1	VT1A	*P. oeningensis*	3	1,43	1,54	1,60			0						4	0,95	1,02	1,12			4	1,24	1,30	1,40			3	0,99	1,12	1,19		
G1	LP5B	*P. oeningensis*	1		1,40				2	1,45		1,55			2	0,97		0,99			2	1,21		1,21			2	0,94		1,17		
E	LUM12	*P. oeningensis*	2	1,38		1,66			2	1,53		1,74			2	0,95		1,09			1		1,45				1		1,31			
Dd	LUM10	*P. oeningensis*	1		1,56				2	1,43		1,67			2	0,96		1,07			2	1,02		1,29			2	1,00		1,24		
	GM	*P. oeningensis*	10	1,45	1,57	1,73	0,027	0,085	9	1,58	1,69	1,99	0,040	0,120	10	0,96	1,06	1,11	0,015	0,047	10	1,19	1,28	1,36	0,017	0,053	9	1,18	1,29	1,40	0,022	0,067
	SA	*P. oeningensis*	12	1,34	1,50	1,77	0,034	0,117	13	1,34	1,55	1,91	0,042	0,150	14	0,90	1,02	1,18	0,018	0,068	12	1,04	1,24	1,44	0,032	0,112	15	0,98	1,13	1,41	0,031	0,118
	VC	*P.* cf. *oeningensis*	14	1,37	1,51	1,63	0,020	0,073	11	1,28	1,55	1,82	0,046	0,152	14	0,94	1,06	1,21	0,022	0,083	15	1,11	1,26	1,38	0,018	0,070	16	0,98	1,10	1,29	0,021	0,085

3D: 2) Length anteroconid, Width anteroconid, Length/Width, Length a/Width a. Juvenile specimens are excluded.

P/3 (excl. juveniles)			Length a (mm)						Width a (mm)						Length / Width						Length a / Width a					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. oeningensis*	89	0,39	0,53	0,70	0,006	0,053	87	0,38	0,56	0,81	0,010	0,089	76	0,75	0,93	1,04	0,006	0,054	86	0,69	0,97	1,61	0,017	0,158
H	NOM1	*P. oeningensis*	5	0,43	0,49	0,54	0,019	0,042	5	0,35	0,52	0,79	0,073	0,163	3	0,93	0,98	1,07			5	0,65	1,00	1,37	0,119	0,266
G3	SOL	*P. oeningensis*	22	0,46	0,53	0,63	0,011	0,051	22	0,41	0,58	0,82	0,019	0,091	14	0,89	0,94	1,00	0,009	0,035	21	0,71	0,94	1,22	0,032	0,147
G3	PJE2	*P. oeningensis*	5	0,44	0,53	0,56	0,022	0,049	5	0,50	0,59	0,66	0,030	0,068	4	0,89	0,98	1,10			5	0,83	0,89	0,98	0,025	0,056
G3	PJE1	*P. oeningensis*	12	0,41	0,53	0,64	0,023	0,078	12	0,47	0,56	0,75	0,026	0,089	7	0,88	0,98	1,11	0,031	0,082	11	0,85	0,95	1,23	0,039	0,129
G3	TOR3B	*P. oeningensis*	4	0,49	0,55	0,61			4	0,51	0,55	0,58			4	0,91	1,00	1,05			4	0,88	0,99	1,05		
G3	TOR3A	*P. oeningensis*	4	0,40	0,51	0,56			4	0,52	0,57	0,62			2	0,97		0,99			4	0,65	0,89	1,00		
G3	TOR1	*P. oeningensis*	8	0,39	0,50	0,55	0,019	0,055	8	0,41	0,51	0,59	0,023	0,065	6	0,89	0,97	1,07	0,032	0,079	8	0,85	0,99	1,20	0,040	0,113
G2	BOR	*P. oeningensis*	14	0,33	0,46	0,59	0,020	0,074	13	0,40	0,51	0,72	0,025	0,091	11	0,85	0,96	1,18	0,028	0,093	13	0,61	0,93	1,23	0,048	0,173
G1	VT1B	*P. oeningensis*	2	0,34		0,54			1		0,52				1		0,98				1		1,04			
G1	VT1A	*P. oeningensis*	3	0,39	0,47	0,52			3	0,47	0,50	0,54			0						3	0,78	0,94	1,11		
G1	LP5B	*P. oeningensis*	1		0,35				1		0,44				1		0,97				1		0,80			
E	LUM12	*P. oeningensis*	2	0,39	0,45	0,51			2	0,47		0,53			2	0,90		0,95			2	0,83		0,96		
Dd	LUM10	*P. oeningensis*	1		0,49				1		0,68				1		0,93				1		0,72			
	GM	*P. oeningensis*	10	0,37	0,46	0,58	0,020	0,063	10	0,42	0,53	0,58	0,015	0,049	10	0,69	0,88	1,07	0,034	0,109	9	0,80	0,93	1,02	0,021	0,064
	SA	*P. oeningensis*	13	0,30	0,42	0,66	0,026	0,094	13	0,31	0,47	0,65	0,026	0,093	12	0,88	0,96	1,09	0,019	0,066	12	0,60	0,93	1,18	0,046	0,159
	VC	*P.* cf. *oeningensis*	15	0,33	0,42	0,49	0,011	0,041	15	0,41	0,49	0,62	0,016	0,061	10	0,84	0,97	1,13	0,028	0,087	14	0,71	0,86	1,11	0,035	0,129

3E: P^3 size measurements of *P. oeningensis*. 1) Length, Width, Width mesial hyperloph, Width distal hyperloph

P3/ (excl. juveniles)			Length (mm)						Width (mm)						Width mh (mm)						Width dh (mm)					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
H	CAR1	*P. oeningensis*	103	1,37	1,65	1,87	0,011	0,107	94	2,12	2,62	3,01	0,021	0,205	93	1,28	1,61	2,04	0,017	0,166	90	1,34	1,72	2,09	0,018	0,172
H	NOM1	*P. oeningensis*	7	1,33	1,44	1,54	0,031	0,081	5	2,19	2,40	2,58	0,063	0,140	5	1,39	1,51	1,65	0,053	0,119	5	1,47	1,59	1,73	0,049	0,110
G3	SOL	*P. oeningensis*	34	1,47	1,62	1,81	0,014	0,081	28	2,14	2,36	2,86	0,033	0,177	34	1,29	1,62	1,98	0,026	0,150	31	1,34	1,70	2,02	0,029	0,161
G3	PJE2	*P. oeningensis*	7	1,35	1,56	1,76	0,060	0,160	3	2,56	2,64	2,74			6	1,13	1,44	1,64	0,079	0,193	6	1,12	1,49	1,72	0,093	0,227
G3	PJE1	*P. oeningensis*	2	1,60		1,67			1		2,52				1		1,61				1		1,68			
G3	TOR3B	*P. oeningensis*	5	1,25	1,54	1,76	0,098	0,220	5	2,17	2,55	2,98	0,144	0,321	4	1,26	1,59	1,72			5	1,38	1,71	1,87	0,087	0,195
G3	TOR3A	*P. oeningensis*	4	1,44	1,56	1,66			0						3	1,35	1,57	1,85			2	1,39		1,97		
G3	TOR1	*P. oeningensis*	6	1,42	1,58	1,72	0,046	0,112	6	2,14	2,50	2,88	0,108	0,265	6	1,50	1,57	1,68	0,027	0,066	6	1,52	1,68	1,84	0,047	0,115
G2	BOR	*P. oeningensis*	5	1,48	1,57	1,64	0,033	0,074	4	2,31	2,42	2,50			4	1,38	1,56	1,63			5	1,46	1,62	1,72	0,046	0,103
G1	VT1B	*P. oeningensis*	0						0						0						0					
G1	VT1A	*P. oeningensis*	1		1,57				0						1		1,66				1		1,77			
G1	LP5B	*P. oeningensis*	7	1,33	1,50	1,59	0,033	0,086	3	2,16	2,21	2,28			8	1,21	1,52	1,81	0,073	0,206	7	1,38	1,70	1,94	0,073	0,192
E	LUM12	*P. oeningensis*	0						1		2,31				1		1,28				1		1,36			
Dd	LUM10	*P. oeningensis*	0						0						0						0					
	GM	*P. oeningensis*	10	1,46	1,59	1,76	0,030	0,096	9	2,20	2,56	2,75	0,062	0,186	9	1,13	1,43	1,66	0,064	0,191	9	1,22	1,50	1,71	0,060	0,180
	SA	*P. oeningensis*	9	1,31	1,49	1,71	0,041	0,123	8	1,89	2,23	2,50	0,074	0,209	9	0,99	1,27	1,57	0,054	0,162	9	1,03	1,39	1,77	0,063	0,190
	VC	*P.* cf. *oeningensis*	3	1,47	1,49	1,52			1		2,07				1		1,39				1		1,54			

3E: 2) Length postlobus, Length/Width, Width mesial hyperloph/Length, Width mesial hyperloph/Width. Juvenile specimens are excluded.

P3/ (excl. juveniles)			Length pl (mm)						Length / Width						Width mh / Length						Width mh / Width					
Zone	Locality	Species	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD	N	Min.	Mean	Max.	SE	SD
H	CAR1	*P. oeningensis*	122	0,70	0,94	1,23	0,008	0,091	82	0,54	0,63	0,78	0,005	0,043	88	0,74	0,98	1,23	0,011	0,104	76	0,47	0,62	0,79	0,007	0,065
H	NOM1	*P. oeningensis*	8	0,71	0,81	0,89	0,021	0,058	5	0,57	0,62	0,63	0,013	0,029	5	0,90	1,02	1,10	0,035	0,078	5	0,57	0,63	0,68	0,018	0,040
G3	SOL	*P. oeningensis*	44	0,76	0,90	1,15	0,013	0,086	24	0,61	0,69	0,78	0,010	0,049	29	0,76	1,01	1,24	0,018	0,099	25	0,49	0,70	0,83	0,014	0,071
G3	PJE2	*P. oeningensis*	7	0,75	0,91	1,02	0,041	0,108	3	0,56	0,60	0,64			6	0,84	0,94	1,08	0,036	0,089	3	0,55	0,58	0,61		
G3	PJE1	*P. oeningensis*	3	0,74	0,88	1,00			1		0,63				1		1,01				1		0,64			
G3	TOR3B	*P. oeningensis*	5	0,73	0,86	1,01	0,056	0,125	5	0,57	0,60	0,71	0,027	0,061	4	0,99	1,08	1,26			4	0,56	0,62	0,72		
G3	TOR3A	*P. oeningensis*	4	0,75	0,85	0,93			0						3	0,94	1,00	1,11			0					
G3	TOR1	*P. oeningensis*	6	0,77	0,89	0,99	0,034	0,083	6	0,59	0,63	0,66	0,011	0,028	6	0,95	0,99	1,09	0,021	0,052	6	0,56	0,63	0,72	0,023	0,056
G2	BOR	*P. oeningensis*	6	0,84	0,92	0,99	0,026	0,064	4	0,61	0,65	0,71			4	0,84	0,98	1,09			3	0,55	0,64	0,71		
G1	VT1B	*P. oeningensis*	0						0						0						0					
G1	VT1A	*P. oeningensis*	0						0						1		1,06				0					
G1	LP5B	*P. oeningensis*	8	0,76	0,88	1,00	0,024	0,069	3	0,66	0,69	0,72			5	0,78	0,97	1,18	0,074	0,166	2	0,67		0,71		
E	LUM12	*P. oeningensis*	1		1,01				0						0						1		0,55			
Dd	LUM10	*P. oeningensis*	0						0						0						0					
	GM	*P. oeningensis*	11	0,79	0,86	0,93	0,014	0,046	9	0,57	0,63	0,75	0,021	0,062	9	0,64	0,91	1,11	0,045	0,134	8	0,48	0,56	0,63	0,018	0,052
	SA	*P. oeningensis*	9	0,76	0,88	1,05	0,039	0,116	8	0,61	0,66	0,78	0,021	0,060	9	0,67	0,86	1,03	0,041	0,124	8	0,52	0,57	0,63	0,017	0,048
	VC	*P.* cf. *oeningensis*	4	0,77	0,84	0,87			1		0,71				1		0,94				1		0,67			

3F: P^2 size measurements of *P. oeningensis*. Length, Width, Width distal hyperloph, Length postlobus, Length/Width. Juvenile specimens are excluded.

P2/ (excl. juveniles)			Length (mm)						Width (mm)						Width dh (mm)						Length pl (mm)						Length / Width					
Zone	Locality	Species	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD	N	Min	Mean	Max	SE	SD
H	CAR1	*P. oeningensis*	95	0,64	0,84	1,10	0,008	0,082	95	1,37	1,70	1,99	0,013	0,131	99	0,28	0,59	0,81	0,011	0,112	98	0,50	0,65	0,86	0,007	0,067	89	0,40	0,50	0,61	0,005	0,046
H	NOM1	*P. oeningensis*	9	0,59	0,72	0,81	0,026	0,078	8	1,34	1,52	1,68	0,042	0,118	10	0,17	0,49	0,63	0,042	0,132	9	0,49	0,60	0,71	0,022	0,066	6	0,42	0,48	0,60	0,027	0,066
G3	SOL	*P. oeningensis*	18	0,74	0,86	1,02	0,015	0,064	16	1,49	1,68	1,86	0,028	0,110	18	0,53	0,63	0,81	0,017	0,073	18	0,52	0,64	0,77	0,017	0,072	16	0,47	0,52	0,56	0,006	0,024
G3	PJE2	*P. oeningensis*	6	0,82	0,89	0,96	0,024	0,060	5	1,70	1,79	1,89	0,038	0,086	6	0,65	0,71	0,85	0,030	0,074	6	0,60	0,70	0,81	0,033	0,081	5	0,45	0,51	0,55	0,021	0,046
G3	PJE1	*P. oeningensis*	1		0,87				1		1,68				1		0,64				1		0,78				1		0,52			
G3	TOR3B	*P. oeningensis*	3	0,89	0,92	0,97			3	1,65	1,68	1,71			3	0,66	0,72	0,79			3	0,57	0,62	0,70			3	0,52	0,55	0,58		
G3	TOR3A	*P. oeningensis*	1		0,89				0						0						1		0,66				0					
G3	TOR1	*P. oeningensis*	2	0,78		0,84			1		1,53				1		0,59				2	0,64		0,68			1		0,51			
G2	BOR	*P. oeningensis*	6	0,74	0,87	1,00	0,043	0,106	4	1,40	1,54	1,68			4	0,57	0,59	0,61			7	0,53	0,65	0,71	0,023	0,061	4	0,52	0,58	0,68		
G1	VT1B	*P. oeningensis*																														
G1	VT1A	*P. oeningensis*	1		0,77				2	1,54		1,55			2	0,60		0,66			1		0,55				1		0,50			
G1	LP5B	*P. oeningensis*	2	0,75		0,86			2	1,34		1,45			2	0,38		0,45			2	0,56		0,60			1		0,59			
E	LUM12	*P. oeningensis*																														
Dd	LUM10	*P. oeningensis*																														
	GM	*P. oeningensis*	7	0,71	0,82	0,90	0,024	0,065	7	1,52	1,57	1,66	0,023	0,060	7	0,56	0,60	0,72	0,022	0,058	7	0,49	0,58	0,63	0,017	0,046	7	0,47	0,52	0,58	0,014	0,037
	SA	*P. oeningensis*	5	0,71	0,84	0,91	0,037	0,083	5	1,36	1,47	1,55	0,042	0,093	5	0,48	0,58	0,65	0,030	0,066	5	0,49	0,56	0,62	0,024	0,053	5	0,52	0,57	0,59	0,013	0,029

CHAPTER 4

Speciation, evolution and competition in pikas (Ochotonidae, Lagomorpha, Mammalia) from the early and middle Miocene of Southwestern Europe

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4.1 Abstract

Recent revision of the systematics of high-crowned pikas (Chapters 2 & 3) necessitates updating and re-evaluating part of the phylogenetic affinities of *Prolagus* in the late early to early late Miocene. In this light, we investigated possible evolutionary relations among the monotypic genus *Lagopsis* SCHLOSSER, 1884 and the polytypic *Prolagus* POMEL, 1853 from the high resolution succession of the Calatayud-Montalbán Basin (Spain). The excellent fossil record and age control in this area permit establishing hypotheses on speciation and evolutionary trends in Spain. Multivariate analyses of size and shape characteristics of preserved P_3 molars were used to demonstrate the intraspecific variation and the disparity between the species of the four lineages present. The combination of these analyses with the stratigraphic and paleobiogeographic distribution of these lineages as well as the species coexistence data within assemblages aims to unravel patterns of biotic interaction between the species and lineages through time.

The evolutionary history of both *Lagopsis* and *Prolagus* is characterized by periods of stasis complemented by or intermitted with anagenesis. The Iberian Peninsula was stage to three speciation events within *Prolagus* during three separate time intervals in the Early Miocene. Two different modes of geographic speciation have been construed for the youngest two speciations, allopatric and parapatric speciation respectively. From the available data we deduced that competition in combination with climate has probably played a significant role in the evolutionary and co-existence patterns of the ochotonid lineages present in the Daroca-Villafeliche area. We inferred the occurrence of competitive exclusion by the delayed settlement of a presumed allopatric competitor from a nearby region, and the occurrence of competition-reducing limiting similarity between co-occurring species within fossil assemblages.

4.2 Introduction

The pika family, Ochotonidae THOMAS, 1897, represents a significant part of the Miocene small-mammal record of Western Europe in which they are often abundantly present. Fossil ochotonids, whose systematics are largely based on isolated teeth, are known for their relatively conservative evolutionary change in which phases of stasis and anagenesis are occasionally intermitted by speciation events.

Lagopsis Schlosser, 1884 and *Prolagus* Pomel, 1853 are the most commonly found pika genera in mammal assemblages from the late early and middle Miocene of Western Europe (López-Martínez, 1989). *Prolagus* represents a species rich, long-lived and widely distributed genus comprising multiple evolutionary lineages, most of which had relatively limited geographical ranges. *Lagopsis*, on the other hand, was less long-lived and is characterized by a single lineage showing anagenetic evolution and its species were relatively widespread. Such marked differences in the species diversity between genera are also known in extant lagomorphs (Chapman & Flux, 2008).

Recently, progress has been made in further establishing and refining the taxonomy and biostratigraphy of Spanish late early and middle Miocene *Lagopsis* and *Prolagus* based on material from the magnetostratigraphically calibrated mammal succession in the Calatayud-Montalbán Basin (Chapters 2 & 3). The new data necessitate reinterpretation of part of the phylogeny of these high-crowned ochotonids in Western Europe. Secondly, it provides the basis for establishing hypotheses on evolutionary processes that took place in Spain during the late early to early late Miocene.

Previous overviews of the phylogenetic affinities of early and middle Miocene ochotonids in Europe have been provided by López-Martínez & Thaler (1975) and López-Martínez (1986, 1997). These overviews have established various evolutionary trends and indicated several knowledge gaps in the data available at that time, while providing hypotheses for some of the less well-constrained phylogenetic affinities and speciation events.

Our first objective was to unravel the evolutionary trends of ochotonid lineages present in the early Miocene to early late Miocene succession Calatayud-Montalbán Basin (Fig. 4.1), in particular with regard to phases of speciation and anagenesis, in which we attempt to identify the possible mechanisms of speciation and evolutionary change that characterize the lineages in question.

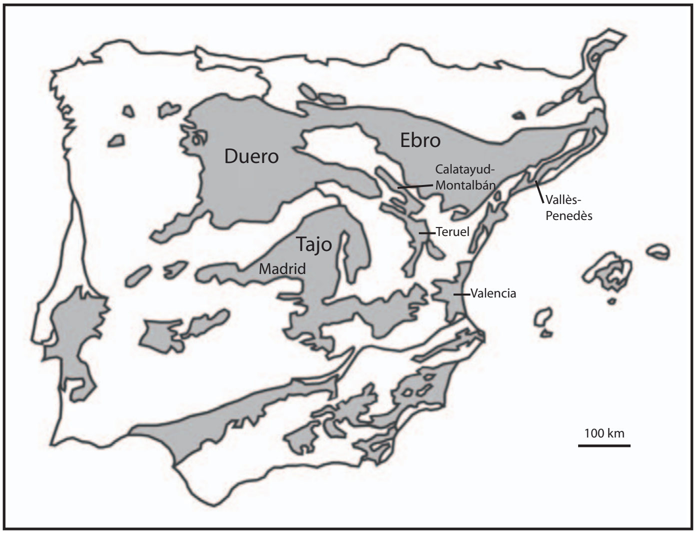


Figure 4.1: Schematic distribution of the main Cenozoic basins on the Iberian Peninsula (modified after Domingo *et al.*, 2007).

Secondly, we aim to identify and establish possible signs of competition between the fossil ochotonid species in the study area, in particular with regard to changes in paleobiogeography and background climate on a larger scale.

For this purpose, presence-absence data and size data of a record comprising a series of 40 localities that includes four lineages and seven species were analysed. This data set provides a good representation of the available fossil record from the end of Iberian local zone A to H (MN3-MN9) in the Calatayud-Montalbán Basin (Chapters 2 & 3). A set of absolute and relative tooth size measures of the occlusal surface of the P_3 were analyzed using multivariate analyses in order to get a grip on the intra- and interspecific variation in tooth morphology through time and within assemblages.

4.3 Material and methods

4.3.1 Material and measurement

The presence of ochotonid species from the study area in the assemblages under consideration is shown in Table 4.1A. The analyzed ochotonid assemblages include the following evolutionary lineages: the *L. penai* (Royo, 1928) – *L. verus* (Hensel, 1856) lineage, the *P. lopezmartinezae* n. sp., Chapters 2 – *P. tobieni* López, 1977 lineage, the *P. vargasensis* n. sp., Chapters 3 – *P. major* López, 1977 lineage and the *P. oeningensis* (König, 1825) lineage (Chapters 2 & 3). The annotation *ex. interc*. (*exemplum intercentrale*; Drooger, 1952, 1993) in Table 4.1A indicates in this case that identification at the species-level is unresolved and that the material belongs to either one of the two chronospecies provided.

The P_3, P^2 and P^3 are the most useful elements for the ochotonids under consideration. The P_3 in particular is diagnostic at the species level and is the element of interest in our multivariate analysis. Figure 4.2 shows the three main morphological groups characterizing the studied lineages along with the tooth cusp nomenclature and tooth size measurements employed by Hordijk & van der Meulen (Chapters 2 & 3). The anteroconid in *Lagopsis* is not isolated and its protoconulid is always absent in contrast to *Prolagus*. The centroflexid and the protoconulid mark the main differences between the two morphological groups in *Prolagus*. One group has a shallow or nearly absent centroflexid and small or nearly absent protoconulid and is represented by *P. lopezmartinezae* and *P. tobieni* in this study. The other group is characterised by a deep centroflexid, which is the merger of the centroflexid with the distal part of the mesoflexid, and the presence of a distinctly developed protoconulid. The latter group is represented by *P.* cf. *oeningensis*, *P. oeningensis*, *P. vargasensis* and *P. major*. In this case *P.* cf. *oeningensis* represents a primitive stage of evolution in the *P. oeningensis* lineage that does not strictly fit the diagnosis of *P. oeningensis*, which is discussed in more detail by Hordijk & van der Meulen (Chapter 3). Therefore, our *P. oeningensis* s.l. includes *P.* cf. *oeningensis* whereas *P. oeningensis* s.s. does not. A state of the art of the inferred phylogenies for *Prolagus* and *Lagopsis* summarizing the existing phylogeny during the early and middle Miocene derived from the literature in which we have integrated our results and views is outlined in Appendix 4.2.

Correlations of Spanish assemblages to the MN system and local biozones are after Daams *et al*. (1999a). The numerical ages of some MN-correlated Spanish assemblages are known to differ from those in central Western Europe (Lindsay, 2001; van Dam, 2003; Kälin & Kempf, 2009; van der Meulen *et al*., in review). For comparison in the time domain, numerical age estimates are used.

Table 4.1:

A											B					C			
Locality	Code	Repository	MN zone	Local zone	Age (Daams *et al.*, 1999)	Age (van Dam *et al.*, 2006)	*Lagopsis* Lineage 1	*Prolagus* Lineage 2	*Prolagus* Lineage 3	*Prolagus* Lineage 4	Lineage 1 P3+p3	Lineage 2 P3+p3	Lineage 3 P3+p3	Lineage 4 P3+p3	deciduous #	Lineage 1 p3	Lineage 2 p3	Lineage 3 p3	Lineage 4 p3
Carrilanga 1	CAR1	NCBN	9	H	10,50	11,57		tobieni		oeningensis		13		300	10		3		72
Nombrevilla 1	NOM1	IVAU	9	H	11,00	10,76		tobieni		oeningensis		1		17	3				3
Solera	SOL	NCBN	7/8	G3	11,75	12,01	verus	tobieni		oeningensis	26	85		151	31	8	12		14
Paje 2	PJE2	MNCN	7/8	G3	12,17	12,20		tobieni		oeningensis		1		18	13				4
Paje 1	PJE1	MNCN	7/8	G3	12,30	12,34				oeningensis				23	6				5
Toril 3B	TOR3B	MNCN	7/8	G3	12,59	12,11	verus	tobieni		oeningensis	18	53		13	42	7	25		4
Toril 3A	TOR3A	MNCN	7/8	G3	12,60	12,12	verus	tobieni		oeningensis	1	49		14	22		15		2
Toril 1	TOR1	NCBN	7/8	G3	12,62	12,14	verus	tobieni	major	oeningensis	18	4	2	19	5	4	3	1	6
Borjas	BOR	NCBN	6	G2	13,20	13,26	verus			oeningensis	12			23	2	4			9
Manchones	MAN	IVAU	6	G2	13,25	13,31	verus	tobieni	major	oeningensis	481	8	4	338	48	n.a.	3	1	n.a.
Valalto 1B	VT1B	NCBN-MNCN	6	G1	13,30	13,36	verus		major	oeningensis	11		7	3	4	1		3	1
Valalto 1A	VT1A	MNCN	6	G1	13,35	13,41	verus	ex. interc.	major	oeningensis	24	4	4	6	19	8	2	2	
Las Planas 5B	LP5B	NCBN-MNCN	6	G1	13,47	13,56	verus		major	oeningensis	48		12	18	23	11		5	1
Armantes 7	ARM7*	IVAU	6	F			verus		major		49		11		5	10		3	
Valalto 2C	VT2C	NCBN	6	F	13,68	13,74	verus	ex. interc.	vargasensis		89	2	9		6	12		2	
Las Umbrias 22	LUM22	MNCN	6	F	13,73	13,76	verus		vargasensis		17		11		4	3		1	
Las Planas 4BA	LP4BA	MNCN	5	E	13,94	13,96	verus	ex. interc.	vargasensis		21	2	14		7	2		3	
Las Planas 4A	LP4A	IVAU-NCBN	5	E	13,96	13,98	verus		vargasensis		63		3		22	13		1	
Las Umbrias 12	LUM12	MNCN	5	E	14,01	14,03	verus			oeningensis	27			4	17	6			1
Las Umbrias 10	LUM10	MNCN	5	Dd	14,07	14,09	verus			oeningensis	19			2	4	2			1
Las Umbrias 9	LUM9	MNCN	5	Dd	14,16	14,18	verus		vargasensis		26		1		3	4			
Las Umbrias 3	LUM3	MNCN	5	Dd	14,37	14,37	penai		vargasensis		47		1		2	7			
Valdemoros 3F	VA3F	MNCN	5	Dd	14,52	14,50	penai	ex. interc.			34	2			6	6			
Valdemoros 1A	VA1A	IVAU-NCBN	5	Dd	14,64	14,61	penai				76				7	10			
Valdemoros 3B	VA3B	IVAU-MNCN	5	Dc	14,85	14,84	penai	ex. interc.			84	***			24	21			
Vargas 5	VR5	MNCN	5	Dc	15,32	15,32	penai	ex. interc.	vargasensis		84	4	***		3	9	1		
La Col D	COL-D	MNCN	5	Db	15,87	15,84	penai	ex. interc.			20	1			0	6			
Fuente Sierra 3	FTE3	MNCN	5	Da	15,92	15,88	penai		vargasensis		18		3		3	5		1	
Fuente Sierra 2	FTE2	MNCN	5	Da	15,93	15,89	penai		vargasensis		17		12		5	6		2	
Olmo Redondo 9	OR9	NCBN	5	Da	15,95	15,91	penai		vargasensis		27		3		1	6			
Vargas 2B	VR2B	MNCN	5	Da	15,96	15,92	penai		vargasensis		***		2		0				
Vargas 2A	VR2A	MNCN	4	Cb	15,98	15,94	penai		vargasensis		15		1		3	3			
Olmo Redondo 8	OR8	NCBN	4	Cb	15,99	15,95	penai		vargasensis		18		2		6	6		1	
Vargas 1A	VR1A	NCBN	4	Cb	16,14	16,11	penai	lopezmartinezae	vargasensis		28	2	11		7	6		3	
Vargas 4BB	VR4BB	MNCN	4	Cb	16,15	16,12	penai	lopezmartinezae	vargasensis		44	1	8		4	8			
Vargas 4A	VR4A	MNCN	4	Cb	16,18	16,15	penai		vargasensis		53		9		2	9		1	
San Roque 3	SR3	MNCN	4	Ca	16,35	16,33	penai	lopezmartinezae			64	3			12	18	1		
Villafeliche 2A	VL2A	IVAU	4	B	16,64	16,63	penai	lopezmartinezae			106	4			14	21	1		
San Marcos	SAM	MNCN	4	B	16,70	16,69	penai	lopezmartinezae			182	54			14	58	14		
Olmo Redondo 2	OR2	NCBN	4	B	16,73	16,72	penai	lopezmartinezae			130	15			3	39	1		
San Roque 4A	SR4A	MNCN	3	A	17,02	17,00	penai	lopezmartinezae			48	18			3	10	1		
La Grive M	GM	IVAU**	7/8				verus			oeningensis				24					8
Sansan	SA	IVAU**	6							oeningensis				27					10
Vieux-Collonges	VC	IVAU**	4-5				penai			cf. oeningensis	19			26		3			9

← *Table 4.1:* Listing of analyzed assemblages and material. A: Ochotonid lineages and species present in the Calatayd-Daroca record (Hordijk & van der Meulen, (Chapter 2 & 3). Repository institutes. IVAU: Instituut voor Aardwetenschappen Utrecht (Institute of Earth Sciences Utrecht), Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands. MNCN: Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences), Department of Paleobiology, Madrid, Spain. NCBN: Netherlands Centre for Biodiversity Naturalis (National Museum of Natural History Naturalis), Leiden, the Netherlands. Correlaton to MN zones and local zones are after Daams *et al*. (1999a). Numerical age estimates are after Daams *et al*. (1999a) and van Dam *et al*. (2006). Comparative localities: Vieux-Collonges a mixed MN 4-5 assemblage, Sansan is the reference locality for MN 6 and La Grive M for MN 7/8 (de Bruijn *et al*., 1992). Numerical age estimates for Sansan are ~13.6 Ma (Daams *et al*. 1999b) and ~14.1 Ma (Kälin & Kempf, 2009). Costeur *et al*. (2007) list rough age estimates for the fissure fillings of Vieux-Collonges (~16.0 Ma) and La Grive M (~12.3 Ma). B: The sum of the P^3 and P_3 present of every ochotonid lineage in the assemblages, the number of deciduous teeth (incl. recognizable fragments) present within the assemblages. C: The number of P_3 of *Lagopsis* and *Prolagus* specimens included in the DCA, PCA and CVA. Asterisks: * ARM7 is from outside the Aragonian type area, in the vicinity of the Armantes section (Krijgsman *et al*., 1994); ** comparative material stored at IVAU, excl. *L. verus* from La Grive M, which presence is inferred from (de Bruijn *et al*., 1992); *** scant material, the taxon is identified by other teeth than the P^3 or P_3.

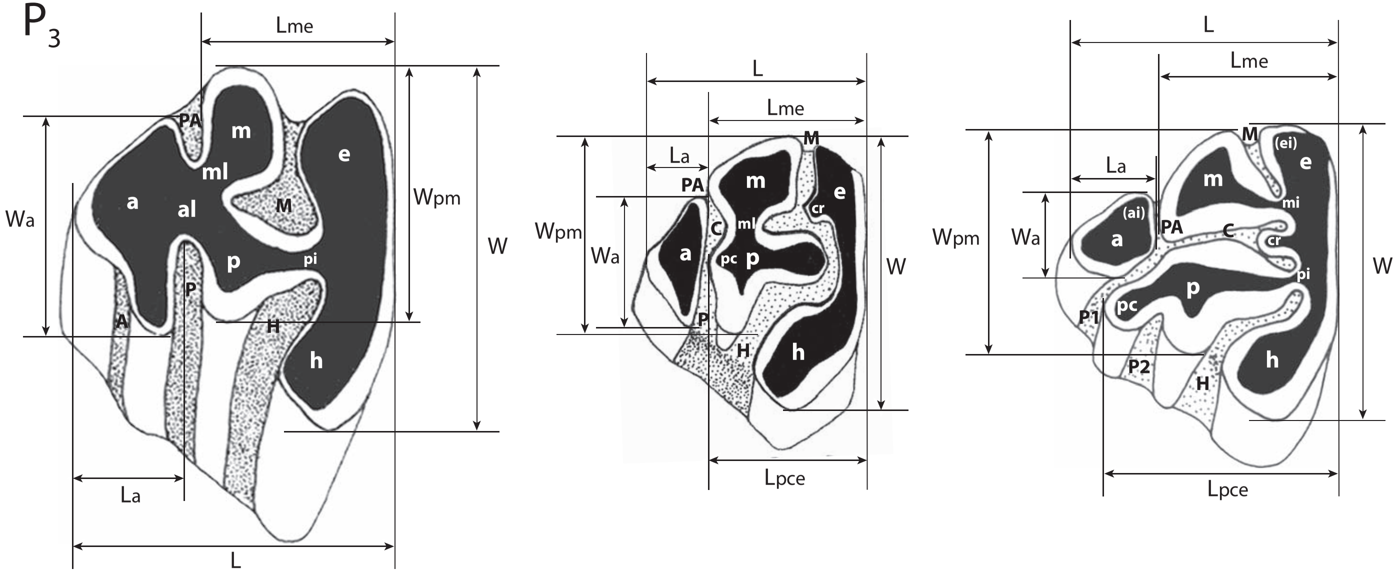
Table 4.2: Listing of P_3 measurement variables used in the PCA and CVA. The measurements used are shown in fig. 4.2. Asterisks denote variables present in *Prolagus* only, which are included in the genus specific CVA analysis.

Absolute parameters	Relative parameters	Species & lineages	N (P_3)
L	L/W	*L. verus*	95
W	Lme/W	*L. penai*	257
Lme	Lpce/W*		
Lpce*	Wpm/W	*P. tobieni*	61
Wpm	La/W	*P.* ex. interc.	3
La	Wa/W	*P. lopezmartinezae*	18
Wa	W/L		
	Lme/L	*P. major*	15
	Lpce/L*	*P. vargasensis*	15
	Wpm/L		
	La/L	*P. oeningensis*	141
	Wa/L	*P.* cf. *oeningensis*	9
	La/Wa		
	Wa/La		

4.3.2 Multivariate analysis

The multivariate analyses performed are Principal Component Analysis (PCA) and a particular kind of Canonical Correspondance Analysis (CCA) with which a Canonical Variate Analysis (CVA) has been obtained using the procedure described by Ter Braak & Šmilauer (2002). All analyses are performed using CANOCO for Windows 4.5 (Ter Braak & Šmilauer, 2002). Data handling and associated summary of statistical results for the analyses are specified in Appendix 4.1.

The data set comprised multivariate measurement data of P_3 size and shape, both absolute values of measured sizes and relative variables representing ratios of a measured size and length or width (Table 4.2). Not all preserved specimens in fossil assemblages were intact. Specimens



no centroflexid
no protoconulid

shallow/absent centroflexid (C)
small/absent protoconulid (pc)

deep merged centroflexid (C)
developed protoconulid (pc)

Lagopsis verus
Lagopsis penai }

Prolagus tobieni
Prolagus lopezmartinezae }

Prolagus oeningensis
Prolagus cf. *oeningensis* }
Prolagus major
Prolagus vargasensis }

Figure 4.2: Measurements and nomenclature on the P_3 of *Lagopsis* and *Prolagus*. Measurements are after Hordijk & van der Meulen (Chapter 2). L: length; W: width; Lme: length metaconid-entoconid; Lpce: length protoconulid-entoconid; Wpm: width protoconid-metaconid; La: length anteroconid; Wa: width anteroconid. Nomenclature follows Hordijk & van der Meulen (Chapter 2) which is based on the descriptive terminology of López-Martínez (1974, 1989). Tooth cusps and connections (white letters). a: anteroconid; p: protoconid; m: metaconid; h: hypoconid; e: entoconid; pc: protoconulid; cr: crochet; al: anterolophid; ml: metalophid; mi: metaisthmid; pi: protoisthmid. The anteroisthmid (ai) and entoisthmid (ei) are not shown and represent the metaconid-anteroconid and the lingual entoconid-metaconid connection, respectively. *Lagopsis* lacks a protoconulid and thus Lpce. Inflexions (black letters). A: anteroflexid; PA: paraflexid; P: protoflexid (1 & 2); M: mesoflexid; H: hypoflexid; C: centroflexid. *Prolagus* is represented by two main morphological groups on the basis of the development of the centroflexid and the protoconulid. Tooth drawings are modified after López-Martínez (1988, 1989).

with any missing data within the chosen set of variables have been excluded from the analysis. Our criteria thus considerably reduced the original set of P_3 specimens suitable for analysis (Table 4.1B-C). Tooth size measures, nomenclature and measurement data are summarized in Chapters 2 & 3.

PCA is an ordination technique assuming a linearly increasing or decreasing distribution of all measured values for all specimens, when plotted along a gradient, or rather an optimized ordering of samples that maximizes the before-mentioned linearity. It is aimed at finding the specimen order or hypothetical gradient that accounts for as much of the variance in the data matrix as possible, thus maximizing the spread of individual specimens along the component axes. A PCA was performed on the complete data set that includes all suitable specimens of both *Lagopsis* and *Prolagus* (table 4.1C); this provides a general overview in morphological variability of included specimens and species. Secondly, a PCA was performed on two chronospecies in *Lagopsis*, *L. penai* and *L. verus*. The latter analysis aims to examine the separation between the two chronospecies based on measured characteristics, without the *a priori* division in to one of the two chronospecies, as opposed to the CVA where the axes are designed to maximize the separation between the centroids of specimens assigned to the same species. The taxon-free PCA approach can thus provide multivariate taxonomic arguments complementary to the morphological qualitative and univariate criteria used by Hordijk & van der Meulen (Chapter 2).

As an alternative for PCA, a DCA (Detrended Correspondance Analysis) was considered for the analysis of the whole data set. The sizes and shape variables of P_3 can potentially vary independently, as a consequence of which a more unimodal distribution of character values along ordination axes might have been more appropriate, as assumed in DCA, rather than a linear distribution of measured characters as in PCA. A rough estimate to see if the data is strongly associated with a unimodal response model is to perform a DCA and look how many standard deviations the greatest gradient length is. If it is larger than four, the data show a strong unimodal response (Ter Braak & Šmilauer, 2002). Since this was not the case with our data (see Appendix 4.1), we decided to perform PCAs.

CVA is a form of discriminant analysis that examines the structure between multiple groups of multivariate data. The multivariate data are arranged by maximizing the separation between the centroids of specified groups. In this case, specimens assigned to the same species were classified as a group with two exceptions. Although not a true species, *P.* cf. *oeningensis* specimens constituted their own group, separate from *P. oeningensis* s.s. in order to investigate the effect of their slight diffence in the stage of evolution and their separation from *P. vargasensis*. Similarly, *P.* ex. interc. *lopezmartinezae-tobieni* does not represent a true species, but is analysed separately from the two species within the lineage in order to elucidate its similarity or dissimilarity to either of them.

In our procedure, a CVA is obtained by performing a CCA of which the derived eigenvalues (λ) are used to approximate the eigenvalues (θ) more commonly employed in CVA (Eq. 1).

$$\theta = \frac{\lambda}{(1-\lambda)} \qquad \text{Equation 1}$$

A CVA is obtained for each individual genus in order to maximize the separation between the congeneric lineages and species without interference from distantly related taxa. In the case of *Lagopsis*, which is represented here by two species only, the CVA will result in a single axis which is the linear combination of character values that best separates the species' centroids. In the analysis of the seven predefined *Prolagus* species groups, three variables that are related to a specific feature in the P_3 of this genus and which is absent in *Lagopsis*, were added to the analysis (Table 4.1C, Table 4.2).

In order to further visualize the distribution of CVA scores of specimens in terms of the (dis) similarity between species and between lineages through time, modeled probability density functions (PDF) of CVA scores are plotted. These indicate the frequency of specimens of the different species along the axes, and actually depict the distribution of morphologies within one species, where 'morphologies' refer to the CVA axis score, or rather the linear combination of characters that best separates the different species. For each defined species group, a continuous cumulative distribution function (CDF) related to a shifted log-logistic probability distribution (Eq. 2) was fitted to the discrete cumulative frequency distribution of axis scores. The best fit was defined as the function that minimizes the sum of squared vertical and horizontal errors between the observed cumulative distribution of CVA scores and the associated predicted CDF values of the cumulative distribution function. For this, the CVA scores of each species group were first rescaled to values between 0 and 1 by subtracting the minimum value and subsequent dividing by the difference between the maximum and minimum values. The corresponding PDF (Eq. 3) is the derivative of this modeled CDF. Tails of the PDF curves are cut at the CVA values found at the frequencies 2.5 and 97.5 % in the CDF. The resulting PDF of the shifted log-logistic distributions thus incorporate 95% (i.e. 47.5% on both sides of the median) of the data distribution of each species group and represent the modeled frequency distribution of the morphological variability of the species.

CDF:

$$F(c;\ \mu,\sigma,\xi) = \frac{1}{1+\left(1+\frac{\xi(c-\mu)}{\sigma}\right)^{-\frac{1}{\xi}}}$$

Equation 2

PDF:

$$f(c;\ \mu,\sigma,\xi) = \frac{\left(1+\xi\frac{c-\mu}{\sigma}\right)^{-\frac{1}{\xi+1}}}{\sigma\left(1+\left(1+\xi\frac{c-\mu}{\sigma}\right)^{-\frac{1}{\xi}}\right)^{2}}$$

Equation 3

Where c = CVA score, and where $\mu \in (-\infty,\infty)$, $\tau \in (0,\infty)$, and $\xi \in (-\infty,\infty)$ are respectively the location, scale and shape parameter.

4.4 Results

4.4.1 Separation of the *Lagopsis* and *Prolagus* species groups

The ordination of the PCA successfully separates the two genera and the species groups (Fig. 4.3A) although overlap between species remains. The separation on the first PCA axis is mostly determined by the variables related to the width of the anteroconid (Fig. 4.3B). The character contribution on the second axis is determined by the absolute variables, with the exception of Wa, which has a limited contribution to this axis. The first PCA axis succesfully separates 1) the *Lagopsis* group and the *Prolagus* group with a deep centroflexid (but not their individual species), and 2) the species in the *Prolagus* group lacking a deep centroflexid, i.e. *P. lopezmartinezae* and *P. tobieni*. The distribution of *P. tobieni* specimens is very similar to that of the two chronospecies of *Lagopsis*, which is in agreement with the general similarity in shape between these species based on visual arguments. The second PCA axis shows separation between 1) the *Prolagus*

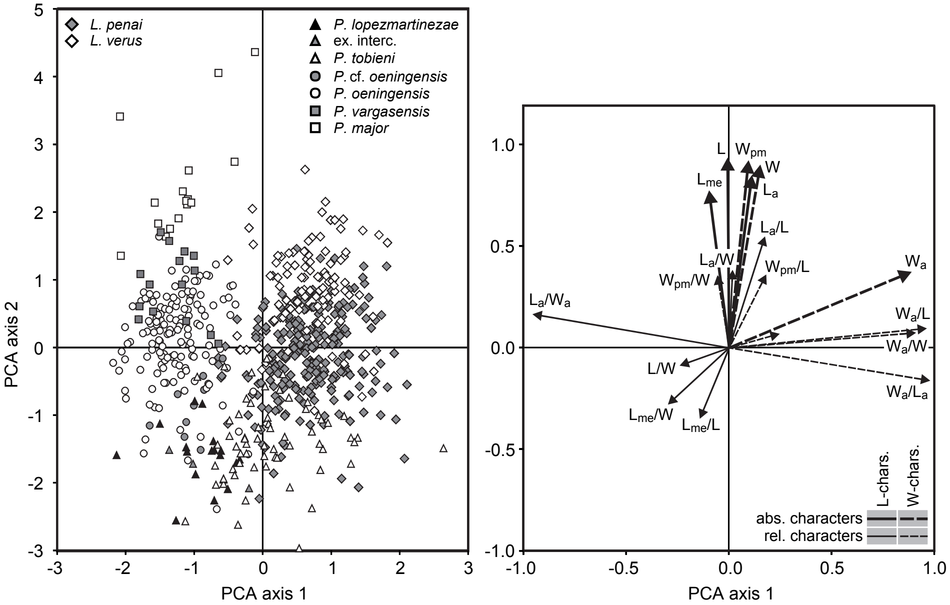


Figure 4.3: PCA ordination results of P_3 characters in *Lagopsis* and *Prolagus*. Included specimens and parameters are summarized in tables 1C and 2. A: Specimen scores; B: Character loadings.

lineages, 2) the species in the *Prolagus* group with a deep centroflexid, and 3) the *Lagopsis* species. *P. lopezmartinezae* and *P. tobieni*, on the other hand, show no separation along PCA2. With the exception of *P. major*, none of the species is completely isolated and all show overlap in their distributions along the two axes. *P. vargasensis* overlaps with part of the *P. oeningensis* data. *P.* cf. *oeningensis* is distinctly separate from *P. major* and *P. vargasensis*, but overlaps with *P. oeningensis* while being separate from the bulk of the distribution of this species.

4.4.2 Separation of the *Lagopsis* species

The first and second axis of the PCA of *L. penai* and *L. verus* explain 47.7% and 30.3% of the morphometric variance respectively (Fig. 4.4A; Appendix 1B). The intraspecific variation, which is represented by the first PCA axis, is thus larger than their interspecific difference expressed on the second axis. There is reasonable separation between the two species, despite evident overlap. The two axes show a remarkably consistent division between the character loadings (Fig. 4.4B): The variables primarily related to either length (negative scores) or width (positive scores) are separated on the first axis (with one exception, Wpm/W) and thus associated mostly with intraspecific variation. The second axis shows a distinct separation between the absolute sizes (positive scores), that of width (W) and protoconid-metaconid width (Wpm) in particular, and the relative sizes or shape parameters (negative scores), which distinguish the two chronospecies. The CVA analysis of the *Lagopsis* data shows again considerable intraspecific variation, but additionally a relatively gradual, but temporally fairly well constrained, shift towards more positive CVA1 values (Fig. 4.5). This shift is due to the increase in size (see lower panel of this figure), and coincides with the succession of *L. penai* to *L. verus*, as indicated by the symbols. The character loadings indicate that the absolute sizes, with the exception of metaconid-entoconid length, and the length and

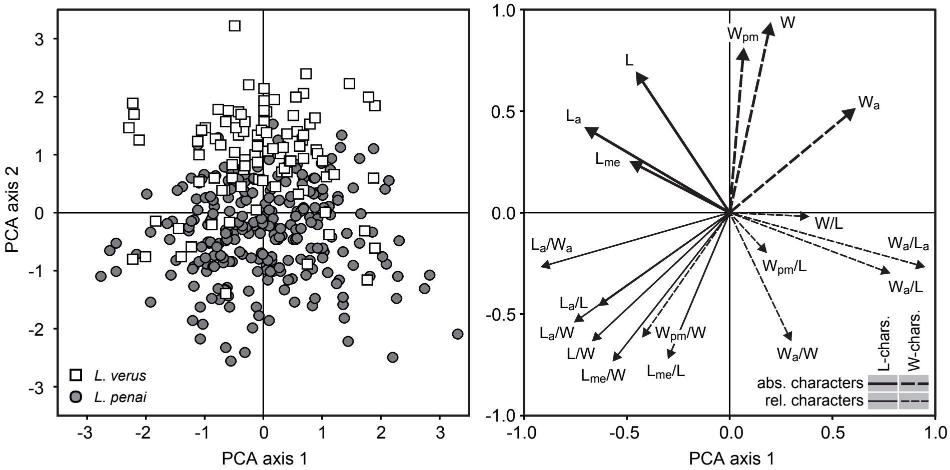


Figure 4.4: PCA ordination results of P_3 characters in *Lagopsis*. A: Specimen scores; B: Character loadings.

metaconid-entoconid length relative to width (L/W and Lme/W) in the opposite direction, are the most important discriminating factors in this analysis.

The distribution of specimen scores through time is in good agreement with the morphological qualitative and univariate criteria used by Hordijk & van der Meulen (Chapter 2), which have not been included in the set of multivariate measurement data analysed here. The evolutionary change in size and shape between *L. penai* and *L. verus* is somewhat limited in comparison to the intraspecific variation, but the modeled frequency distribution of the variability of these species (fig. 4.5) is sufficiently distinct for characterizing assemblages of *L. penai* and *L. verus*. The CVA axis scores of *L. verus* in the levels younger than ~13.2 Ma are more similar to those of *L. penai* than those of most *L. verus* specimens older than this level. This deviation coincides with a notable shift in relative abundance from a general high relative abundance of *L. verus* in the small-mammal communities of the region prior to ~13.2 Ma, to a distinctly lower abundance after this level (Chapters 2 & 5). *P. tobieni* is relatively well represented after 13 Ma and shows a rough similarity in its shape parameters (fig. 4.3).

4.4.3 Separation of the *Prolagus* species

Figure 4.6 shows the results of the CVA of *Prolagus* species revealing distinct patterns in the size and shape of its species and lineages. The first axis strongly separates the two morphological groups within the genus (fig. 4.2), i.e. the lineage lacking a developed protoconulid and deep centroflexid, *P. lopezmartinezae* – *P. tobieni*, and the two lineages with a well developed protoconulid and deep centroflexid, *P.* cf. *oeningensis* – *P. oeningensis* and *P. vargasensis* – *P. major*. Secondly, the centroids of the species and lineages of the latter group are separated along this axis as well, although there is overlap in the distribution of specimens. Protoconulid length (Lpce) and length (L) have the largest contribution on the first CVA axis. Most other variables contribute on this axis in the same direction with the exception of the characters related to anteroconid width (Wa). The CVA2 axis shows a comparable distribution of centroids in comparison to the CVA1 axis and is therefore omitted here. The third CVA axis provides a good separation of *P. lopezmartinezae* and *P. tobieni*, while all the other species are closely centered at zero. The character loadings on this axis are

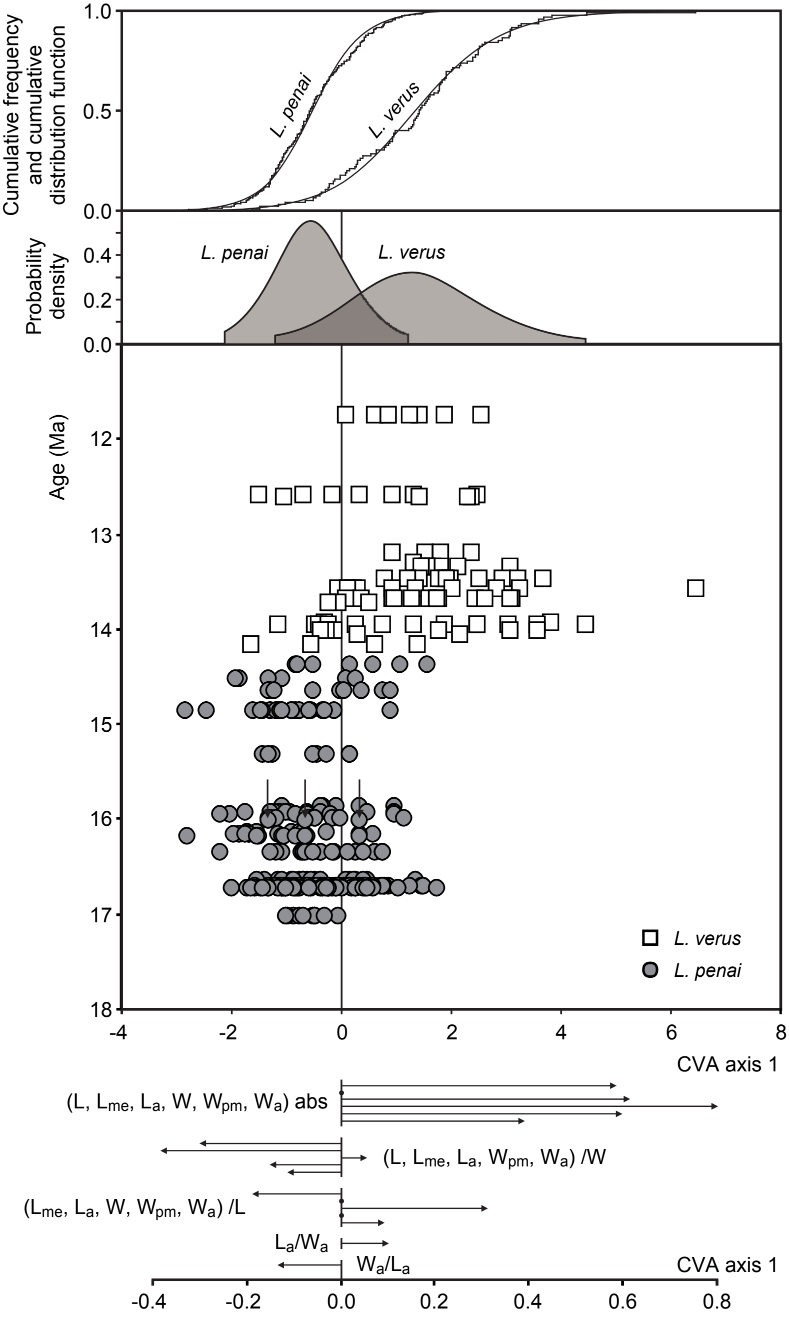


Figure 4.5: CVA ordination results of P_3 characters in *Lagopsis*. The top panel shows the discrete cumulative frequency distributions, the fitted cumulative distribution functions and the modelled probability density functions of the CVA scores of *L. penai* and *L. verus*. The area represents 95% of the data distribution. The middle panel shows the specimen scores through time. The lower panel clarifies the character loadings on the CVA axis.

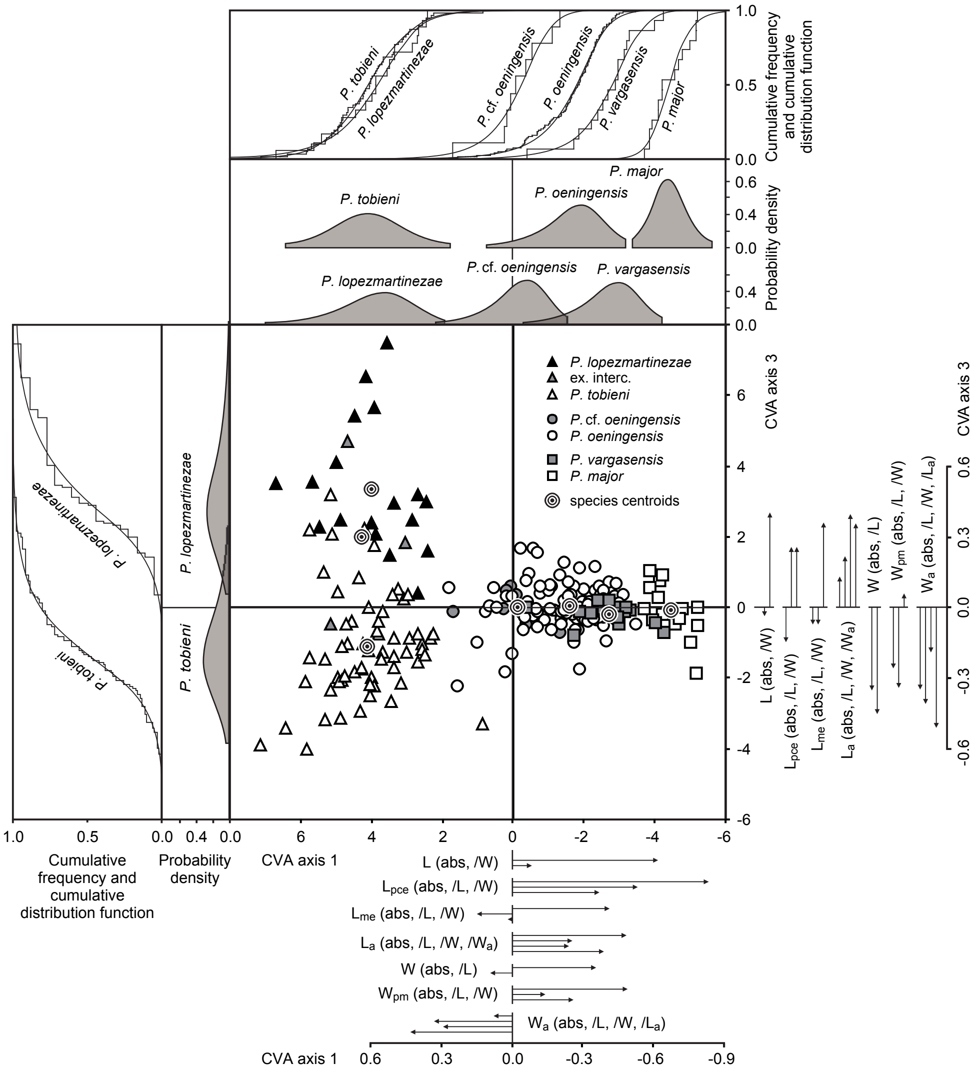


Figure 4.6: CVA ordination results of P_3 characters in *Prolagus*. The centre panel shows the specimen scores along the first and third CVA axes. The panels on the top and the left-hand side depict the discrete cumulative frequency distributions and the fitted cumulative distribution functions along with the modelled probability density functions that show the distribution of morphologies, in this case CVA axis scores, within the *a priori* defined species groups. The area of the modelled probability distributions incorporates 95% of the data distribution of the respective species groups. Here, the species with a well developed protoconulid are omitted on the CVA3 axis for clarity. In the top panel, the specified species groups are schematically separated in two time slices to indicate evolutionary time. The character loadings on the CVA axes are shown on the bottom and right-hand side. See Appendix 4.1 for additional information.

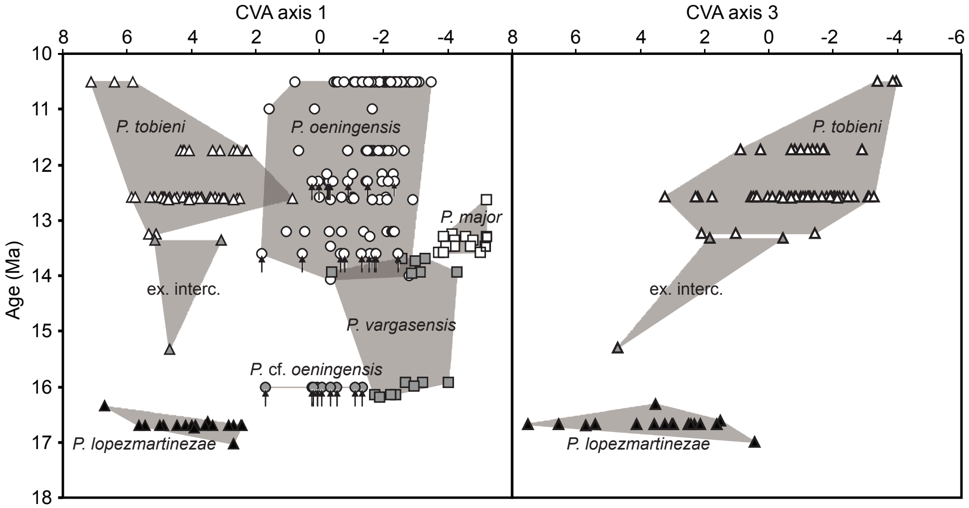


Figure 4.7: Temporal distribution of CVA scores. The grey envelopes (i.e. the smallest convex hull encompassing all conspecific specimens) and symbols denote different species. The left panel shows specimen of the *Prolagus* P_3 specimens along the first CVA axis versus geological age. Arrows denote *P. oeningensis* specimens from France (Vieux-Collonges, Sansan, La Grive M). The right panel shows P_3-specimen scores of *P. lopezmartinezae* and *P. tobieni* specimens along the third CVA axis versus geological age. The species with a well developed protoconulid have been omitted for clarity.

generally separated between length variables opposite to width variables. The largest contributions are related to relative parameters of length, width and anteroconid length and width (Wa/La, W/L, L/W, La/W).

The modeled frequency distributions of the morphological variability of the *Prolagus* species along the first and third CVA axes illustrate pronounced differences between the species and lineages. The analyzed assemblages of the morphologically very similar species *P.* cf. *oeningensis* (Vieux-Collonges, France) and *P. vargasensis* (Spain) show good separation along the first CVA axis. Similarly, *P. oeningensis* and *P. major*, which may co-occur within the same assemblages, show distinctly different frequency distributions along this axis. On the other hand, *P. vargasensis* shows marked overlap with the distributions of both *P. oeningensis* and *P. major*. However, *P. vargasensis* has not been found associated with either *P. oeningensis* or *P. major*, the latter of which is considered its descendent chronospecies.

Figure 4.7 shows that the *Prolagus* CVA scores plotted against time reveal evolutionary change of its species groups. On the first CVA axis, two patterns stand out: 1) the first known *P. vargasensis* in Spain are distinctly different from contemporary *P.* cf. *oeningensis* in France, and 2) the evolution of *P. vargasensis* to *P. major* coincides with the continuous presence of *P. oeningensis* in the Daroca-Villafeliche succession. The evolutionary change from *P. lopezmartinezae* to *P. tobieni* through time is evident on the third CVA axis (figure 4.7). This trend confirms the long time interval of unresolved species assignment, which is primarily due to lack of fossil material in the phase of transition between the species. From the specimen scores of *Prolagus* ex. interc. *lopezmartinezae-tobieni*, however, it can be hypothesized that the specimen from Vargas 5 (zone Dc) will most likely be assignable to *P. lopezmartinezae* in case new fossil material would become available. The two specimens from Valalto 1A (zone G1) show overlap with both chronospecies, which prohibits a clear hypothesis for species assignment, but at first glance they seem to fit the distribution of *P. tobieni* best.

4.5 Discussion

The multivariate analyses have provided independent confirmation of the species identifications and evolutionary relationships as interpreted in Chapters 2 and 3. Our interpretation of the early and middle Miocene phylogeny of *Prolagus* and *Lagopsis* is shown in Fig. 4.8 and further outlined in Appendix 4.2. This summary was based on published data in which we have integrated our results and views. Before we focus on the speciations, evolutionary trends and signs of competitive interaction, we will give special attention to the phylogenetic affinity of the species in the *Prolagus* group having a well developed protoconulid and a P_3 with a deep centroflexid. *P.* cf. *oeningensis, P. oeningensis, P. vargasensis,* and *P. major* constitute two anagenetic lineages (Chapter 3). The origin of that of the latter two species will be discussed below.

4.5.1 Origin of the *P. vargasensis-P. major* lineage

P. vargasensis is the oldest known representative of the *Prolagus* group under discussion in Spain. This species is only known from Spain and thus considered endemic, but the fossil record lacks

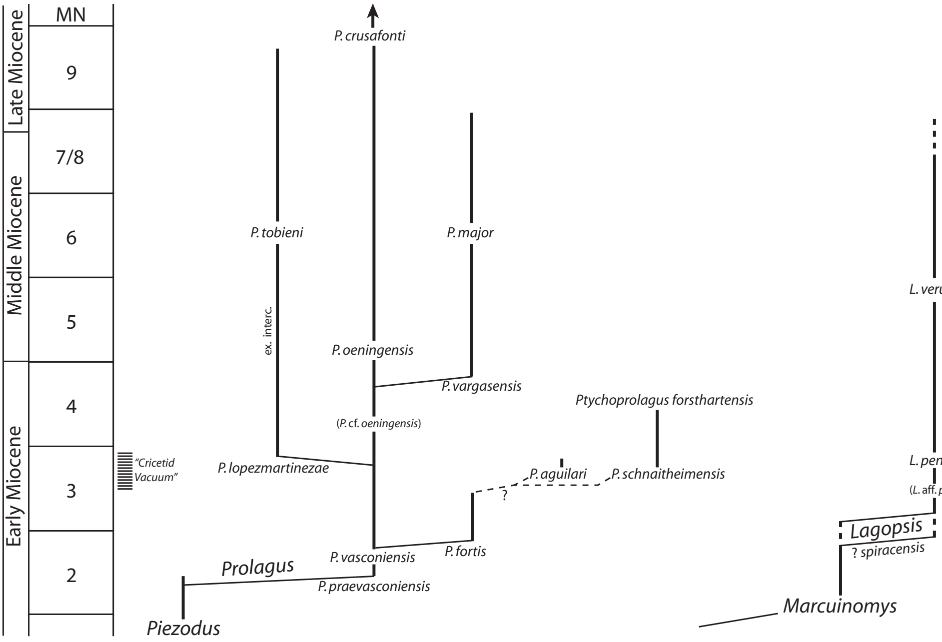


Figure 4.8: Schematic overview of inferred phylogenetic affinities and stratigraphic ranges of *Prolagus* and *Lagopsis* in Western Europe during the early to early late Miocene. The length of MN zones is standardized for clarity and convenience and does not reflect a linear time axis. For details, see Appendix 4.2.

a potential ancestor within the local succession of its first known occurrence. A few options for its phylogenetic origin can be considered. The similar sized species *P. aguilari* López-Martínez, 1997, which is solely known from Southern France, has a transitional character mosaic in the P_3-structure that is more primitive in comparison to *P. vargasensis* in which the deep centroflexid is fully formed. This difference in stage of evolution is in agreement with the age of ~17.5 Ma for *P. aguilari* (Aguilar *et al.*, 2003) and ~16.15 Ma for the oldest known *P. vargasensis* (Table 4.1A). However, *P. aguilari* appears to be an unlikely ancestor of *P. vargasensis* on the basis of its derived P_3 characters such as the large size of the anteroconid and the relatively reduced entoconid that are both absent in *P. vargasensis*.

In analogy to the suggestion made by Alvarez Sierra *et al.* (1991) and López-Martínez (1997) for a possible origin of *P. major*, the relatively large sized *P. fortis* of Ramblian age from the Ebro Basin, which, except for its large size, is morphologically identical to *P. vasconiensis* Viret, 1930, is another candidate that may have given rise to *P. vargasensis* in the Early Aragonian. The hypothetical evolution of *P. fortis* to *P. vargasensis* would imply that the same evolutionary transition would have taken place in this lineage simultaneously and parallel to that of *P. vasconiensis* to *P. oeningensis*. Although this hypothesis cannot be ruled out completely, there is currently no supporting fossil evidence despite the intensive and fairly complete sampling of the Neogene mammal record of the Iberian Peninsula (Alba *et al.*, 2001). Transitional forms between *P. vasconiensis* to *P. oeningensis*, on the other hand, have been found north of Spain in western Central Europe (Appendix 4.2, Chapter 3). In our opinion, *P. fortis* is therefore not a likely ancestor of *P. vargasensis*.

We prefer instead the scenario in which *P. vargasensis* descends from *P.* cf. *oeningensis* (i.e. *P. oeningensis* s.l.; see Appendix 4.2). The tooth morphology of early *P. vargasensis* is very similar to that of contemporary *P.* cf. *oeningensis* in western Central Europe. The most conspicuous distinctive feature is their size difference, which is evident in Figs 4.3, 4.6 & 4.7. It is therefore well conceivable that *P. vargasensis* stems from a population of *P.* cf. *oeningensis* that had migrated south from western Central Europe to Spain during the late early Aragonian. The inferred occurrence of this migration seems reasonable, since the first appearance of *P. vargasensis* coincides with the late early Aragonian immigration of other lineages in the basin, e.g. the cricetids *Democricetodon franconicus* Fahlbusch 1966 and *Eumyarion* Thaler 1966 (van der Meulen *et al.*, in review; Chapter 3).

López-Martínez (1989) reported the presence of a few specimens of *P.* cf. *oeningensis* from the locality of Sant Mamet in the Vallès-Penedès Basin (Catalunya, Spain; Fig. 4.1). This basin can be considered a key dispersal corridor due to its location at the bottleneck between France and Spain, and its near-coast position. Differences in the arrival time of various late Early Miocene rodents in more coastal regions in comparison to the Calatayud-Montalbán Basin have been established (van der Meulen *et al.*, in review), highlighting the importance of these regions for dispersals. Sant Mamet closely underlies marine deposits that have been related to the Langhian transgression phase and its age has been magnetostratigraphically dated to the lower part of C5Br, which corresponds to an earliest Langhian (earliest middle Aragonian) age (Garcès Crespo, 1995). This locality currently represents the southernmost known occurrence of *P.* cf. *oeningensis* at that time. Although it slightly postdates the first appearance of *P. vargasensis*, it unequivocally shows that *P.* cf. *oeningensis* has been able to invade Spain south of the Pyrenees prior to the marine incursions that submerged part of the Vallès-Penedès Basin during the Langhian. Its absence from the Daroca-Villafeliche area suggests that this species most likely has not reached the Calatayud-Montalbán Basin.

4.5.2 Speciation

The classic discrete geographic modes of speciation are often regarded unsatisfactory in modern evolutionary biology and are rather considered as endmembers in a continuum of speciation mechanisms (Gavrilets, 2003; Butlin *et al.*, 2008; Fitzpatrick *et al.*, 2008; Mallet, 2008). The original focus on geography has shifted toward the mechanisms for evolving reproductive isolation (Doebeli & Dieckmann, 2003; Rundle & Nosil, 2005). From a paleontological perspective, the fossil record may, and with sufficient resolution can, provide crucial insight in the paleobiogeographic history of species evolution in geological time for which the geographic modes of speciation apply fairly well.

Based on the available data, we hypothesize that the first appearance of *P. vargasensis* is the result of parapatric speciation. This mode of speciation has been described as speciation occurring when sister species evolve while adapting to adjacent but spatially segregated habitats (or ecotones), across a contact zone (Bush, 1994, 2001; Losos & Glor, 2003) and has been associated with the invasion of new habitats or colonization of neighbouring habitats. Both modelling and field studies suggest this type of speciation is plausible and potentially common (Schilthuizen, 2000; Gavrilets, 2003). In terms of mechanisms for evolving reproductive isolation, the pattern fits within the concept of ecological speciation (Rundle & Nosil, 2005).

The presence of an ecological boundary or gradient between northeastern Spain (Ebro region and Vallès-Penedès Basin) and the Calatayud-Montalbán Basin is suspected on the basis of the presence of the Aragonian Range in the Iberian Chain, which represents an altitudinal gradient in the region that is also likely to have been present to some degree in the Miocene (Casas-Sainz & Cortés-Gracia, 2002; Casas-Sainz & de Vicente, 2009). The environment of the more central Iberian Peninsula tends to deviate to some degree from the northern areas. Faunas from the Ebro and Vallès-Penedès basins in preceding and following time intervals respectively are known for their relatively higher resemblance to French faunas and different local environment in comparison to other regions in Spain (Alvarez Sierra *et al.*, 1991; Casanovas-Vilar, 2007; Casanovas-Vilar & Agustí, 2007)[1].

In our view, other modes of speciation are less likely. Vicariant speciation, which assumes the presence of a physical barrier separating large populations in different regions (Bush, 1994, 2001), is considered improbable, but cannot be ruled out entirely. *P.* cf. *oeningensis* has so far not been detected in the region prior to the evolution of *P. vargasensis*. Peripatric speciation, which is associated with a founder event (Mayr, 1982; Bush, 2001), is considered unlikely on the basis of a rodent immigration phase marking a brief period of enhanced ecological connectivity with northern regions (van der Meulen *et al.*, 2005, in review). The lack of a potential ancestor in our record preceding and at the first known occurrence of *P. vargasensis* argues against sympatric speciation.

The pattern associated with the speciation of *P. vargasensis* also appears to fit the fossil record of the genus *Democricetodon* FAHLBUSCH, 1964 that is preserved in the same succession, but occurs at an older level. Van der Meulen *et al.* (2003, in review) have suggested that *D. hispanicus* FREUDENTHAL, 1967, which marks the first record of this genus in the Villafeliche-Daroca area in the top of zone A at the end of the "cricetid vacuum" (San Roque 4A), is probably a Spanish

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[1] The present-day distribution of *Lepus* LINNAEUS, 1758 in Europe shows a species range boundary between *Lepus europaeus* PALLAS, 1778 in north-eastern Spain and central Europe and *Lepus granatensis* ROSENHAUER, 1856 on the Iberian Peninsula along the Ebro River (Alves *et al.*, 2008), which marks the southernmost extent of a central European species that may have been comparable to the distribution of *P.* cf. *oeningensis* in the latest Early Miocene.

descendant of *D. franconicus*, or, alternatively, that these species share a very close common ancestor. This recurring pattern of southern range expansion with the associated first appearance of an apparently regionally derived species suggests that parapatric speciation, as it is interpreted here, can be expected in the region, although it is not necessarily common.

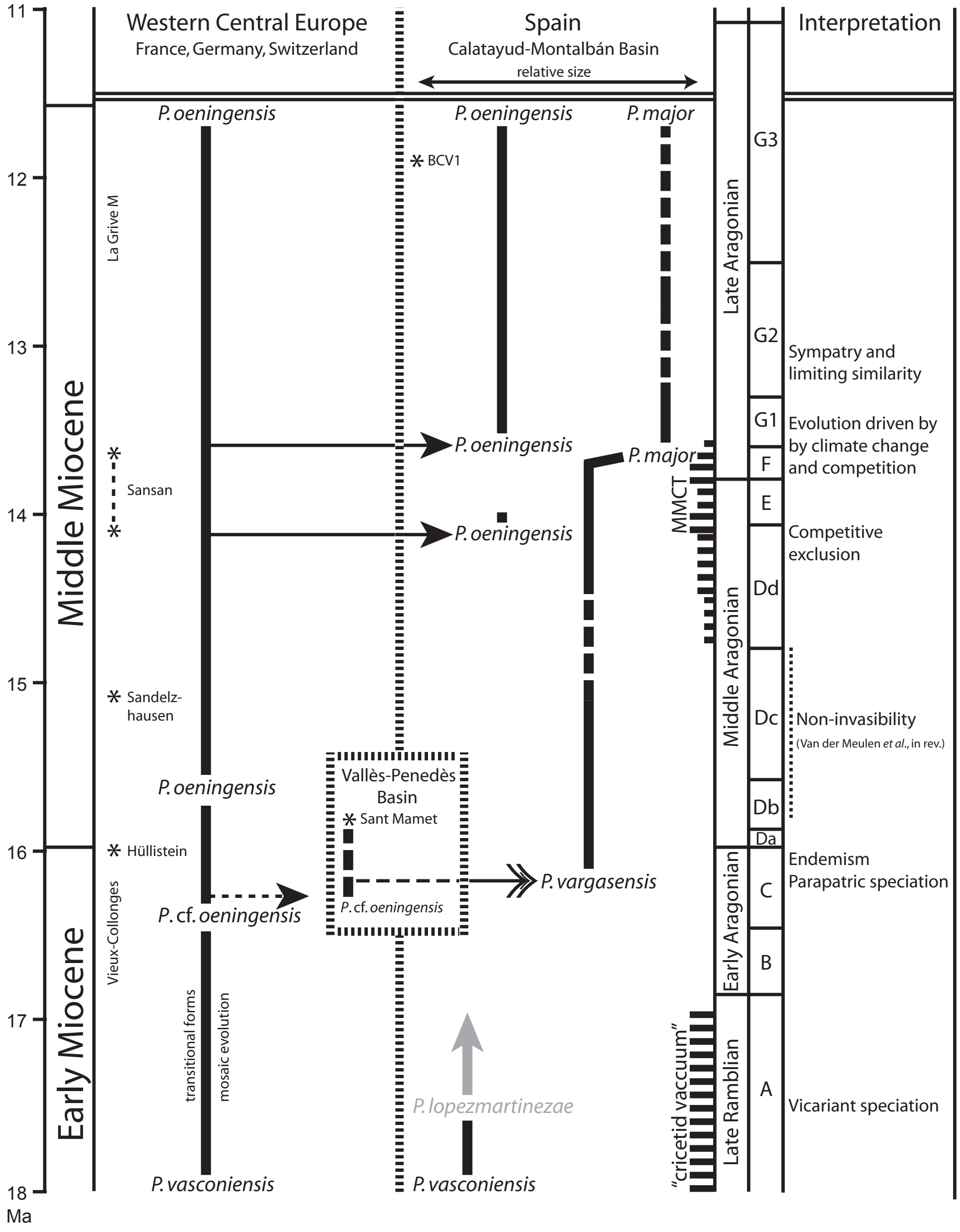
The speciation of *P. lopezmartinezae* follows a clearly different geographic and temporal pattern in comparison to that of *P. vargasensis*, which we associate with an allopatric mode, i.e. dichopatric or vicariant speciation, in accordance with previous views (López-Martínez, 1997). The local fossil records in Spain and in western Central Europe reflect anagenetic trends in which *Prolagus vasconiensis* gives rise to *P. lopezmartinezae* in Spain and to *P. oeningensis* s.l. (*P*. cf. *oeningensis*) in western Central Europe, respectively. The surmised barrier is most likely ecological in nature, since the developing Pyrenees or other potential obstacles have not proved to be problematic for the dispersal of the ancestral species *P. vasconiensis*. Likewise, the sympatric *L. penai* lineage appears unaffected by this barrier as well. The well-established presence of the ancestor in the local fossil records of both regions rules out peripatric speciation. Similarly, the anagenetic trends in which the ancestral species is completely replaced by its descendants, indicates that non-allopatric modes of speciation can also be considered highly improbable.

4.5.3 Evolution and competitive interaction

As is clear from Fig. 4.8, evolutionary change in the four lineages studied is limited to anagenesis in the middle and early late Miocene. An important part of the chronospecies distinction and definition relies on shifts in the relative frequency of particular morphological details within the variation of assemblages (Chapters 2 & 3). The definition of chronospecies in these types of lineages is therefore to some degree a matter of taste. However, Figs. 4.4-4.7 reveal distinct shifts in the ordination of size and shape parameters within lineages representing evolutionary change. Our approach provides an additional and potentially indispensable means for testing and defining chronospecies by taking into account the variance in size and shape (Duijnstee *et al.*, 2010).

Despite the seemingly arbitrary nature of chronospecies definition, the transition from *L. penai* to *L. verus* on the basis of morphological observation data (Chapter 2) and on that of measured size and shape parameters (Figs 4.4 & 4.5) are in excellent agreement and can be well constrained to a narrow time interval around ~14.2 Ma. The frequency distribution of *Lagopsis* P_3 lengths figured by de Bruijn & van Meurs (1967: 123) shows a very similar pattern in comparison to the modeled probability density distribution shown in fig. 4.5 and is in excellent agreement with our interpretation of the timing of the transition of chronospecies, in contrast to that of the latter authors and López-Martínez (1989) who placed it at a younger level. The moderate but yet distinct shift in the range of morphological variance during a relatively short period of time suggests some form of selection pressure may have been imposed temporarily. The occurrence of a bottleneck in population-size appears less likely, since the relative abundance of the lineage in Spain remained unaffected, although in the northern part of its range it appears to have declined at this time (Kälin & Kempf, 2009).

The evolution of *P. vargasensis* to *P. major* is an example of relatively rapid and pronounced anagenesis. The general size and shape of the P_3 of *P. vargasensis* has remained markedly unchanged for almost ~2.5 Myrs, but the transition to *P. major* is characterized by rapid size increase taking place at the end of Zone F around ~13.6 Ma (Table 4.1; Figs. 4.6 & 4.7). The evolutionary transition slightly postdates the main cooling step of the Middle Miocene Climate Transition (MMCT), a phase of global climate cooling that has been associated with expansion of the East Antarctic ice-sheet (Flower & Kennett, 1994). The main shift observed in marine stable oxygen



isotopes (Mi3b), which occurred at the end of the MMCT, has been dated to between 13.95 and 13.76 Ma in the Mediterranean (Abels *et al.*, 2005; Mourik, 2010). This climatic cooling step is the culmination of the cooling phase that is thought to have caused the faunal turnover and marks the transition between the middle and late Aragonian (boundary Zones E-F) (Krijgsman *et al.*, 1994, Daams *et al.*, 1999a; van der Meulen *et al.*, 2005). Therefore, the evolution of *P. vargasensis* to *P. major* appears to be an example of punctuated anagenesis, presumably triggered by environmental

← *Figure 4.9:* Schematic overview of local stratigraphic ranges, migrations and inferred phylogenetic relations of early and middle Miocene *Prolagus* lineages bearing a well developed protoconulid and a deep centroflexid in the P_3 in Western Central Europe and Spain. The Spanish endemic sister lineage, indicated in grey, and continues into the Vallesian (not shown). Columns represent geological time: the ATNTS2004 on the left (Lourens *et al.*, 2005), the Spanish continental stages on the right (Daams *et al.*, 1999a, 1999b; Larrasoaña *et al.*, 2006). Black horizontal arrows denote migrations and the double headed arrow indicates a combined migration-speciation event. Dashed range intervals indicate (temporary) absence from the Calatayud-Montalbán Basin and presumed presence in other parts of Spain. Comparative localities are indicated on the left hand side in region columns, where asterisks denote numerically dated localities. The estimated ages of Vieux-Collonges and La Grive M are given with Table 4.1. Hüllistein (Switzerland) is dated to around 16 Ma (Kälin & Kempf, 2009). Sant Mamet (Vallès-Penedès Basin) is dated to the lower part of C5Br, at approximately ~15.8 Ma (Garcés Crespo, 1995). The age of Sandelzhausen is estimated at around ~15.1 Ma based on the presence of two species of *Megacricetodon* Fahlbusch 1964 (Abdul Aziz *et al.*, 2008; Wessels & Reumer, 2009) in combination with a normal polarity chron (Abdul Aziz *et al.*, 2008), which can be correlated to the magnetostratigraphically calibrated rodent biostratigraphy in Switzerland and chron C5Bn.2n, respectively (Kälin, 1997; Kempf *et al.*, 1997; Kälin & Kempf, 2009). The age of Sansan (Table 4.1) is based on two correlation possibilities, Daams *et al.* (1999b) and Kälin & Kempf (2009) respectively, both of which are in agreement with paleomagnetic data (Sen & Ginsburg, 2000). Barranc de Can Vila 1 (BCV1), in which *P. oeningensis* is present (Casanovas-Vilar *et al.*, 2008), has been dated at 11.9 Ma (Moyà-Solà *et al.*, 2009). The last known occurrence of *P. major* in Torremormojón 6A (late G3) has been dated in the Duero Basin to the early late Miocene (C5r.2r) at about ~11.2 Ma (López-Martínez *et al.*, 1986; Krijgsman *et al.* 1996), while its last known occurrence in the Calatayud-Montalbán Basin is earlier in G3 (Table 4.1; Chapter 3).

and faunal change. In our opinion, however, the event should also be considered in the context of competitive interaction, in particular in relation to the immigration of *P. oeningensis*, as we will now illustrate.

The *P. oeningensis* and *P. vargasensis* – *P. major* lineages are morphologically similar and closely related, as we have argued above. It is of interest to reconstruct the circumstances under which they became part of the same community with due consideration of the limitations and potential of the fossil record (Kidwell & Flessa, 1996; Hadly, 1999; Alves *et al.*, 2008; Tomašových & Kidwell, 2009; Terry, 2010). We assume for convenience's sake that species co-occurrence in a single locality is indicative of their sympatry. Figure 4.9 shows the sequence of events and the biostratigraphical distribution of the taxa concerned. With the exception of its earliest known middle Aragonian occurrence in the Vallès-Penedès Basin, the *P. oeningensis* lineage has so far not been found in Spain prior to the levels of Las Umbrías 10 and 12 (zone Dd-E boundary interval, MN5; Table 4.1A), despite the commonness of this lineage north of the peninsula. In these two assemblages (14.09 and 14.03 Ma, respectively) *P. vargasensis* is lacking. In the two assemblages in between LUM10 and 12 (Chapter 5; van der Meulen *et al.*, in review) and during the subsequent half million years spanning most of Zones E and F, *P. oeningensis* is absent while *P. vargasensis* has returned. The alternating presences of *P. oeningensis* and *P. vargasensis* can be explained by spatial shifts of their respective habitats caused by climatic fluctuations during the MMCT, which is also reflected in the rodent fossil record (van der Meulen *et al.*, 2005). We assume from the close similarity between the two cognate species that their niches, and the habitats in which they are found, are also similar to a certain degree. Unless the unlikely situation of fully synchronous shifts of habitats and species (Bulleri, 2008) would hold true, we may assume that the distributions of *P.*

oeningensis and *P. vargasensis* have temporarily overlapped. In view of the dense sampling in this time interval, the two lineages belonged to the same paleocommunity (Chapter 5), but avoided each other at the locality scale by competitive exclusion. Similarly, competitive exclusion may also have delayed the successful immigration of *P. oeningensis* earlier in zone Dd due to a competitive disadvantage of this species relative to *P. vargasensis* during the beginning of the MMCT.

The short phase of habitat shifts during which the two species were part of the same paleocommunity suggests the possibility of the occurrence of ecological character displacement for reducing competition[2]. In this case ecological character displacement includes the temporal domain which can be interchanged with that of geography. However, our data show no clear temporal pattern indicating that any of the species is either larger or smaller in the temporary presence or absence of the other in the paleocommunity. In addition, *P. oeningensis* from our French comparative reference assemblages (i.e. Sansan and La Grive M) show no apparent difference with those in Spain that would indicate character displacement or release on a geographical scale (Fig. 4.7; Chapter 3).

Shortly after the distinct size increase at the end of zone F that marks the evolution of *P. vargasensis* to *P. major*, *P. oeningensis* returns at the beginning of zone G1 (Table 4.1, Fig. 4.9). From this time on *P. oeningensis* is consistently present and regularly co-occurs with *P. major* in the same assemblages during the late Aragonian. The increased size difference between the two lineages relative to *P. vargasensis* suggests that the evolution of *P. major* provided niche space for *P. oeningensis*, which had been unavailable previously in the presence of *P. vargasensis*, and resulted in the possible co-occurrence of these lineages within assemblages. Several causes may have evoked or influenced the evolution of *P. major*. One option is competitive pressure by *P. oeningensis*. As is shown by the brief presence of *P. oeningensis* in the late middle Aragonian, this potential colonizer from the north appears to be relatively nearby and may have applied competitive pressure along their mutual range boundary. This pressure is likely to have increased over time during the MMCT, which at some point may have tipped the competitive balance between the two, ultimately inducing an evolutionary response in *P. vargasensis*. However, the absence of any obvious evolution in *P. vargasensis* with the first appearance of *P. oeningensis* in the area and the stable size of *P. vargasensis* over a period spanning almost 2.5 Myrs suggests that competition is not likely to be the only factor inducing evolutionary change.

Alternatively, climate change and the associated changes in the local environment may have forced the evolutionary response resulting in the evolution of *P. major*, while facilitating the opportunity for *P. oeningensis* to settle in the Daroca-Villafeliche area. The MMCT is considered to have shifted and expanded the number of available habitats as well as having initiated the rodent community turnover (van der Meulen *et al.*, 2005). The evolution of *P. major* however postdates the main change of the MMCT by more than 100 kyr.

Our preferred option involves both biotic interaction and climate change. The invasibility of the region is known to have increased during the MMCT after a considerable isolation phase (van

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[2] Brown & Wilson (1956: 63) summarized ecological character displacement as follows: “Character displacement is the situation in which, when two species of animals overlap geographically, the difference between them are accentuated in the zone of sympatry and weakened or lost entirely in the parts of their ranges outside this zone.” Although it is not explicitly analyzed, Smith *et al.* (1990) have reported several features suggesting this mechanism in two extant ochotonids from Asia, *Ochotona alpina* (Pallas, 1773) and *Ochotona hyperborea* (Pallas, 1811). *O. hyperborea* is smaller than the former in the zone of sympatry and its range of utilized habitats is more restricted in the presence of *O. alpina*. In the absence of the latter, *O. hyperborea* is larger than the average of the species.

der Meulen *et al.*, 2005, in review; Chapter 5). Climate induced changes in the local environment probably provided more advantageous habitat conditions for *P. oeningensis*, thus increasing its competitiveness along its range boundary adjacent to *P. vargasensis* over time, and increasing the opportunity to reinvade and colonize the Calatayud-Montalbán Basin as the climate transition progressed. Likewise, climate change and associated local community change altering the regional competitive balance over an extended period of time (several 100 kyr) may have reduced the competitiveness of *P. vargasensis*, while providing the opportunity for evolutionary change with a wider available range of habitats. In the end, the progressive transition in the environment is possibly more favorable for the widely distributed generalist already more familiar with the new conditions (*P. oeningensis*) than for the likely more specialist endemic (*P. vargasensis*) that may be more inclined to adapt or perish. Therefore, the combination of increasing competitive pressure from nearby *P. oeningensis* and climate-induced ecological changes may have contributed to the evolution of *P. major*.

Regardless of the cause for the evolution of *P. major*, the presence-absence patterns of the two closely related morphologically similar lineages (Table 4.1; Fig. 4.9) suggests substantial biotic interaction. On the basis of our multivariate analysis we hypothesize that following the phase of competitive exclusion the concept of limiting similarity (MacArthur & Levins, 1967) provides a reasonable explanation for the observed evolutionary pattern. The sympatric lineages in *Prolagus* show a clear separation in Figs. 4.6 & 4.7, while the non-sympatric contemporary species *P. vargasensis* and *P. oeningensis* show a distinctly higher degree of similarity in their frequency distribution of morphological variability, which we associate with stronger competition. The long term settlement of *P. oeningensis* appears to have remained impossible until the transition toward the larger sized *P. major* emptied just enough previously occupied niche space for *P. oeningensis* to successfully colonize the area. The potentially sympatric species *L. verus*, *P. major*, *P. oeningensis* and *P. tobieni* show sufficiently different sizes and tooth morphologies, and subsequently different niche preferences, to allow for their coexistence.

In addition to *Prolagus*, *Democricetodon* shows a comparable pattern in a slightly older time interval in the same succession (van der Meulen *et al.*, 2003). The inferred parapatric speciation of *D. hispanicus* from *D. franconicus* and the subsequent invasion of the latter species at a level following marked size evolution of *D. hispanicus* via *D. decipiens* FREUDENTHAL & DAAMS, 1988 to *D. moralesi* VAN DER MEULEN, PELÁEZ-CAMPOMANES & DAAMS, 2003, strongly resembles the pattern of two subsequent invasions intermitted by evolutionary divergence observed in *Prolagus*, indicating that the occurrence of this mechanism may not be uncommon in Spain.

The study of limiting similarity has for a major part been theoretical and has been considered somewhat controversial at times, but competition remains a plausible mechanism in evolutionary ecology (Abrams, 1983; Schluter, 2000; Meszéna *et al.*, 2006; Calsbeek & Cox, 2010). The present study adds an example of the influence of competitive interaction on evolution and community composition in fossil assemblage sequences in the terrestrial realm. The patterns observed in *Prolagus* and *Democricetodon* strongly resemble the McPhail model of a double invasion and character displacement in sticklebacks at the scale of laboratory experiments and of several kyrs of a natural pond system discussed by Schluter (2000) and Pritchard & Schluter (2001). Despite differences in specific details, the similarity between their model and the patterns in the stratigraphic record in the Calatayud-Montalbán Basin is striking. In our opinion, this strengthens our inference of competition and limiting similarity in the evolutionary patterns of the *P. oeningensis* and the *P. vargasensis*-*P. major* lineages.

4.6 Conclusions

The rich small-mammal fossil record from the Daroca-Villafeliche succession provides valuable new information on the phylogeny and evolutionary history of high-crowned pikas in Western Europe. Various multivariate analyses on a set of absolute and relative measures from the P_3 occusal surface of *Lagopsis* and *Prolagus* have been applied to capture both temporal and non-temporal morphological variation in ochotonid lineages. This type of analysis proofs to be a useful tool for discerning morphological trends within and between chronospecies and for establishing the disparity between lineages while keeping track of intraspecific variation.

The schematic phylogenetic trees of *Lagopsis* and *Prolagus* in Western Europe during the early and middle Miocene, shown in fig. 4.8, result from the integration of our new data from the Calatayud-Montalbán Basin with the phylogenetic and paleobiogeographic data available in the literature. Our reconstruction of the *Prolagus* phylogeny largely agrees with that of López-Martínez (1997) and provides the current state of the art. It differs mainly in the interpretation of the *P. major* lineage. Several cladogenetic speciation phases in *Prolagus* have taken place during the early Miocene (MN2-4), while during the middle Miocene evolutionary change is limited to the anagenetic evolution of chronospecies, the turnover rate of which is low and result in species longevities of several million years.

The Iberian Peninsula represents an important region for speciation in *Prolagus* during the early Miocene. By combining the biostratigraphy, multivariate morphological data, the paleobiogeography and the phylogeny, distinctive patterns in the evolutionary history of *Prolagus* in this region have been demonstrated. We hypothesize that the Iberian *P. lopezmartinezae* lineage and western Central European *P. oeningensis* lineage evolved from *P. vasconiensis* in allopatry and that the *P. vargasensis* lineage likely arose by parapatric speciation from *P. oeningensis* s.l. (*P.* cf. *oeningensis*) during the latest early Aragonian (latest Burdigalian), after which the latter two lineages continued in allopatry during the early middle Aragonian (early Langhian).

Secondly, we hypothesize that competitive exclusion between *P. vargasensis* and *P. oeningensis* may have delayed the permanent settlement of the latter species in the Calatayud-Montalbán Basin and that the punctuated anagenetic evolution of *P. vargasensis* to *P. major* may have been evoked by the combined influence of climate change, the associated small-mammal community turnover and competitive interaction with *P. oeningensis* associated with the MMCT. Biotic interaction appears to have played a significant role in the stratigraphic presence-absence and co-existence patterns in the Daroca-Villafeliche area and in the evolution of the two morphologically similar lineages on a wider scale. Evidence indicating ecological character displacement as changes in intraspecific variability in time and space has not been found. At the species and community level on the other hand, the multivariate analysis clearly shows that the disparity in P_3 size and shape between sympatric ochotonid species is more pronounced than between contemporaneous non-coexisting ochotonid species in the region and from nearby regions. We conclude that reduction of competition by means of limiting similarity allows for the coexistence of the four pika lineages in part of the succession in the Calatayud-Montalbán Basin.

Appendix 4.1

The multivariate data-set consists of taxonomically identified P_3 specimens on which a total of 18 (*Lagopsis*) or 21 (*Prolagus*) absolute and relative parameters have been measured on each specimen (Table 4.2). The program CANOCO (Ter Braak & Šmilauer, 2002) has originally been designed for application in (plant) ecology, but has been used for ordination in a wide range of research fields. The program requires a data matrix of "samples" and "species" (primary data) to which a set of "environmental parameters" for each sample (explanatory data) can be added.

In the PCA, individual P_3 specimens are loaded as "samples" and the measured morphological parameters as "species", where the measured values are a substitute for "abundance". Species assignments are later added as labels to individual specimens.

In the CCA, from which CVA eigenvectors are derived, individual P_3 specimens are again treated as "samples" and the assigned chronospecies as "species" with an abundance of 1 for the species the specimen has been assigned to, and an abundance of 0 for all other species in the analysis. The specimen specific set of morphological parameters are loaded as "environmental parameters" in a separate matrix.

Listed in the tables below are summaries of statistics of the various analyses performed. The cumulative percentage of variance of species data gives the cumulative fraction of the total species variance that is actually explained by the axes. In the CVA, "species-environment correlation" measures the strength of the relation between the position of species and the morphological parameters for a particular axis. The cumulative percentage of variance of species-environment relation (appendix tables C1 & D1) describes the cumulative contribution of the CVA axes to the maximum amount of variance of the species data that can be explained by the morphological parameters.

Appendix tables C2 & D2 show the forward selection of morphological characters. The marginal effects column lists the morphological characters in order of the variance they explain individually, i.e. when that specific character is used as the only variable in the analysis. The conditional effect column gives the morphological characters in order of their inclusion in the model, starting with the character with the highest marginal effect, then the character is added that explains the highest amount of variance in addition to the first one that is already included, then the character that has the highest explanatory potential in addition to the previous two, etc. In a Monte Carlo test the significance was assessed of each character at the time of inclusion (Monte Carlo F-values and P-values are listed, $P<0.05$ reveals significant characters).

A: Summary statistics of PCA on *Lagopsis* and *Prolagus* P_3 characters. Ordination results are shown in Figure 4.3.

	axis 1	**axis 2**	**axis 3**	**axis 4**
Lengths of gradient in DCA (in Standard Deviations)	0.589	0.367	0.289	0.188
Eigenvalues in PCA	0.639	0.238	0.067	0.028
Cumulative % variance of species data	63.9	87.7	94.4	97.2
Sum of all eigenvalues	1.000			

B: Summary statistics of PCA on *Lagopsis* P_3 characters. Ordination results are shown in Figure 4.4.

	axis 1	**axis 2**	**axis 3**	**axis 4**
Lengths of gradient in DCA (in Standard Deviations)	0.608	0.369	0.195	0.166
Eigenvalues in PCA	0.477	0.303	0.111	0.064
Cumulative % variance of species data	47.7	78.0	89.1	95.5
Sum of all eigenvalues	1.000			

C1: Summary statistics of CVA on *Lagopsis* P_3 characters. Ordination results are shown in Figure 4.5.

	axis 1	**axis 2**
Eigenvalues in CCA [λ]	0.417	0.583
Eigenvalues in CVA [$\theta=\lambda/(1-\lambda)$]	0.715	1.398
Species-environment correlations	0.646	0.000
Cumulative % variance of species data	41.7	100.0
Cumulative % var. of species-environment relation	100.0	0.0
Sum of all eigenvalues	1.000	
Sum of all canonical eigenvalues	0.417	

C2: Forward selection of *Lagopsis* P_3 characters.

Marginal Effects			**Conditional Effects**				
	λ	**% var. in species data**		**λ**	**F**	**P**	**% var. in species data**
W	0.31	31	W	0.31	160.8	0.001	31
La	0.21	21	La/Wa	0.05	23.8	0.001	5
Wpm	0.20	20	La	0.00	1.5	0.246	0
L	0.20	20	La/W	0.00	2.0	0.161	0
Lme	0.10	10	Wpm	0.01	1.7	0.190	1
Wa	0.10	10	Wpm/W	0.00	2.5	0.116	0
La/L	0.09	9	Wa/La	0.00	0.9	0.361	0
Lme/W	0.08	8	Wa/W	0.01	2.0	0.178	1
W/L	0.07	7	L	0.00	0.5	0.499	0
L/W	0.06	6	L/W	0.03	16.6	0.001	3
Lme/L	0.02	2	Wa	0.00	1.4	0.238	0
Wpm/L	0.02	2	Wa/L	0.00	1.5	0.244	0
Wpm/W	0.02	2	Lme/W	0.00	1.0	0.376	0
Wa/La	0.01	1	Lme/L	0.01	1.1	0.260	1
La/Wa	0.01	1	W/L	0.00	0.4	0.526	0
Wa/W	0.01	1					
Wa/L	0.01	1					
La/W	0.00	0					

D1: Summary statistics of CVA on *Prolagus* P_3 characters. Ordination results for axes 1 and 3 are shown in Figure 4.6-4.7, accounting for 23.6% of the variance in the species data and 56.4% of the maximum amount of variance explained by the morphological parameters.

	axis 1	**axis 2**	**axis 3**	**axis 4**
Eigenvalues in CCA [λ]	0.891	0.690	0.525	0.240
Eigenvalues in CVA [θ=λ/(1-λ)]	8.174	2.226	1.105	0.316
Species-environment correlations	0.944	0.831	0.724	0.490
Cumulative % variance of species data	14.8	26.3	35.1	39.1
Cumulative % var. of species-environment relation	35.5	63.0	83.9	93.4
Sum of all eigenvalues	6.000			
Sum of all canonical eigenvalues	2.511			

D2: Forward selection of *Prolagus* P_3 characters.

Marginal Effects			**Conditional Effects**				
	λ	**% var. in species data**		**λ**	**F**	**P**	**% var. in species data**
Lpce	0.84	14.0	Lpce	0.84	42.27	0.001	14.0
L	0.76	12.7	Wa/La	0.38	20.79	0.001	6.3
Lpce/L	0.70	11.7	Lpce/L	0.30	17.08	0.001	5.0
Wpm	0.66	11.0	L	0.35	21.75	0.001	5.8
Wa/La	0.65	10.8	Lme/W	0.13	8.71	0.001	2.2
La	0.64	10.7	Wpm/W	0.07	4.08	0.002	1.2
Lme	0.63	10.5	Wa	0.03	1.89	0.099	0.5
La/Wa	0.58	9.7	Wa/L	0.05	3.17	0.034	0.8
W	0.55	9.2	La/L	0.01	1.11	0.369	0.2
Lpce/W	0.55	9.2	La	0.04	2.31	0.048	0.7
Wa/L	0.52	8.7	La/Wa	0.01	0.59	0.710	0.2
Wa/W	0.44	7.3	Wpm	0.00	0.46	0.827	0.0
La/W	0.39	6.5	Lme	0.08	5.41	0.002	1.3
La/L	0.37	6.2	Lpce/W	0.04	2.33	0.061	0.7
Wpm/W	0.35	5.8	L/W	0.04	2.78	0.027	0.7
Wpm/L	0.25	4.2	W/L	0.03	1.82	0.121	0.5
W/L	0.25	4.2	Lme/L	0.04	2.69	0.040	0.7
L/W	0.24	4.0	Wa/W	0.02	1.95	0.091	0.3
Lme/L	0.20	3.3	Wpm/L	0.02	0.74	0.522	0.3
Lme/W	0.20	3.3	La/W	0.00	0.38	0.829	0.0

Appendix 4.2

Supplementary information associated with the schematic overview of inferred phylogenetic affinities and stratigraphic ranges of *Prolagus* Pomel, 1853 and *Lagopsis* Schlosser, 1884 shown in figure 4.8.

EARLY AND MIDDLE MIOCENE PHYLOGENY AND PALEOGEOGRAPHY OF *PROLAGUS* AND *LAGOPSIS*: A STATE OF THE ART

Lagopsis and *Prolagus* independently evolved rootless hypsodont teeth from different ancestors in Europe during the early Miocene (López-Martínez, 1986, 1989; Chapter 2). The evolution of *Prolagus* from *Piezodus* Viret, 1929 in MN2 has been well established (López-Martínez, 1974; Tobien, 1975; López-Martínez & Thaler, 1975; Ringeade, 1979). The ancestry of *Lagopsis* has been related to the early Miocene genus *Marcuinomys* Lavocat, 1951 (Tobien, 1963; Bucher, 1982; López-Martínez, 1984, 1986, 1989). Its emergence most likely took place either in the younger part of MN 2 or in the earliest MN3, depending on the interpretation of the generic characteristics and diagnosis used (Chapter 2).

Prolagus underwent a series of speciations throughout its temporal range, while *Lagopsis* is characterized by the absence of cladogenetic speciation events. The abundance distribution of *Lagopsis* relative to *Prolagus* shows a distinct latitudinal gradient in Western Europe (Mein, 1984; López-Martínez *et al.*, 1987; López-Martínez, 2001). *Lagopsis* is distinctly more abundant on the Iberian Peninsula, while *Prolagus* is more prolific in more northern parts of Western Europe in the interval of stratigraphic range overlap, which has been associated with a latitudinal humidity gradient.

Prolagus

Prolagus praevasconiensis Ringeade, 1979 represents the transitional species between *Piezodus* and *Prolagus*, showing the loss of roots in the cheek teeth and the progressive development of the third lobe in the M_2 from the small archaic hypoconulid, which serves as a functional replacement of the M_3 that is lost in *Piezodus*. Its descendent species, *Prolagus vasconiensis* Viret, 1930 (*in* Roman & Viret, 1930), appears to have evolved in the region of France (Ringeade, 1979), but is ultimately found throughout Western Europe from Germany to Spain. *P. vasconiensis* has been shown to be the last common ancestor of all subsequent lineages of *Prolagus* that evolved during the early Miocene (López-Martínez, 1997).

The emergence of *Prolagus fortis* López-Martínez & Sesé, 1991 (*in* Alvarez Sierra *et al.*, 1991) marks the first known speciation event of *Prolagus*. *P. fortis* has only been found at various localities in the Ebro Basin, Northern Spain, in local zones Y2 (MN2) and Z (MN3) (Alvarez Sierra *et al.*, 1991; = *P. vasconiensis in* Murelaga *et al.*, 2004). The two lineages in this time interval mainly differ in their size. *P. fortis* has originally been described as a large subspecies of *P. vasconiensis*, but was raised to the species level by López-Martínez (2001).

The late Ramblian (MN3) is characterized by a small radiation phase in *Prolagus* during which three endemic *Prolagus* lineages evolved in separate regions within Western Europe. López-Martínez (1997) noted the coincidence of this radiation with the so-called "cricetid vacuum" and associated this conjunction with a global rather than a local evolutionary forcing mechanism. The "cricetid vacuum" is characterized by the absence of cricetids, with the exception of the conspicuous derived genus *Melissiodon* Schaub, 1920, and is recognized throughout Western Europe, which in Spain generally corresponds to local biozone A (Daams & Freudenthal, 1990). The interval marks the transition phase between the last archaic resident cricetid *Eucricetodon* Thaler, 1966 and the modern cricetid invader *Democricetodon* Fahlbusch, 1964. At this moment it is not possible to establish whether the radiation is in any way linked to the absence of cricetids and whether one or both of these trends are related to changes in global climate. Paleogeographic reconstructions indicate that large scale basin rearrangements during the early Miocene may have been a potentially contributing factor as well in the timing and distribution of mammal migrations from the east into Western Europe and in influencing the bioprovinciality in this region and time interval (Meulenkamp & Sissingh, 2003; Popov *et al.*, 2004).

Prolagus aguilari López-Martínez, 1997 is one of the three lineages that emerged during the "cricetid vacuum" and has so far only been found in few localities in Southern France (López-Martínez, 1997; Aguilar *et al.*, 2003). Its closest ancestor has not been identified, but only two candidates are presently known from the fossil record, *P. vasconiensis* and *P. fortis*. *P. fortis* and *P. aguilari* have similar sized teeth, indicating that the former species is possibly more closely related to *P. aguilari* than *P. vasconiensis* is.

Prolagus schnaitheimensis Tobien, 1975, an endemic species from the region of Germany, is a second lineage that evolved in the "cricetid vacuum" (Tobien 1975; Ziegler & Fahlbusch, 1986). Its size appears to be somewhat similar to that of *P. fortis* and *P. aguilari*, suggesting a possibly closer affinity with these species than with contemporary *P. vasconiensis*, although only measurements of upper teeth have been published that show overlap with those of *P. vasconiensis* also (Ziegler & Fahlbusch, 1986). *P. schnaitheimensis* has been found associated with *P. vasconiensis*, indicating that these species have diverged enough to allow coexistence, but this is inconclusive with respect to their phylogenetic affinity.

P. schnaitheimensis shares some synapomorphies in the P_3 morphology with *P. aguilari*, such as the shape and relative size of the anteroconid, while these species also have diverging apomorphies, like in the development of the centroflexid (López-Martínez, 1997). The morphological resemblance suggests that these two lineages are likely to be closely related (López-Martínez, 1997). The relative stratigraphic position of their ranges in terms of succession and/or overlap remains unclear, but the type localities of these species have a similar age. Their closest common ancestor may possibly have been derived from *P. fortis*, which appears to agree with the primitive nature of *P. schnaitheimensis* noted by Tobien (1975). However, the evidence for the exact phylogenetic origin of *P. schnaitheimensis* and *P. aguilari* is still wanting and other plausible scenarios that include *P. vasconiensis* remain possible.

López-Martínez (1997) has shown by the example of *P. aguilari* from Beaulieu (France) that the most notable morphological change in the late early Miocene is the mosaic evolution in the P_3 morphology in various lineages. The deep centroflexid in the P_3 is formed from the primitive morphology of *P. vasconiensis* and *P. fortis* by the merger of the initial centroflexid with the internal part of the mesoflexid (López-Martínez, 1997; Chapter 3). *P. schnaitheimensis* has not evolved the deep centroflexid, but does show the variation in the combination of derived and primitive characters that is associated with mosaic evolution.

Ptychoprolagus forsthartensis Tobien, 1975, known from Germany and the Czech Republic, evolved from *Prolagus schnaitheimensis* in MN4 (Tobien, 1975; Ziegler & Fahlbusch, 1986; Fejfar & Kvaček, 1993). The phylogenetic affinity between these species has been well established, but due to the currently low resolution in this interval, the timing of the evolution of *Pt. forsthartensis* remains to be determined more precisely. This lineage has not been reported from younger levels.

Prolagus lopezmartinezae n. sp. Hordijk & Van der Meulen, Chapter 2 from Spain is a third endemic lineage to evolve during the late Ramblian. Its evolution from Spanish populations of *P. vasconiensis* in zone A has been well documented by López-Martínez (1984), although referred to as *Prolagus* aff. *tobieni* López-Martínez, 1977, and is confirmed by recent data (Chapter 2).

Prolagus tobieni evolved from *P. lopezmartinezae* during the middle Miocene (Chapter 3). The timing of its evolution is however unclear, because of its rarity in the Daroca-Villafeliche area in the interval spanning MN5 and part of MN6, which hampers establishing a more precise age for the transition between these chronospecies. *P. tobieni* is known from the Calatayud-Montalbán record from at least zone G2 upto zone I (Pedregueras 2A; Chapter 5). The interval following local biozone I remains to be analysed further for its presence. However, it is expected that its last known occurrence is most likely close to the level of its extinction, since this species is not reported in representative and well studied assemblages from a slightly younger interval in the late Miocene, such as that from Can Ponsic (López-Martínez & Thaler, 1975; López-Martínez, 1988).

Prolagus oeningensis (König, 1825) *sensu lato* (i.e. *P.* cf. *oeningensis*) evolves from *P. vasconiensis* in western Central Europe (Huin, 1979; Bulot, 1988, *et al.* 2009; Ziegler & Fahlbusch, 1986; Bolliger, 1992, 1997; Kälin, 1993, 1997; López-Martínez, 1989, 1997; Sabol *et al.*, 2007; Prieto *et al.*, 2009; Chapter 3). This transition is characterized by the formation of a deep centroflexid in the P_3. Both *P. oeningensis* and *P. aguilari* show this trend, although not simultaneously, but it is fully developed only in the former lineage.

P. oeningensis sensu stricto. evolved from *P. oeningensis s.l.* in MN5 in western Central Europe (Ziegler & Fahlbusch, 1986; Bolliger, 1997; Kälin, 1997; López-Martínez, 1997; Angelone, 2009), but appears to have remained absent on the Iberian Peninsula during most of MN5 (Chapter 3). Data from northern Spain and from coastal regions of the Iberian Peninsula in this interval is however lacking.

Prolagus crusafonti López, 1975 (*in* López-Martínez & Thaler, 1975) most likely evolved from *P. oeningensis* in the late Miocene in Western Europe (López-Martínez & Thaler, 1975; López-Martínez, 1988; Angelone, 2009; Chapter 3). López-Martínez (1988) indicated the strong affinity with *P. oeningensis*, but argues that the exact history of the evolution of *P. crusafonti* is unresolved, since neither populations containing an association of the two forms nor a single transitional form have been found. *P. oeningensis* may have evolved to *P. crusafonti* in a small (peripheral) region of its geographic range, after which *P. crusafonti* displaced *P. oeningensis* over its entire range, or *P. oeningensis* may have evolved to *P. crusafonti* over all (or most) of its range. Their species diagnoses, however, do not allow their distinction in case they are sympatric (Chapter 3). In order to clarify the issue raised by López-Martínez, well dated successions covering this species transition in different regions are required. The lineage of *Prolagus vasconensis* to *P. crusafonti* is generally considered as the main anagenetic lineage ("lignée principal" of López-Martínez, 1997), from which the remaining lineages branch off.

The *P. crusafonti* lineage is the only lineage of *Prolagus* known to have survived MN9 after which it rediversified (López-Martínez & Thaler, 1975; López-Martínez, 1989, 2001; Angelone, 2007). Angelone (2007) mentions the remote possibility that a hypothetical late Miocene *P. oeningensis*-like species from South-Eastern Europe whose phylogenetic affinity is unknown may have colonized the eastern (pen)-insular bioprovince of Italy during the late Miocene, but this inference has not been substantiated.

Prolagus vargasensis n. sp., Chapter 3 first appears in the fossil record of the Calatayud-Montalbán Basin in MN4 (local biozone Cb). This species lacks local predecessors and is thus considered an immigrant species in the area, while it is currently only known from Spain (Chapter 3). This lineage most likely stems from *P. oeningensis* s.l. (see section 4.5.1, this chapter).

The large endemic species *Prolagus major* LÓPEZ-MARTÍNEZ, 1977 has been shown to have most likely evolved from *P. vargasensis* at the end of local biozone F in MN6 in Spain (Chapter 3). Two alternative hypotheses for the phylogenetic origin of *P. major* have been proposed earlier. López-Martínez (1977, 1989) postulated that *P. major* has possibly been derived from *P. oeningensis* during the middle Miocene, presumably in zone E (late MN5). Alvarez Sierra *et al.* (1991) and López-Martínez (1997) have suggested that *P. major* possibly arose from *P. fortis* somewhere between MN3 (zone Z) and MN6 (zone F). At that time, the first hypothesis was supported by limited fossil evidence (one P_3) that was stratigraphically close to *P. major*. This specimen has been reexamined and reassigned to *P. vargasensis* (Chapter 3), partly invalidating the first hypothesis. The close affinity between the lineage leading to *P. major* and the *P. oeningensis* lineage is however supported in our view. The second hypothesis is hampered by a considerable gap in the stratigraphic record of the species involved, i.e. between *P. fortis* and *P. vargasensis*, lacking any fossil evidence for a direct phylogenetic link. This alternative remains theoretically possible, but is considered unlikely (see section 4.5.1, this chapter).

Lagopsis

The species *spiracensis* BAUDELOT & CROUZEL, 1974 is considered to be the transitional species between the genera *Marcuinomys* and *Lagopsis* in MN2, but there is no general agreement on its generic assignment (Chapter 2). Unlike Baudelot & Crouzel (1974), who prefer its inclusion in *Lagopsis*, López-Martínez (1984) prefers to assign this species in *Marcuinomys*. For the moment, we consider the generic assignment of *spiracensis*, and consequently the timing of the emergence of *Lagopsis*, as unresolved.

Primitive *Lagopsis* has been described from Spain and France (Bucher, 1982; López-Martínez, 1984; Murelaga *et al.*, 2004). Yet, its taxonomy of chronospecies is not well constrained and is in need of revision (Chapter 2). The evolution of *Lagopsis penai* (ROYO, 1928) in the "cricetid vacuum" from this more primitive precursor on the other hand has been well established (López-Martínez, 1984, 1989) and is approximately coeval with the evolution of *P. lopezmartinezae* (Chapter 2).

The evolutionary succession from *Lagopsis penai* to *L. verus* (HENSEL, 1856) has been widely established throughout Western Europe (De Bruijn & Van Meurs, 1967; Bucher, 1982; López-Martínez, 1989; Bolliger, 1997; Kälin, 1997; Prieto *et al.*, 2009; (Chapter 2). However, the distinction between these chronospecies has been applied differently between studies and regions, resulting in different opinions on the timing of its transition (Chapter 2). The set of criteria applied in the high resolution record from the Calatayud-Montalbán Basin appears to provide a means of consistent species assignment. However, the chosen diagnostic features remain to be tested on assemblages from regions outside Spain with good numerical dating, such as the succession in Switzerland (Kempf *et al.*, 1997; Kälin & Kempf, 2009).

The late Miocene genus *Paludotona* DAWSON, 1959 (not shown in Fig. 4.8) which is endemic to (pen)-insular Italy, has been suggested as a possible descendant lineage of *Lagopsis* (López-Martínez, 1986, 1989; Dawson, 2008). On the basis of morphology and paleogeography, this appears to be plausible. However, its biochronologic range (MN11- MN13) and a radiometric age estimate stratigraphically close to the type locality (Rook *et al.*, 1996, 2000) significantly postdate the last known occurrence of *Lagopsis* (*L. verus*, MN7/8, Western Europe). We consider the supposed occurrence of this genus in Buszhor 1 (Vallesian, Moldavia) reported in the NOW-database (Fortelius, 2009; dataset downloaded Dec. 30, 2009) and discussed by Nargolwalla (2009) as unsubstantiated, which is in agreement with the faunalisting by Nesin & Nadachowski (2001). The supposed close phylogenetic affinity between *Lagopsis* and *Paludotona* has as yet to be verified. If that would be confirmed, the timing and whether or not this involved anagenetic evolution or a cladogenetic event remain to be established as well.

CHAPTER 5

Persistence and abundance of Miocene pikas (Ochotonidae, Lagomorpha, Mammalia) in small-mammal communities from north-eastern Central Spain

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5.1 Abstract

In this paper we analyse the community-structure of the small-mammal primary consumers from the rich Miocene small-mammal succession in the Calatayud-Montalbán Basin, which comprise lagomorphs (i.e. pikas) and rodents from the time interval between ~17 to 10 Ma. Previous analyses had been focused only on the rodents, while the role of other primary consumers has remained unexplored. Ochotonids are regularly and often abundantly present in the small mammal assemblages from the succession and therefore provide a significant source of information.

Community members within a community can be divided into two groups: the resident and transient community members. The patterns of community assembly, disassembly and turnover are illustrated in terms of Community Age (e.g. the mean residence time of the community members at a particular level). Our study aims to test the earlier analyses on rodent assemblages and to investigate the persistence-abundance patterns of the small-mammal primary consumers in the succession.

Our results indicate that the ochotonidae are mostly core components of the Aragonian small-mammal community structure and consolidate the pattern established in earlier studies on rodents. Phylogeny is shown to affect the persistence-abundance patterns at the family level. Moreover, our results confirm that commonness and rarity of lineages are related to temporal and possibly spatial patterns.

5.2 Introduction

The extant families Ochotonidae Thomas, 1897 (pikas) and Leporidae Fischer, 1817 (rabbits and hares) that presently represent the order Lagomorpha Brandt, 1855, are all non-hibernating herbivores and are characterized by caecophagy (Hirakawa, 2001; Chapman & Flux, 2008). This reingestion strategy increases their digestive efficiency allowing for the combination of a small body size with a tough fibrous diet. Various studies (e.g. Smith & Foggin, 1999; Lai & Smith, 2003; McIntire & Hik, 2005; Retzer, 2007; Wesche *et al.*, 2007) have shown that extant pikas may play significant roles in the faunas and ecosystems in which they thrive, because of their burrowing (excluding rock-dwelling species), grazing and hoarding activities and by providing an important food source as prey for a host of predators, such as birds of prey, mustelids, canids, felids, ursids and snakes (Smith *et al.*, 1990).

Pikas represent a significant part of the Miocene small-mammal record of Spain in which they are frequently and regularly abundantly present. This family represents the folivorous guild alongside the generally more granivorous or omnivorous rodents and the non-vegetarian insectivores in fossil small-mammal assemblages and are therefore of potential significance in paleoecological analysis. Like that of extant ochotonids, the habitat of their fossil representatives is associated with various kinds of grassland and woodland ecosystems, but also with more densely vegetated habitats (López-Martínez, 2001). Generally comparable types of predators are known to have been present in the region during the Miocene (Azanza *et al.*, 1993; Peigné *et al.*, 2006). The commonness of pikas in Miocene fossil assemblages from Spain, both in terms of relative abundance and temporal occurrence frequency, suggests that some of the lineages present may potentially represent core members of small-mammal communities as well.

Rodents constitute the main portion of these small-mammal communities, both in terms of diversity and relative abundance. Van der Meulen *et al.* (2005) and van der Meulen & Peláez-Campomanes (2007) have therefore focussed on studying the rodent community structure and dynamics from the rich, dense and well dated succession near Villafeliche in the Calatayud-Montalbán Basin (Daams *et al.*, 1999a, 1999b; van der Meulen *et al.*, in review) and have established characteristic regularities in the distribution of residence times of the rodent community members.

In this paper we will expand the community analysis to include the lagomorphs, which are in this case represented by the family of pikas, and test the results achieved on the basis of rodents. Lagomorphs and rodents are closely related orders (Murphy *et al.*, 2001; Springer *et al.*, 2004), but they show quite different phylogenetic patterns in time (López-Martinez, 2008). The role of pikas in late early to early late Miocene small-mammal communities is as yet entirely unexplored. In addition, we will further investigate the persistence-abundance patterns of this group of small-mammal primary consumers in fossil small-mammal assemblages.

The systematics, biostratigraphy and evolution of the ochotonids from the Daroca-Villafeliche succession have recently been established and updated (Chapters 2, 3 & 4). Four lineages are recognized in the late early to early late Miocene succession from the Daroca-Villafeliche record, representing seven chronospecies of two genera, the monotypic genus *Lagopsis* Schlosser, 1884 and *Prolagus* Pomel, 1853 (López-Martínez, 1989; Chapters 2 & 3).

Our main objectives are 1) to analyse the temporal range patterns, the changes in relative abundance of the pika lineages in the succession from the Calatayud-Montalbán Basin; 2) to establish the community age pattern of the small-mammal primary consumers and compare it with the results obtained by van der Meulen *et al.* (2005), i.e. the main community age pattern, the recognition of two groups characterised by their residence time and the "seniority rule"; 3) the recognition of different persistence-abundance groups within the small-mammal primary consumers and their possible interpretation.

5.3 Material and methods

5.3.1 Fossil assemblages

For reasons of consistency, we use the rodent data of van der Meulen *et al.* (2005) and van der Meulen & Peláez-Campomanes (2007) and the locality ages provided by Daams *et al.* (1999a) on the basis of the magnetostratigraphic analysis by Krijgsman *et al.* (1994, 1996) in which we include the new lagomorph data. The still ongoing revision of various hamster genera (see van der Meulen *et al.*, in review) will be used in a future analysis (Peláez-Campomanes) also incorporating the data of van Dam *et al.* (2006) and García-Paredes (2006 unpublished, *et al.*, 2009).

Our analysis is limited to the small-mammal primary consumers, which represent the bulk of the assemblages and constitute one main trophic group. The order of the insectivores, which is consistently present in fossil assemblages (van den Hoek Ostende & Furió, 2005), represents the trophic group of animal consuming small-mammals and is therefore not included in our analysis. The insectivore mean relative abundance within the assemblages analysed is in the order of a few (~3) percent, ranging roughly between absence and 15% in individual localities (van den Hoek Ostende, pers. comm. 2009).

Complementary data required for the calculation of inferred ranges of community members before and after the studied interval are obtained from López-Martínez (1984), Daams *et al.* (1987) and van Dam (2001). Ochotonid taxonomy and phylogeny follows chapters 2, 3 and 4. Although *Prolagus crusafonti* López, 1975 has not been found in the studied interval of the succession at Villafeliche, we consider *Prolagus oeningensis* (König, 1825) and *P. crusafonti* as successive chronospecies as is discussed in chapter 3. The temporal range of the latter chronospecies in the adjacent Teruel Basin (van Dam, 2001) is considered to represent a continous lineage with the former.

Relative abundance estimates of rodent species in previous studies have been based on the sum of their first two upper and lower molars, which are generally their most taxonomically distinct teeth (Daams *et al.*, 1988; van Dam & Weltje, 1999; van der Meulen *et al.*, 2005). Since species assignment of ochotonids is primarily based on premolars while their molars are poor diagnostic elements, we estimate the relative abundance of ochotonids as the double sum of their upper and lower third premolars in analogy to the four elements used for rodents. The total number of available third premolars is shown in Table 5.1. In a few cases the presence of a particular taxon is demonstrated by the presence of a dental element in the absence of the preferred premolar, in which case the occurrence is counted as 0.5 premolars.

The ochotonid assemblages from Olmo Redondo 5, Valdemoros 7A-7F, Las Planas 5L, Villafeliche 9 and Pedregueras 2C were unfortunately not available for analysis. Material from Las Umbrías 11 and Las Umbrías 14 is potentially incompletely represented. If applicable, the confirmed presence of a lineage is indicated in Table 5.1 on the basis of other material (P^2, P^4-M^2, M_2, fragments). In most of these cases the presence of *Lagopsis* has been demonstrated, while that of the various *Prolagus* lineages could not be established. Possible omissions therefore correspond to the presence of the latter genus. Overall, the general inferred range pattern appears to be largely unaffected by this incidental lack of material.

5.3.2 Determination of local range lengths

Evolutionary lineages are the taxonomic unit of interest in our analysis; chronospecies are therefore collapsed to within a single lineage. In calculating the inferred residence times of lineages, we follow the procedure and associated assumptions relating to community undersampling and taphonomy outlined by van der Meulen *et al.* (2005) and van der Meulen & Peláez-Campomanes (2007) in order to reconstruct paleocommunities from fossil assemblages.

As a first step, range lengths are calculated based on the method of Barry *et al.* (2002), in which the probability (P_i) of finding one specimen of taxon i in the localities adjacent to those containing the observed first or last occurrence is estimated (Eq. 1).

Table 5.1:

Presence of *Lagopsis* and *Prolagus* lineages

Locality	loc. code	Repository	MN zone	Local zone	Age (Ma)	*L. penai - L. verus*	*P. lopezmartinezae - ex. interc. - P. tobieni*	*P. vargasensis - P. major*	*P. oeningensis*
						P3+p3	P3+p3	P3+p3	P3+p3
Pedregueras 2C	PE2C	IVAU	9	I	10,00		ND		P
Pedregueras 2A	PE2A	NCBN & IVAU		I	10,25		1		84
Carrilanga 1	CAR1	NCBN		H	10,50		13		300
Nombrevilla 1	NOM1	IVAU		H	11,00		1		17
Nombrevilla 2	NOM2	MNCN	7/8	G3	11,50		24		445
Solera	SOL	NCBN		G3	12,75	26	85		151
Paje 2	PJE2	MNCN		G3	12,17		1		18
Paje 1	PJE1	MNCN		G3	12,30				23
Las Planas 5H	LP5H	NCBN		G3	12,52	1			15
Toril 3B	TOR3B	MNCN		G3	12,59	18	53		13
Toril 3A	TOR3A	MNCN		G3	12,60	1	49		14
Toril 2	TOR2	NCBN		G3	12,61	2	5		6
Toril 1	TOR1	NCBN		G3	12,62	18	4	2	19
Alcocer	AC2	NHM		G3	12,70				13
Villafeliche 9	VL9	NCBN		G3	12,85	ND	ND	ND	ND
Las Planas 5K	LP5K	NCBN	6	G2	13,05				3
Las Planas 5L	LP5L	NCBN		G2	13,12	ND	ND	ND	ND
Borjas	BOR	NCBN		G2	13,20	12			23
Manchones	MAN	IVAU		G2	13,25	481	8	4	338
Valalto 1B	VT1B	MNCN & NCBN		G1	13,30	11		7	3
Valalto 1A	VT1A	MNCN		G1	13,35	24	4	4	6
Las Planas 5C	LP5C	MNCN		G1	13,46	66		3	20
Las Planas 5B	LP5B	NCBN		G1	13,47	48		12	18
Valalto 2C	VT2C	NCBN		F	13,68	89	2	9	
Valalto 2B	VT2B	NCBN		F	13,70	1		0,5	
Las Umbrías 21	LUM21	MNCN		F	13,72	34		2	
Las Umbrías 22	LUM22	MNCN		F	13,73	17		11	
Las Umbrías 20	LUM20	MNCN	5	E	13,77	52		13	
Las Planas 4C	LP4C	IVAU		E	13,85	8		2	
Las Umbrías 19	LUM19	MNCN		E	13,93	44		4	
Las Planas 4B	LP4B	IVAU		E	13,94	150			
Las Planas 4A	LP4A	IVAU & NCBN		E	13,96	63		3	
Las Umbrías 14	LUM14	MNCN		E	13,97	1		0,5	
Las Umbrías 18	LUM18	MNCN		E	13,98				
Las Umbrías 17	LUM17	MNCN		E	13,99	19		3	
Las Umbrías 12	LUM12	MNCN		E	14,01	27			4
Las Umbrías 16	LUM16	MNCN		E	14,02	91		3	
Las Umbrías 11	LUM11	MNCN		E	14,04	15		0,5	
Las Umbrías 10	LUM10	MNCN		Dd	14,07	19			2
Las Umbrías 9	LUM9	MNCN		Dd	14,16	26		1	
Las Umbrías 8	LUM8	MNCN		Dd	14,18	56			
Las Umbrías 7	LUM7	MNCN		Dd	14,19	35			
Valdemoros 7G	VA7G	MNCN		Dd	14,23	10	0,5		
Valdemoros 7F	VA7F	MNCN		Dd	14,26	P	ND	?	
Valdemoros 7E	VA7E	MNCN		Dd	14,29	P	ND	ND	
Las Umbrías 5	LUM5	MNCN		Dd	14,30	16			
Las Umbrías 4	LUM4	MNCN		Dd	14,32	18			
Valdemoros 7D	VA7D	MNCN		Dd	14,33	P	ND	ND	
Las Umbrías 3	LUM3	MNCN		Dd	14,37	47		1	
Vargas 11	VR11	MNCN		Dd	14,39	12	1		
Valdemoros 6B	VA6B	MNCN		Dd	14,40	3	0,5		
Las Umbrías 2	LUM2	MNCN	5	Dd	14,41	9	0,5		
Las Umbrías 1	LUM1	MNCN		Dd	14,43	20			
Valdemoros 3F	VA3F	MNCN		Dd	14,52	34	2		
Valdemoros 3E	VA3E	NCBN & MNCN		Dd	14,55	2	0,5		
Valdemoros 6A	VA6A	MNCN		Dd	14,56	51			
Valdemoros 7C	VA7C	MNCN		Dd	14,58	P	ND	ND	
Valdemoros 7B	VA7B	MNCN		Dd	14,62	P	ND	ND	
Valdemoros 1A	VA1A	IVAU & NCBN		Dd	14,64	76			
Valdemoros 7A	VA7A	MNCN		Dd	14,65	P	ND	ND	
Valdemoros 8B	VA8B	MNCN		Dd	14,69	23			
Valdemoros 8C	VA8C	MNCN		Dd	14,71	15			
Vargas 8C	VR8C	MNCN		Dd	14,73	23			
Vargas 8B	VR8B	MNCN		Dd	14,75	31			
Vargas 7	VR7	MNCN		Dd	14,82	49			
Valdemoros 3D	VA3D	MNCN		Dc	14,83	5			
Valdemoros 3B	VA3B	IVAU & MNCN		Dc	14,85	84	0,5		
Valdemoros 11	VA11	MNCN		Dc	15,20	5			
Vargas 6	VR6	MNCN		Dc	15,25	16			
Vargas 5	VR5	MNCN		Dc	15,32	84	4	0,5	
Villafeliche 4B	VL4B	IVAU		Dc	15,30	14	1		
Villafeliche 4A	VL4A	MNCN & NCBN		Dc	15,51	67	1	0,5	
Valdemoros 8A	VA8A	MNCN		Db	15,70	162			
Fuente Sierra 4	FTE4	MNCN		Db	15,85	11	1		
La Col D	COL-D	MNCN		Db	15,87	20	1		
La Col C	COL-C	MNCN		Da	15,89	132	4		
La Col B	COL-B	MNCN		Da	15,91	1			
Fuente Sierra 3	FTE3	MNCN		Da	15,92	18		3	
Fuente Sierra 2	FTE2	MNCN		Da	15,93	17		12	
Olmo Redondo 9	OR9	NCBN		Da	15,95	27		3	
Vargas 2B	VR2B	MNCN		Da	15,96	0,5		1	
La Col A	COL-A	MNCN		Da	15,97	10	0,5		
Vargas 2A	VR2A	MNCN	4	Cb	15,98	15		1	
Olmo Redondo 8	OR8	NCBN		Cb	15,99	18		2	
Fuente Sierra 1	FTE1	MNCN		Cb	16,00	7		0,5	
Olmo Redondo 5	OR5	NCBN		Cb	16,02	ND	ND	ND	
Vargas 3	VR3	MNCN		Cb	16,13	2			
Vargas 1A	VR1A	NCBN		Cb	16,14	28	2	11	
Vargas 4BB	VR4BB	MNCN		Cb	16,15	44	1	8	
Vargas 4B	VR4B	MNCN		Cb	16,16				
Vargas 4A	VR4A	MNCN		Cb	16,18	53		9	
Olmo Redondo 4A	OR4A	IVAU		Ca	16,32	15	0,5		
San Roque 3	SR3	MNCN		Ca	16,35	64	3		
Artesilla	ART	MNCN		Ca	16,51	140	1		
Villafeliche 2A	VL2A	IVAU		B	16,64	106	4		
Olmo Redondo 3	OR3	NCBN		B	16,65	65	2		
San Roque 5	SR5	MNCN		B	16,66	77	7		
San Roque 2	SR2	NCBN		B	16,67	118	2		
San Marcos	SAM	MNCN		B	16,70	182	54		
Olmo Redondo 2	OR2	NCBN		B	16,73	130	15		
Olmo Redondo 1	OR1	NCBN		B	16,76	81			
San Roque 1	SR1	NCBN		B	16,78	208	10		

← *Table 5.1:* Listing of analyzed small-mammal assemblages, ochotonid material (P_3 & P^3) and their repository. Values indicated by P denote confirmed presence, but unknown relative abundance; ND designates absence of data;? refers to a possible but unconfirmed presence and is considered as absence in range calculations. Numerical age estimates are after Daams *et al.* (1999a). Correlation to MN zones and local zones follow van der Meulen *et al.* (in review). Abbreviated repository institutes are IVAU: Instituut voor Aardwetenschappen Utrecht (Institute of Earth Sciences Utrecht), Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands; MNCN: Museo Nacional de Ciencias Naturales (National Museum of Natural Sciences), Department of Paleobiology, Madrid, Spain; NCBN: Netherlands Centre for Biodiversity Naturalis (National Museum of Natural History Naturalis), Leiden, the Netherlands.

$$P_i = 1 - (1 - p_i)^r \qquad \text{Eq. 1}$$

The probability of finding a specimen of species *i* in the locality containing the first or last occurrence is $p_{i,}$ and r represents the cumulative number of specimens in the localities for which P_i is estimated. The absence of species *i* in an assemblage is considered a true local extinction in case P_i is 0.8 or higher. In case P*i* is lower, it is assumed present. In accordance with van der Meulen *et al.* (2005), but in contrast to Barry *et al.* (2002) who used the mean abundance of a taxon over its range, the frequency in the localities containing the first and last occurrences of a lineage over its range (interval) is used to calculate P_i. Fluctuations in relative abundance are ecologically meaningful in the sense that they are commonly related to changing environmental conditions. Global and regional climate varied during the Miocene influencing local habitat conditions (Zachos *et al.*, 2001; Abdul Aziz *et al.*, 2003; Raffi *et al.*, 2006; Holbourn *et al.*, 2007; Abels *et al.*, 2010; Mourik, 2010). Associated fluctuations are distinctly evident in the composition of mammal assemblages (van der Meulen and Daams, 1992; Daams *et al.*, 1999a; van Dam *et al.*, 2006), undermining Barry *et al.*'s (2002) assumption of a constant probability to find a taxon during its range.

As a second step, range gaps spanning a single locality are closed, since such absences may have resulted from chance. Finally, remaining gaps smaller than 200 kyr are closed in order to compensate for a potential sampling bias related to Milankovitch cyclicity at the scale of tens to 100 kyrs. Various studies on the stratigraphy and sedimentology of Spanish Miocene continental successions have demonstrated that the regional paleoenvironment is susceptible to orbital forcing (Abdul Aziz *et al.*, 2000, 2003; Abels, 2008; Abels *et al.*, 2009a, 2009b). Although the presence of Milankovitch cycles has not been established in the sedimentary succession of the study area, sampled levels, which are clay rich, may be related to relatively dry conditions within orbital cycles (Abdul-Aziz, 2001; Abdul-Aziz *et al.*, 2003; van der Meulen *et al.*, 2005).

5.3.3 Community age, community structure and "seniority rule"

Van der Meulen *et al.* (2005) distinguished two main categories in the distribution and duration of rodent lineage residence times. The so-called resident community members have temporal ranges equal to or exceeding the mean residence time (~1.534 Myr) of all included rodent lineages, while transient community members represent lineages with shorter durations.

Secondly, the quantity Community Age (CA) has been defined, which is the mean of the residence times of the community members at the time of the community. In the succession from the Calatayud-Montalbán Basin, CA is significantly negatively correlated with the number of community members. This trend of preferential disappearances of transients while residents

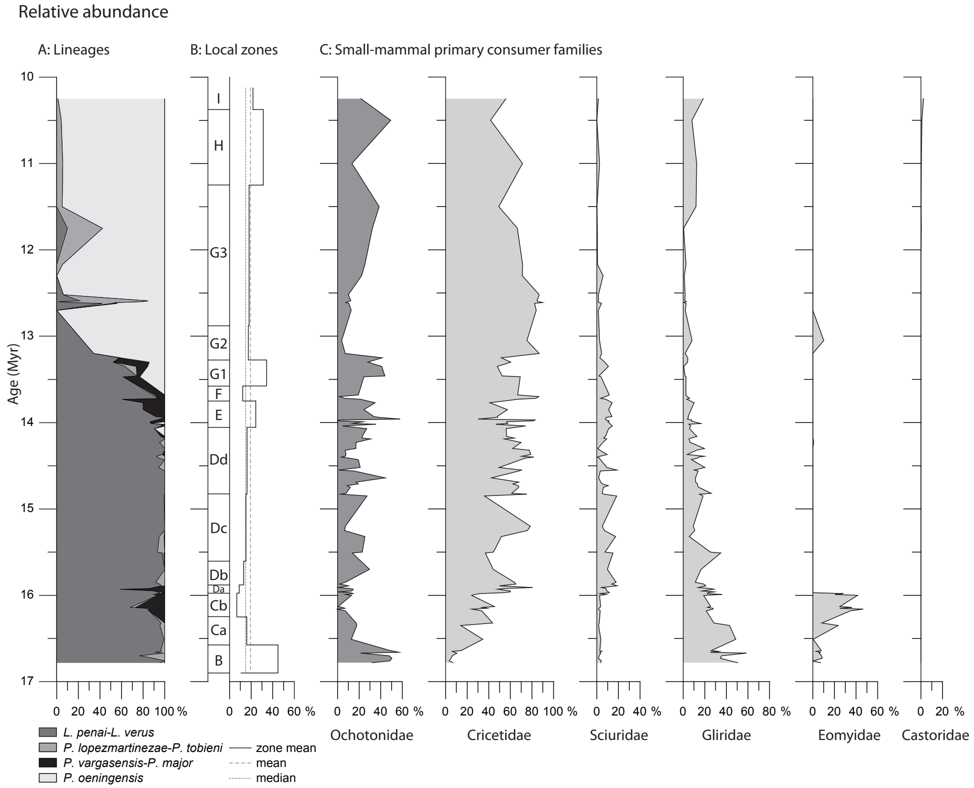


Figure 5.1: (A) Relative abundance of *Lagopsis* and *Prolagus* lineages in the Ochotonidae. Assemblages in which $2(P_3+P^3) < 10$ are omitted in order to reduce bias due to small ochotonid assemblage size, while retaining information of assemblages showing a low relative ochotonid abundance. (B) Average ochotonid relative abundance per biozone and the mean and median relative abundance in the entire studied interval. The relatively low abundance in zone A is in this case only based on the ochotonid abundance in San Roque 4A (suppl. table 5.1). (C) Relative abundances of families of small-mammal primary consumers represented by the lagomorphs and rodents. Assemblages from which the quantity of ochotonids could not be substantiated are excluded (see Table 5.1).

persist during episodes of species loss has been termed "seniority rule". High degrees of ecological disturbance that impare community succession have been assumed to explain the reversed pattern in which residents are associated with early successional stages of vegetation, while transients are associated with later stages. The community membership type of a lineage may change over time and may change over large geographic distances.

A third aspect in the analysis of the rodent community structure involved the definition of different communities in time. Van der Meulen *et al.* (2005) proposed that residents define temporal metacommunities of fossil rodents since they form a core group of most continuous coexisting members, while transients come and go. Phases of community turnover therefore constitute the disappearance of residents and appearance of newcomers and are characterized by a marked decrease in CA. Boundaries between successive metacommunities are drawn somewhat arbitrarily within phases of turnover during which residents are replaced.

5.4 Results & discussion

5.4.1 Relative abundance and temporal range patterns of Ochotonidae

The relative abundance of the lagomorph and rodent families represented in the succession of the Daroca-Villafeliche area is shown in figure 5.1. Differences in generic relative abundance within the Ochotonidae show a distinct but gradual shift from *Lagopsis* dominated to *Prolagus* dominated during the middle Miocene (Fig. 5.1A). This general trend has been documented previously by López-Martínez (1989, 2001) on a longer time interval, but at a considerably lower resolution.

Since the trend in figure 5.1A is entirely based on assemblages from the same composite succession from a small area, it remains unaffected by possible regional scale sampling effects on relative abundance differences. It therefore provides a detailed record in Spain in the context of latitudinal abundance patterns and range shifts of the two genera through time. *Lagopsis* is most abundant in Spain and *Prolagus* is most abundant north of Spain. Mein (1984) and López-Martínez (*et al.*, 1987; 1989, 2001) have associated the gradient in their abundance pattern with latitudinal temperature and humidity gradients across Western Europe.

The main shift of relative genus abundance is primarily brought about by two lineages, *L. penai* Royo, 1928 – *L. verus* (Hensel, 1856) and *P. oeningensis*, both in space and time. In the studied succession, *Lagopsis* is most common during the early middle Miocene, in particular in the interval covering part of zones Dc and Dd in which *Prolagus* is almost or completely absent in the area. *Prolagus* is relatively more abundant during the late middle Miocene. The onset of the abundance shift, which is characterized by the first brief appearance of *P. oeningensis* in the area, approximately coincides with the anagenetic transition between *L. penai* and *L. verus* (Fig. 5.1A; Table 5.1; Chapter 4). Subsequently, during the early phase of the shift, the *P. vargasensis* n. sp., Chapter 3 -*P. major* López, 1977 lineage is relatively abundant and forms a prelude to the rise of the *P. oeningensis* lineage. Similarly, in an older interval marked by community change, i.e. zone C to Da at the end of the early Miocene, the *P. vargasensis*-*P. major* lineage is also relatively well represented within the family. After *P. oeningensis* became the most common ochotonid present in the community in zone G2, *L. verus* had only a few brief comebacks before disappearing from the record alltogether.

Ochotonidae represent on average ~19% of the group of small-mammal primary consumers in the succession, ranging from absence to ~55% (Figs 5.1B and 5.1C). Zone B stands out as an interval during which the ochotonids constitute the most abundant family group. This high relative abundance, which in particular represents *Lagopsis penai*, is intermitted only once by the glirids (San Roque 2), the second most abundant family in this biozone. At the species level in this locality however, *L. penai* remains the most abundant lineage (21.2%) by a small margin. Beside zone B, zones E, G1 and H show an above average relative abundance of Ochotonidae (Fig. 5.1B). Zone Cb on the other hand, is characterized by a distinctly below average relative abundance, which increases again in the subsequent zones Da and Db. Despite the low relative abundance in this zone, the ochotonid diversity in the area comprises three lineages, one more than the three preceding zones and hence does not appear to be reduced. Except for sporadic individual assemblages, phases of consistent ochotonid dominance such as in Zone B have not occured in other intervals of the studied succession. Zones Ca and Cb are characterized by high abundances of glirids and eomyids, respectively, while the cricetids constitute the largest portion of the small-mammal assemblages during the middle and late Aragonian (Fig. 5.1C).

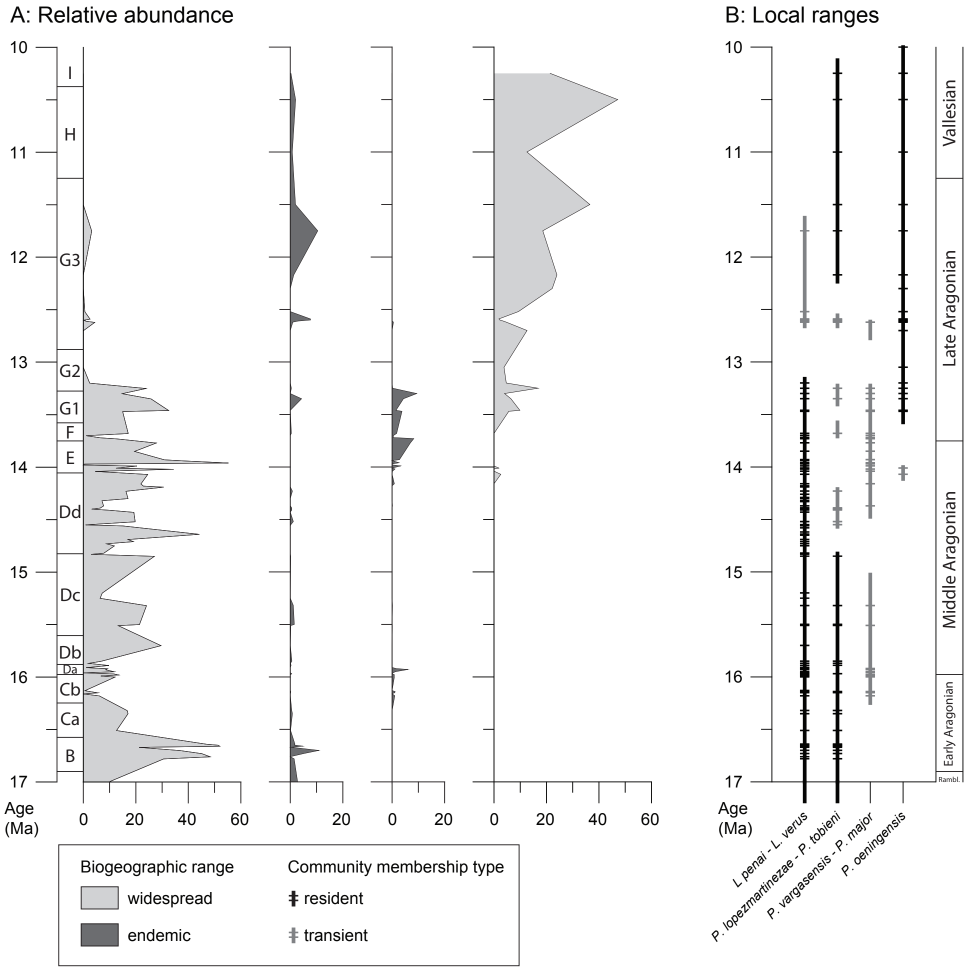


Figure 5.2: (A) Relative abundance and (B) inferred local ranges of the four pika lineages in the Daroca-Villafeliche succession. Three inferred range intervals continue before and after the time interval shown (see fig. 5.3 and text for further explanation). Horizontal lines indicate observed occurrences. Widespread lineages are known throughout Western Europe, endemic lineages are known only from the Iberian Peninsula. Local zonation is after Daams *et al.* (1999a) and van der Meulen *et al.* (in review).

The two abundant successive lineages, i.e. *L. penai-L. verus* and *P. oeningensis* (Fig. 5.2A), are both known to be widespread in Western Europe (Chapters 2 & 3) and thus likely have a good dispersal ability. Contrastingly, the other, markedly less abundant two lineages, *P. lopezmartinezae* n. sp., Chapter 2 – *P. tobieni* López, 1977 and *P. vargasensis-P. major*, are endemic Iberian lineages. These observations are in agreement with the well known geographical pattern in macroecology that widespread species in general tend to be more common, while rare or occasional species tend to be less widely distributed (Hanski, 1982; Hanski & Gyllenberg, 1993; Gibson *et al.*, 1999).

The temporal abundance patterns in Figure 5.2A show quite a few fluctuations in the pattern of *Lagopsis*. Clear temporal regularities in that of *Lagopsis* at the scale of several 100 kyrs cannot be tightly established at this point although these may potentially be present. A number of fluctuations appear to fit, while others do not, with the pronounced 400 kyr cycles in the benthic stable carbon isotope record of the marine realm that has been related to the burial of terrestrial organic carbon (Holbourn *et al.* 2007; Diester-Haass *et al.*, 2009). The lack of clarity may partly be due to the variable sampling resolution and distribution in the succession.

Similarly, the *P. lopezmartinezae-P. tobieni* lineage, which shows its most prominent relative abundance peaks in zones B and G3 while being rare or absent in the interval between these zones, shows slight abundance increases and decreases every couple of 100 kyrs in the lower half of the record, suggesting a potentially cyclic recurrence of environmental conditions, but which cannot be verified with the current data and might be due to chance as well. The *P. vargasensis-P. major* lineage is fairly uncommon, but is regularly present in zones Cb and Da, showing a marked relative abundance peak in the latter zone, and is notably more abundant in the interval spanning zone E to G1. Both intervals, the latter in particular, are characterized by turnover. Both small-mammal turnover phases have been associated with long-period astronomical climate forcing (van Dam *et al.*, 2006).

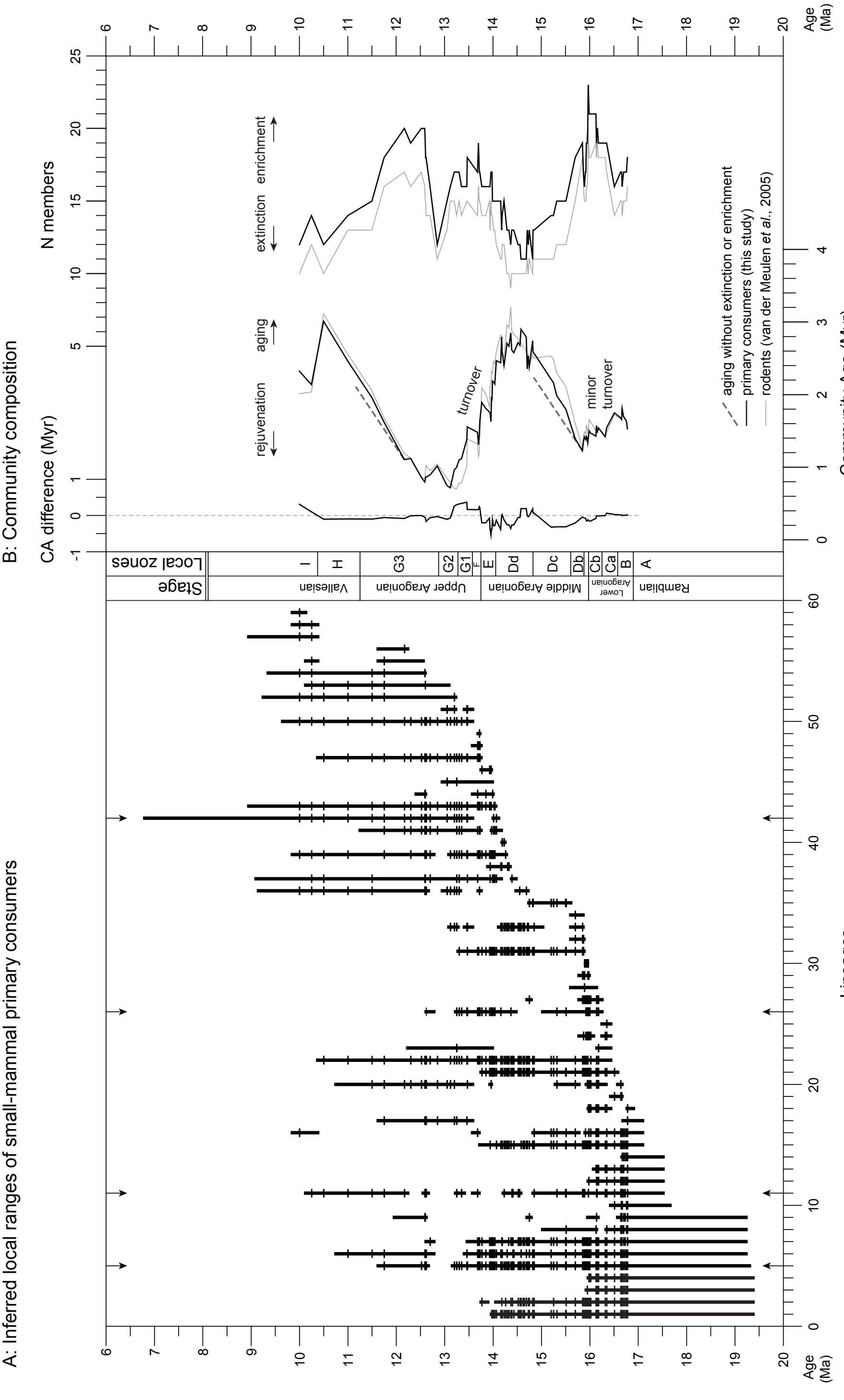
5.4.2 Community membership of ochotonidae

Three resident lineages and one transient lineage are identified on the basis of their inferred ranges in the succession (Figure 5.2B). The *Lagopsis* lineage, whose abundance optimum is in the south of Western Europe (López-Martínez, 2001), has been a resident community member for the major part of the Ramblian upto the middle Aragonian before becoming a transient member in the late Aragonian. Conversely, *P. oeningensis* lineage, which is most abundant in more norther parts of Western Central Europe (López-Martínez, 2001; Chapter 3), starts off as a transient lineage in the middle Aragonian and becomes a resident member in the late Aragonian. The pattern in which relatively "southern" species are displaced by Central European ones in this time interval is well known in the rodent record (van der Meulen *et al.*, 2005).

Although several lineages may occur in the area over a large time span, the *P. lopezmartinezae-P. tobieni* lineage is one of only two lineages of the small-mammal primary consumers that are characterized by two resident phases. This lineage is a resident in both successive Aragonian temporal metacommunities. In between these intervals, the lineage was transient, being present in the area for several short periods of time. It should be noted that the resolution of the fossil record in the interval younger than 13 Ma is distinctly less in comparison to that in the preceding one, which may result in overestimation of the inferred range length. However, the consistent presence of this not particularly abundant lineage next to *P. oeningensis* in all assemblages suggests that the inferred long range interval is justified. Moreover, the consistently low relative abundance does not seem to hamper its persistence and common occurrence in time.

The *P. vargasensis-P. major* lineage is the only transient ochotonid lineage in the study area, while its entire biostratigraphic range on the Iberian Peninsula spans approximately five Myrs (Chapters 3 & 4). Two of its range intervals are, however, fairly long in comparison to many other transient lineages. This pattern is likely related to its endemism and implies that this lineage is never very far away during phases of absence and emphasizes the local nature of the observed range pattern, being restricted to the immediate vicinity of the studied succession or the basin area (van der Meulen *et al.*, 2005).

Figure 5.3


A: Inferred local ranges of small-mammal primary consumers
B: Community composition
Age (Ma)
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Lineages
0
10
20
30
40
50
60
Stage
Local zones
Vallesian
Upper Aragonian
Middle Aragonian
Lower Aragonian
Ramblian
I
H
G3
G2
G1
F
E
Dd
Dc
Db
Cb
Ca
B
A
CA difference (Myr)
-1
0
1
5
10
15
20
25
N members
rejuvenation
aging
extinction
enrichment
turnover
minor turnover
aging without extinction or enrichment
primary consumers (this study)
rodents (van der Meulen et al., 2005)
Community Age (Myr)
0
1
2
3
4

← *Figure 5.3:* (A) Inferred ranges of small-mammal primary consumers. Dashes indicate occurrences in fossil assemblages. Arrows denote ochotonid lineages. (B) Community composition as shown by Community Age (CA) and the number of community members. The black line denotes rodent and lagomorphs (this study) and the grey line rodents only (van der Meulen *et al.*, 2005). The dashed line indicates normal aging trend of a stable community assemblage without extinction or enrichment. The CA difference shows the contribution of the Ochotonidae relative to the analysis solely based on rodents.

5.4.3 The role of Ochotonidae in small mammal community structure

The inferred range pattern of the Ochotonida fits very well with that of the rodents (Figure 5.3). Our analysis of the small-mammal primary consumers confirms and strengthens the Community Age (CA) pattern established by van der Meulen *et al.* (2005) (Figure 5.3B). In comparison to the analysis on rodents only, the CA trend on small-mammal primary consumers is slightly smoothed by both positive and negative contributions of the ochotonids and the peaks and troughs in CA and community richness have slightly shifted in some cases. The Community Age and the number of community members show a strong negative correlation (Table 5.2), which is slightly higher than that reported for the rodents only (van der Meulen *et al.*, 2005). The deviations from linear community aging with time during phases of species loss indicates preferential loss of newcomers, which is in line with "seniority rule" described by van der Meulen *et al.* (2005) in which there is a preferential loss of taxa of which exit residence time (RT_{exit}) is smaller than the CA at that level.

The phase of minor turnover from zone Ca to Da is characterized by community rejuvenation, which among others includes the immigration of *P. vargasensis* and of the cricetids *Eumyarion* THALER, 1966 and *Democricetodon franconicus* FAHLBUSCH, 1966 in the area in zone Cb (van der Meulen *et al.*, in review). These new arrivals enlarge the community that mostly consists of lineages that stem from the Ramblian.

Extinction significantly empoverished the community richness in zones Da and Dc. Zone Db on the other hand is characterized by a brief expansion of the community involving mostly endemic lineages. Following the extinction phase of zone Dc, the early part of zone Dd is characterized by the lowest community richness in the studied succession and CA reaches a maximum. From the perspective of the Ochotonidae, this interval coincides with a phase during which the endemic *Prolagus* lineages are temporarily absent while long-time community member *Lagopsis* remains present, the effect of which is clearly visible in figure 5.3B.

During the remainder of zone Dd, the community expands considerably. CA nevertheless remains high during zone Dd, after which the major community turnover phase takes place during zones E to G2. The early and middle Aragonian community is succeeded by the late Aragonian one with the replacement of resident community members by new lineages, some of which are the new residents. A peak in community richness is reached in zone F, delimiting the new late Aragonian community from the previous one. In the ochotonids, the community

Table 5.2: Partial correlation coefficients between Community Age (CA) and the number of community members of the small-mammal primary consumers, controlling for locality age (N = 102 fossil levels). Asterisks denote a significant correlation (p < 0.01; two-tailed).

	CA	Nmem
CA	1,000	-0.812*
Nmem	-0.812*	1,000

turnover is exemplified by the shift in the relative abundance of *Lagopsis* and *Prolagus* (Fig. 5.1A), which essentially constitutes the displacement of one abundant resident by another. At this large temporal scale, the *Lagopsis* lineage and the *P. oeningensis* lineage appear to play very similar roles within their respective paleocommunities even though these communities are thought to represent different ecological successional stages (van der Meulen *et al.*, 2005; van der Meulen & Peláez-Campomanes, 2007).

Zone G2 represents the interval with lowest CA, which results from the culmination of new arrivals in the three preceding zones and extinction of several remaining residents from the previous community (e.g. *Lagopsis* among others), and marks the end of the middle Miocene community turnover phase.

The community richness trend shows a large peculiar dip at the level of Villafeliche 9 (VL9) at the zone G2-G3 boundary interval (Figure 5.3B), which is not easily explained. Contrastingly, the CA only shows a relatively minor increase. This boundary interval is further characterized by a gap in the record of many lineages, including that of residents, and by the rarity of transient lineages (Figure 5.3A). This may indicate that VL9 is possibly undersampled taxonomically, although the sample size is not particularly small, suggesting a possible taphonomic effect of some sort. However, the observed shift may also represent a true paleoecological response to changes in the local habitat or climate rather than entirely being the result of a sampling artifact. Nevertheless, the fact that the ochotonids from this assemblage could not be analysed (see section 5.3.1) may likely have contributed to the enhanced magnitude of the richness decrease in comparison to the study of van der Meulen *et al.* (2005).

The interval following the low community richness peak is characterized by a strongly enriched community, after which preferential extinction of late-comers results in mildly enhanced aging of the community, similar to the trend observed in zone Dc.

5.4.4 Small mammal community persistence-abundance patterns

As is evident from the results decribed above, relative abundance information represents an important variable next to community membership times. In figures 5.4A-G various aspects of the persistence and abundance patterns of the small-mammal primary consumers analysed are summarized.

A clear relation between the persistence and maximum relative abundance can be observed in the ochotonid lineages (Fig. 5.4A). The highest maximum relative abundance is shown by the most persistent lineages. The rodent lineages show a very similar pattern (Fig. 5.4B), in particular within separate families. The small-mammal primary consumer families, however, show differences in their general maximum abundance levels. Similarly, not all families are equally persistent in the area. The glirids and cricetids show a very similar distribution in the range of their persistence, but the maximum abundance of the former is in general less than that of the latter. The ochotonids are distributed between these two families, but appear to be most similar to the cricetids in this respect. The sciurids and eomyids do not reach the level of persistence shown by the former three families. The different abundance patterns shown by the various families suggest that phylogy or biological species traits may be a significant factor in determining these patterns.

The distribution of small-mammal primary consumer residence times (Figs. 5.4B & C) shows two main gaps of interest: between 1.55 and 1.95 Myr, and between residence times (RT) of 4 and 5 Myr. The first gap represents the division between transient and resident community members. Van der Meulen *et al.* (2005) had taken the mean of the rodent residence times of ~1.54 Myr, which coincided with the trough in the distribution of rodent residence times in their analysis, as the division between transients and residents. We consider the mean value of all residence times, which is ~1.44 Myr in our analysis, to be less meaningful or arbitrary with respect to this division. The median residence time is 0.525 Myrs, indicating that the large majority of residence times (~70 %) represent transient phases. Thirtyone lineages out of 59 are transients over the entire interval.

In our analysis we set the resident-transient division at the lower boundary of the RT gap (1.55 Myr), which closely approximates the original division and maintains the original characterization of community members with the exception of *Simplomys robustus* de Bruijn, 1967 which we propose to include with the transients here. The RT of this species is 1.547 Myrs, which lies at the short edge of the RT gap, fitting better with the RT distribution of transient lineages (Fig. 5.4B).

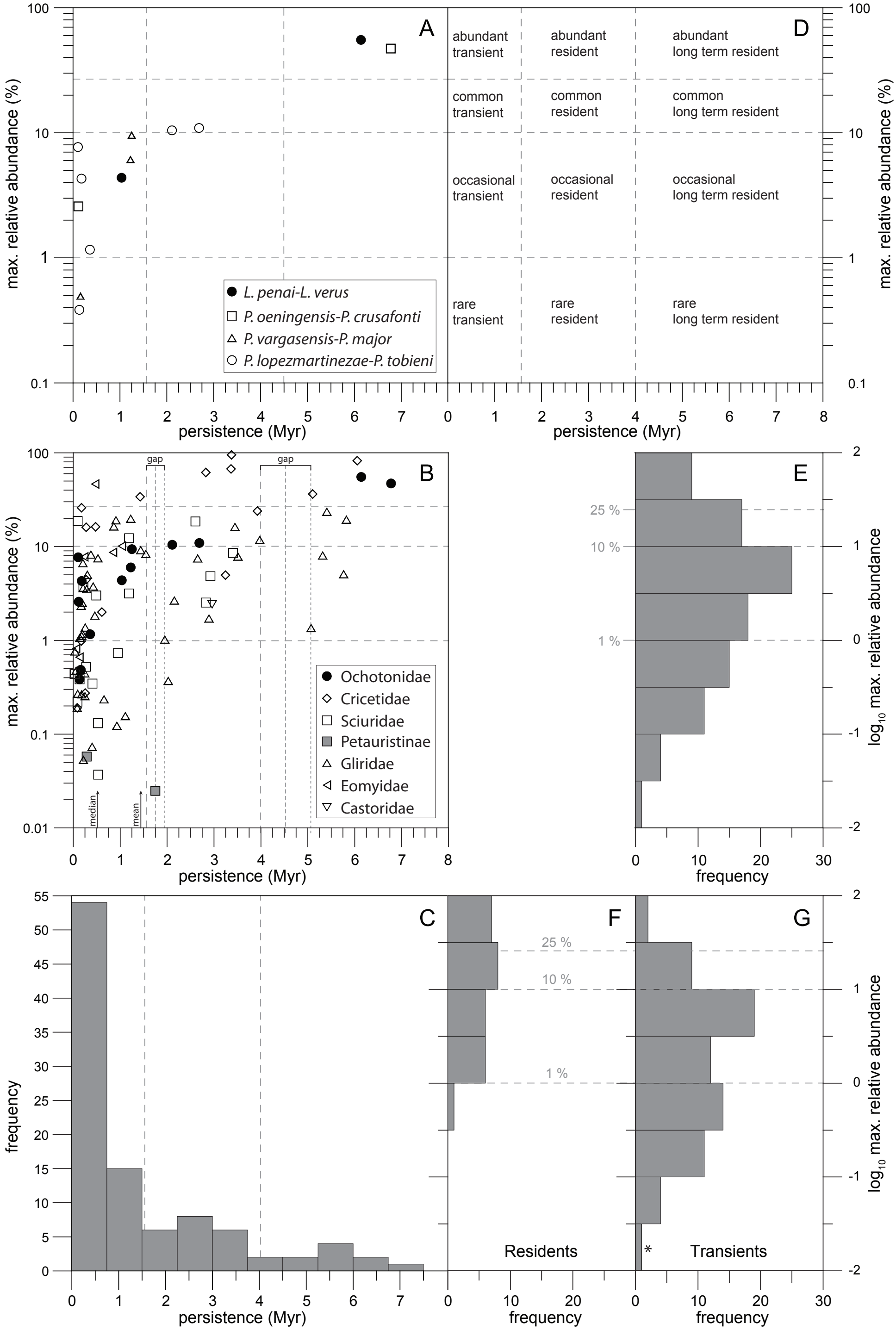
The gap midpoint of 1.75 Myr is a plausible alternative choice for the division in residents and transients. In this case, *S. robustus* would also be considered a transient lineage. Both in the previous option and in this option, the longest RT (1.75 Myr) of a petauristine sciurid results in a status as resident. However, in its long inferred range interval only one occurrence of a single petauristine specimen is recorded, while it spans 27 fossiliferous levels. This seeming discrepancy is due to the large assemblage size of Manchones in which this rare taxon has been found. In our procedure, this strongly influences the chance of finding one specimen in the smaller adjacent assemblages. The long range of this lineage is therefore considered to be caused by a sampling effect and is considered an outlier. The petauristines most likely represent a transient lineage.

A second alternative, in which the division is placed at the upper boundary of the RT gap (1.95 Myr), cirmumvents this problem. The petauristines would be labeled as transients, as would *S. robustus*. However, use of the end of the RT gap as a separator between transients and residents seems counterintuitive. The fact that the transients are all on the other side of this gap argues for a boundary at the beginning (1.55 Myr) or at the midpoint.

The gap in residence times between 4 and 5 Myr subdivides the residents in 'normal' residents and long term residents. The latter group includes lineages of only three families: cricetids, glirids and ochotonids. We provisionally delimit the two resident groups at the short edge of the corresponding RT gap, following the procedure with the previous gap. The long term residents are characterized by extremely long residence times that cover multiple successive fossil metacommunities. This indicates that these organisms occupy a niche that is highly stable in its presence and that is apparently not easily conquered by competitors. In addition, these lineages can cope well with changing environments on a longer time scale, indicating a certain degree of ecological flexibility or adaptability in their survival strategy. Their consistent community membership suggests that they may potentially fulfil a key function in the local ecosystem.

On the basis of the available data, specific persistence-abundance groups can be defined (Fig. 5.4D). The abundance groups are chosen for convenience at the ≤1% (rare), ≤10% (occasional), ≤25% (common) and >25% (abundant) maximum relative abundance levels. The abundance distributions of all community members, resident members and transient members are shown in figures 5.4E-G, respectively. Like the distributions of separate families, the overall distribution of the persistence and abundance data indicates a general positive relation between abundance and persistence.

Transient lineages are found in all abundance groups of which the eomyid *Ligerimys ellipticus* Daams, 1976 represents the only abundant transient (Figs. 5.4B & D). The maximum relative abundance of all but one resident community members is above 1% (Fig. 5.4F). The glirid *Microdyromys legidensis* Daams, 1981 is the only rare resident and its taxonomic status is under


A
max. relative abundance (%)
100
10
1
0.1
persistence (Myr)
0 1 2 3 4 5 6 7 8
● L. penai-L. verus
□ P. oeningensis-P. crusafonti
△ P. vargasensis-P. major
○ P. lopezmartinezae-P. tobieni
D
abundant transient
abundant resident
abundant long term resident
common transient
common resident
common long term resident
occasional transient
occasional resident
occasional long term resident
rare transient
rare resident
rare long term resident
B
0.01
gap
gap
median
mean
● Ochotonidae
◇ Cricetidae
□ Sciuridae
■ Petauristinae
△ Gliridae
◁ Eomyidae
▽ Castoridae
E
25 %
10 %
1 %
log₁₀ max. relative abundance
2
1
0
-1
-2
frequency
0 10 20 30
C
frequency
0 5 10 15 20 25 30 35 40 45 50 55
F
Residents
G
*
Transients

← *Figure 5.4:* Persistence-abundance of small-mammal primary consumers. (A) The $\log_{10}$ maximum abundance in each inferred range interval of ochotonid lineages. (B) The $\log_{10}$ maximum abundance in each inferred range interval of small-mammal primary consumer lineages specified to family. Dashed lines delimit gaps in the distribution of the persistence groups. Arrows at the base denote the median and mean RT. (C) Histogram of the persistence in each range interval of small-mammal primary consumer lineages. (D) Subdivision of persistence-abundance groups. Persistence groups are drawn on the basis of diagrams B and C. Abundance groups are separated for convenience at 1%, 10% and 25% relative maximum abundance. (E) Histogram of $\log_{10}$ maximum abundance in each range interval of small-mammal primary consumer lineages. (F) The $\log_{10}$ maximum abundance in range intervals of resident community members. (G) The $\log_{10}$ maximum abundance in range intervals of transient community members. The asterisk denotes the Petauristinae, whose persistence exceeds 1.55 Myr, but which we consider a transient lineage (see text).

discussion (García-Paredes, 2006). As indicated earlier, we provisionally consider the petauristines as transients in the record. Most range intervals of the resident group have maximum abundances between 1 and 10%. Most long term residents tend to have peak abundances above 10%, to which some the glirids are the exception, which may be related to specific aspects in their life history such as hibernation (Peláez-Campomanes *et al*., 2005). Rare long term residents are not found in the succession, which is to be expected since the extinction vulnerability of rare species can be considered higher than that of more abundant species (Gaston, 2008).

5.4.5 Community membership at different scales

Magurran & Henderson (2003) have demonstrated that, using a data-set spanning 21 years from an extant estuarine fish community, species abundance distributions of an ecological community can be separated in two components. The group of the so-called core species are persistent and abundant and are associated with, in this case, estuarine habitats, while the group of occasional species is characterized by infrequent presence in the record, a typically low abundance and different habitat requirements in comparison to the core species. The commonness and rarity of species in assemblages is related to their persistence in the community.

Van der Meulen *et al*. (2005) and van der Meulen & Peláez-Campomanes (2007) argue that their resident and transient community members on the geological scale may be viewed as long-term equivalents of the core and occasional species as used by Magurran & Henderson (2003) on an ecological scale. In both cases, the two groups are biologically distinquishable. The different community member groups are recognized on the basis of persistence, abundance, and ecological requirements as the most significant commonality between the two studies, although abundance was not yet included in their analysis at that time.

Similar to the study of Magurran & Henderson (2003), our analysis also provides evidence for a relation between abundance and persistence. However, the abundance distributions of resident and transient lineages in comparison to the core and occasional species are different. The maximum abundance of the core species in Magurran & Hederson's (2003) study shows a log normal distribution and their occasional species show a log series distribution. These patterns are not evident in our small mammal record (Fig. 5.4E-G) in which the abundance distribution pattern of the transients approaches a log normal distribution, while that of the residents does not clearly show this shape. In addition, neither group shows a log series distribution or a strong negative skew.

This discrepancy is likely related to the difference in scale and manner of sampling, since it is known for a long time that different time scales of sampling and different sampling methods will result in different abundance distributions (Magurran, 2007). Very rare and/or shortlived species that might be potentially sampled at the ecological time scale may be more strongly undersampled or not sampled at all in the fossil record, resulting in an apparent lack of very rare species in comparison to the ecological scale. In other words, the occasional species at the ecological scale may not be or are barely detected in the fossil record.

Alternatively, the difference in the distribution patterns of the persistence-abundance groups may possibly be explained by a time averaging effect in the fossil record. Samples encompass specimens from a certain period of time during which species abundances may have fluctuated. Smaller scale trends may have been lost, while a longer term abundance trend may be preserved. Residents and transients are likely related to longer term changes in climate, while core and occasional species reflect shorter term (seasonal or annual) variability.

On top of that, the use of the maximum abundance of a species during a particular range interval increases the chance that the abundance of a species is higher when the time interval under consideration is longer. In this case, the contrast between the Myr scale in our analysis and the decadal scale in that of Magurran & Henderson (2003) may have resulted in the log-normal like abundance distribution shape of the transient lineages instead of the log-series shape of the core species.

Magurran (2007) recently drew attention to a paper of Preston (1960) who argued that species-time and species-area relations are equivalent. This assertion appears to be detectable in the fossil record. Peláez-Campomanes *et al.* (2005) have extended and applied the concepts van der Meulen *et al.* (2005) to the spatial domain in geological time. Their study focused on species-richness patterns of European mammal genera using data from the NOW-database (Fortelius, coordinator) by applying the "locality coverage" approach (Jernvall & Fortelius, 2002, 2004) to distinguish between commonness and rarity. Peláez-Campomanes *et al.* (2005) have established among other things that a positive correlation exists between commonness and persistence in fossil European mammal assemblages. Furthermore, they showed that commonness and persistence are sensitive to phylogenetic constraints and that two persistence-occurrence groups can be recognized in the rodent portion of the data.

Yu & Dobson (2000) highlight the fact that commonness and rarity can be defined in multiple ways and that phylogeny may play a significant role in the commonness and rarity of mammals. In the mammal fossil record, the effect of phylogeny is evident from both the viewpoint of relative abundance in a single succession (this study) and of locality occurrence frequency in a large sub-continental scale (Peláez-Campomanes *et al.*, 2005). Despite the very different nature of the data and the applied analyses, the agreement between general conclusions of Peláez-Campomanes *et al.* (2005) and our study suggests a connection between temporal and spatial scales that may be equivalent to that indicated by Magurran (2007). In general, most abundant species are most persistent in contrast to rare species, and are likely to be more widespread or more commonly found in a particular region.

The results in this study indicate that the suggested commonality between comparable community member groups on a geological time scale and ecological time scale (van der Meulen & Peláez-Campomanes, 2007) should be investigated further to establish the main differences, similarities and scale effects between the associated concepts and trends in greater detail. As a next step, comparison to the so-called core and sattellite species groups (Hanski, 1982; Hanski &

Gyllenberg, 1993; Gibson *et al.*, 1999; Magurran, 2007), which are related to the spatial domain and dispersal ability on an ecological scale, seems a logical extension for future attention

5.5 Conclusions

In this paper we have expanded the community analysis based on rodents from the small-mammal record in the Calatayud-Montalbán Basin (van der Meulen *et al.*, 2005) by including the lagomorphs. The temporal relative abundance pattern of the ochotonids confirms the previously documented shift in generic relative abundance from *Lagopsis* to *Prolagus* during the middle Miocene (López-Martínez, 1989, 2001), but at a significantly higher resolution which offers a series of details that are relevant to the timing of and changes in the community structure of the small-mammal primary consumers. Zone B stands out as an interval in which the ochotonids (i.e. *L. penai*) are the dominant group. Three of the four ochotonid lineages present are resident community members, while the remaining one is a recurring transient endemic, exemplifying that ochotonidae represent important core components in the local small-mammal community structure. The endemic ochotonid lineages are fairly uncommon in faunal assemblages, while the two resident lineages that are widespread throughout Western Europe show significantly higher relative abundances throughout their range, which is in agreement with well known patterns in macroecology.

The inclusion of ochotonids in the community structure analysis in terms of community age confirms the dichotomy of transient and resident species established by van der Meulen *et al.* (2005) and supports a further subdivision of the residents in a resident and a long-term resident group that has been discussed by van der Meulen & Peláez-Campomanes (2007). The community age pattern closely resembles the pattern established on the basis of rodents only, confirming the community turnover phase evidenced by the marked drop in CA and the preferential loss of late arrivals during episodes of environmental disturbance, i.e. "seniority-rule", resulting in significant aging of the community.

Analysis of the persistence-abundance relation of the community has revealed that in general, abundant lineages tend to be more persistent. There are however exceptions to this pattern and there are distinct differences between family groups, which implies that phylogeny represents an important factor in small-mammal community anaysis. Preliminary comparison to other studies, both on geological and ecological time scales indicates that further exploration and comparison of existing persistence-abundance patterns and models at various temporal and spatial scales may prove to be a fruitful avenue for future research.

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Supplement Table 5.1: Listing of relevant ochotonid material (P_3 & P^3) from additional assemblages that are not included in the analysis, because these are from outside the analyzed mammal succession and/or interval.

Presence of *Lagopsis* and *Prolagus*						*L. penai - L. verus*	*P. lopezmartinezae* - ex. interc. - *P. tobieni*	*P.* vargasensis - *P. major*	*P. oeningensis*
Locality	loc. code	Repository	MN zone	Local zone	Age (Ma)	P3+p3	P3+p3	P3+p3	P3+p3
Arroyo del Val 6	AR6	IVAU	7/8	G1		30	2	1	134
Armantes 7	ARM7	IVAU	6	F	~13.58	49		11	
Las Planas 4BA	LP4BA	MNCN	5	E		21	2	14	
Regajo 2	RG2	NCBN	5	Dd	14.17	91		0,5	
Torralba 1	TRB1	IVAU	5	D		37		2	
Casetón 2B	CS2B	MNCN	5	Dd	14.77	7			
Casetón 1A	CS1A	MNCN	5	Dd	14.80	35	1		
Valdemoros 9	VA9	MNCN	5	Dc	15.35	3			
Muela Alta	MUE	MNCN	5	Db		13			
Moratilla 4	MOR4	MNCN	5	Db		5			
Moratilla 3	MOR3	MNCN	5	Db	15.76	42	2		
Moratilla 2	MOR2	MNCN	5	Db	15.81	65	1		
Armantes 1	ARM1	IVAU	5	Db		9			
Buñol	BU	IVAU	4	C		23			
San Roque 4A	SR4A	MNCN	3	A	17.02	48	18		
Ateca 3	AT3	IVAU	3	A	~17.30	206	28		

CHAPTER 6

Impact of middle Miocene climate change on small-mammal evolution and community composition in north-eastern Central Spain

Kees Hordijk, Albert J. van der Meulen & Pablo Peláez-Campomanes

6.1 Abstract

The Miocene Climate Optimum and the Middle Miocene Climate Transition represent prominent climate phases in the Neogene. The rich magnetostratigraphically-dated high-resolution small-mammal record from the Calatayud-Montalbán Basin covers both climate intervals. The level of time control and resolution achieved in this succession permits a close comparison to marine isotope records that reflect changes in global climate. In this paper we investigate the correlation between changes in the local small-mammal record in terms of community composition and evolutionary trends of individual lineages and main shifts in the stable oxygen and carbon isotope records of ODP Site 1146 in the South China Sea and the Ras Il Pellegrin section on Malta.

The results demonstrate a close connection between major events and shifts in the small-mammal record in the basin and marked shifts in global climate. The Miocene Climate Optimum coincides with significant aridification in Spain and marked impoverishment of the small-mammal community. This interval is associated with widening of the tropical belt and an increase in the influence of the subtropical high pressure zone in Spain. The Middle Miocene Climate Transition is correlated with a prolonged immigration phase and with marked anagenetic evolution in various lineages. It ultimately results in a community turnover event at the onset of the "ice-house" climate state. The changes in the small-mammal record in the Calatayud-Montalbán Basin reflect a high sensitivity to shifts in global climate, in particular in relation to changes in local humidity.

6.2 Introduction

The middle Miocene encompasses a dynamic time interval in the Cenozoic era which is characterized by major shifts in global climate (Zachos *et al.*, 2001, 2008). The Miocene Climate Optimum (MCO) marks a high temperature phase roughly between ~16.3 Ma and ~15 Ma which intermits the overall Cenozoic cooling trend from a "Greenhouse" world to an "Icehouse" world (Fig. 6.1). The Middle Miocene Climate Transition (MMCT) between ~15 Ma and ~13.7 Ma marks the termination of the Miocene Climate Optimum and represents the second of three major cooling steps that characterize the Cenozoic global cooling trend (Flower & Kennett, 1994; Zachos *et al.*, 2001, 2008; Shevenell *et al.*, 2004; Abels *et al.*, 2005; Holbourn *et al.*, 2005, 2007; Hilgen *et al.*, 2009; Mourik, 2010). This culmination is widely recognized in a distinct shift in marine stable oxygen isotopes to heavier values labelled as the Mi-3b event (Miller *et al.*, 1991,

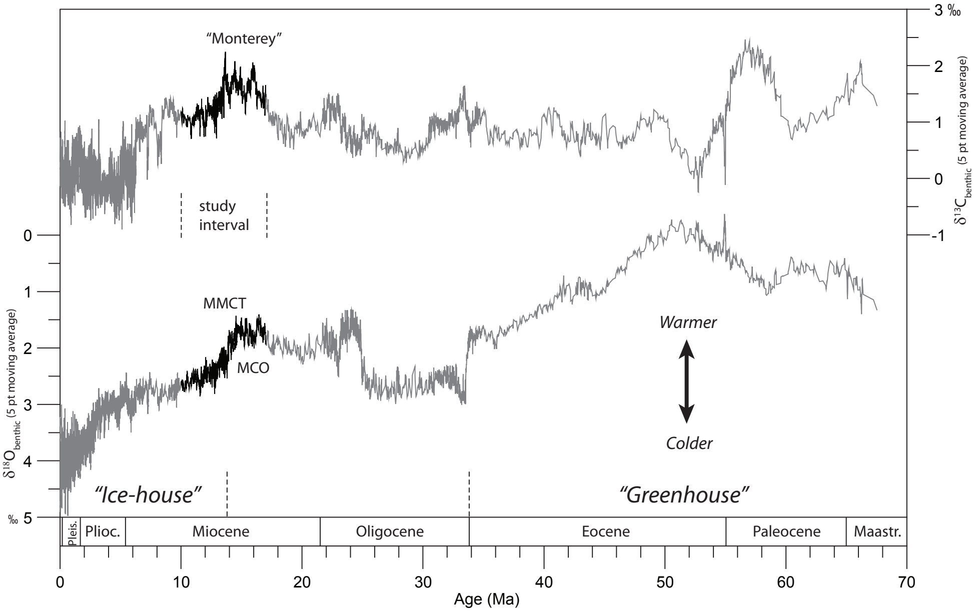


Figure 6.1: Five point moving average of stable oxygen and carbon isotopes of deep-sea benthic foraminifera compiled by Zachos *et al.* (2001 2008) showing the main trends in Cenozoic global climate change. The study interval is shown in black and covers the Middle Miocene Climate Transition (MMCT) and the Miocene Climate Optimum (MCO).

1996), which has recently been ratified as the base of the Serravallian stage, marking the transition into the Earth's "Icehouse" climate state (Hilgen *et al.*, 2009).

The rich, dense and magnetostratigraphically dated mammal succession from the Aragonian type area in the Calatayud-Montalbán Basin spans both the Miocene Climate optimum and the Climate Transition (van der Meulen & Daams, 1992; Krijgsman *et al.*, 1994; Daams *et al.*, 1999a; van der Meulen *et al.*, 2005; van der Meulen *et al.*, in review). Daams *et al.* (1988) and van der Meulen & Daams (1992) have reconstructed the long-term trends in the local paleoenvironment based on rodent species compositions and correlated their findings to then known patterns in global climate. With their studies providing a range of insights and hypotheses, newly developed independent and accurate time control for the mammal succession is now available (Krijgsman *et al.*, 1994, 1996) as well as higher-resolution paleoclimate records from marine successions covering the middle Miocene (e.g. Holbourn *et al.*, 2007). The robust age model constructed for the Aragonian mammal succession on the basis of magnetostratigraphy (Krijgsman *et al.*, 1994, 1996; Daams *et al.*, 1999a) has recently been recalibrated to the ATNTS2004 (Lourens *et al.*, 2005; van Dam *et al.*, 2006; van der Meulen *et al.*, in review). The detailed age models for several high-resolution marine stable oxygen and carbon isotope records covering the early and middle Miocene usually include a tuning to orbital parameters with varying degrees of confidence (Billups *et al.*, 2004; Shevenell *et al.*, 2004; Abels *et al.*, 2005; Holbourn *et al.*, 2005, 2007; Westerhold *et al.*, 2005; Raffi *et al.*, 2006; Tian *et al.*, 2008; Diester-Haass *et al.*, 2009; Hüsing *et al.*, 2010; Mourik, 2010; Mourik *et al.*, 2010). This age control on both data records allow a much more accurate continental to marine comparison.

Recently, periodicities in species turnover patterns in the Spanish Miocene rodent record have been linked to long-period orbital forcing (i.e. 1.2 Myr obliquity nodes and 2.37 Myr eccentricity minima) (van Dam *et al.*, 2006). In this paper, we will focus more directly on the impact of (orbitally-induced) long-term climate changes as recorded in marine successions on the community composition and evolution of small-mammals from the Spanish Miocene fossil record. We will in particular compare the dense small-mammal record from the Calatayud-Montalbán Basin with detailed climate proxy records from the marine realm, ODP Site 1146 in the South China Sea (Holbourn *et al.*, 2007) and the Ras il Pellegrin section on Malta (Abels *et al.*, 2005; Mourik, 2010; Mourik *et al.*, in review) and identify possible synchronies and commonalities in the main trends and events observed. Secondly, the observed patterns in the Spanish mammal succession will be discussed in the context of latitudinal gradients in Western Europe and shifts therein, as inferred from various sources, during the early to middle Miocene.

6.3 Time control

Understanding the accuracy and precision of the age models of the Aragonian type section, ODP Site 1146 and the Ras il Pellegrin section (RIP) is essential for the comparison of data sets. The composite Aragon section containing the succession encompassing over 100 mammal localities spans the interval between ~17 and 10 Ma and is numerically dated by magnetostratigraphy in the interval between ~16.2-13 Ma and provides a consistent framework for the mammal biostratigraphy (Daams *et al.*, 1999a). In the absence of orbital tuning possibilities, fossiliferous levels in the mammal succession are dated by interpolation of sedimentation rates between polarity reversals, which themselves have not yet been astronomically calibrated in this time interval (Lourens *et al*, 2005).ODP Site 1146 in the South China Sea has initially been dated biostratigraphically, correlated to other sites for paleomagnetic constraints, and subsequently tuned to an astronomical target curve on the basis of characteristic cyclic patterns in the stable oxygen isotope record of benthic foraminifera (Holbourn *et al.*, 2007). Mourik *et al.* (in review) provide an alternative tuning, which we will follow here, that is based on the benthic stable carbon isotope record to circumvent a core break issue. The age model of the Ras il Pellegrin section on Malta is based on the integrated stratigraphy including biostratigraphy, magnetostratigraphy and cyclostratigraphy (Abels *et al.*, 2005; Hilgen *et al.*, 2009). The Maltese succession has recently been extended downwards to ~15 Ma and its astronomical age model slightly revised (Mourik, 2010; *et al.*, in review). Recently, Mourik (2010; *et al.*, in review) indicated the possibility of a hiatus of ~80 kyr at the top or bottom of a transitional bed in the section that is characterized by the Mi-3b isotope shift, which adds some uncertainty to the exact age of this event.

The difference between the sources of the three age models has consequences for the precision of correlations. The average temporal resolution in the densest part of the mammal succession, i.e. the early and middle Aragonian, is 46 kyr (van der Meulen *et al.*, 2005), allowing comparison with the astronomically-tuned successions at the 100-kyr scale. The Maltese Ras il Pellegrin section is considered as the best dated of the three sites for the MMCT interval due to the integrated stratigraphy possible, despite the possible short hiatus. This section therefore serves as a reference for both the relatively nearby continental succession in Spain and ODP Site 1146 in the

South China Sea around the global cooling interval. With due consideration of the limitations, sufficiently robust correlations between these records can in our opinion, be made.

6.4 Comparison between the Aragonian mammal succession and ODP site 1146

6.4.1 The Aragonian mammal succession

Several phases and events are recognized in the community composition of the small-mammal succession in the Calatayud-Montalbán Basin (Fig. 6.2A). The community composition in the lower Aragonian largely represents lineages of Ramblian origin, in particular local zone B, which is also characterized by the dominance of herbivores, in particular the ochotonid *Lagopsis penai* Royo, 1928 (Chapter 5). The commonness of pikas indicates the presence of a fairly open grassland environment at that time, which is in agreement with earlier interpretations on the basis of rodents (van der Meulen & Daams, 1992). Zone C is characterized by distinct changes in the community composition with the addition of new arrivals and loss of a few older lineages. The eomyids flourish in this zone, in particular during zone Cb, which is interpreted to indicate a more developed environment structure with additional vegetation tiers relative to zone B (Daams *et al.*, 1988; van der Meulen & Daams, 1992; van Dam *et al.*, 2006; Chapter 5). Zones Da and Dc are characterized by a significant impoverishment of the small-mammal community richness in the study area that has been associated with pronounced aridification of the Iberian Peninsula (Daams *et al.*, 1988; Peláez-Campomanes *et al.*, 2003; van der Meulen *et al.*, 2005; van Dam *et al.*, 2006). Likewise, the herpetological record from the Calatayud-Montalbán Basin indicates dry conditions, in particular during zone Dc (Böhme *et al.*, accepted). In contrast to zones Da and Dc, zone Db shows a distinct diversity increase and is also characterized by endemism. Aridification and change to a more open landscape is also evident in the large mammal record from the area (Daams *et al.*, 1998; DiMiguel *et al.*, 2010). Zones Dd and E comprise a series of immigrations that expand the small-mammal community. Within zone Dd, at around ~14.5 Ma, the immigration rate increased, while zone E is marked by the brief disappearance of recent arrivals, and thus in part reflects a mild regression of the overall enrichment trend. The boundary interval of zones E and F is highlighted by the community turnover during which the early and middle Aragonian community is replaced by the late Aragonian one (van der Meulen & Daams, 1992; van der Meulen *et al.*, 2005).

6.4.2 ODP Site 1146

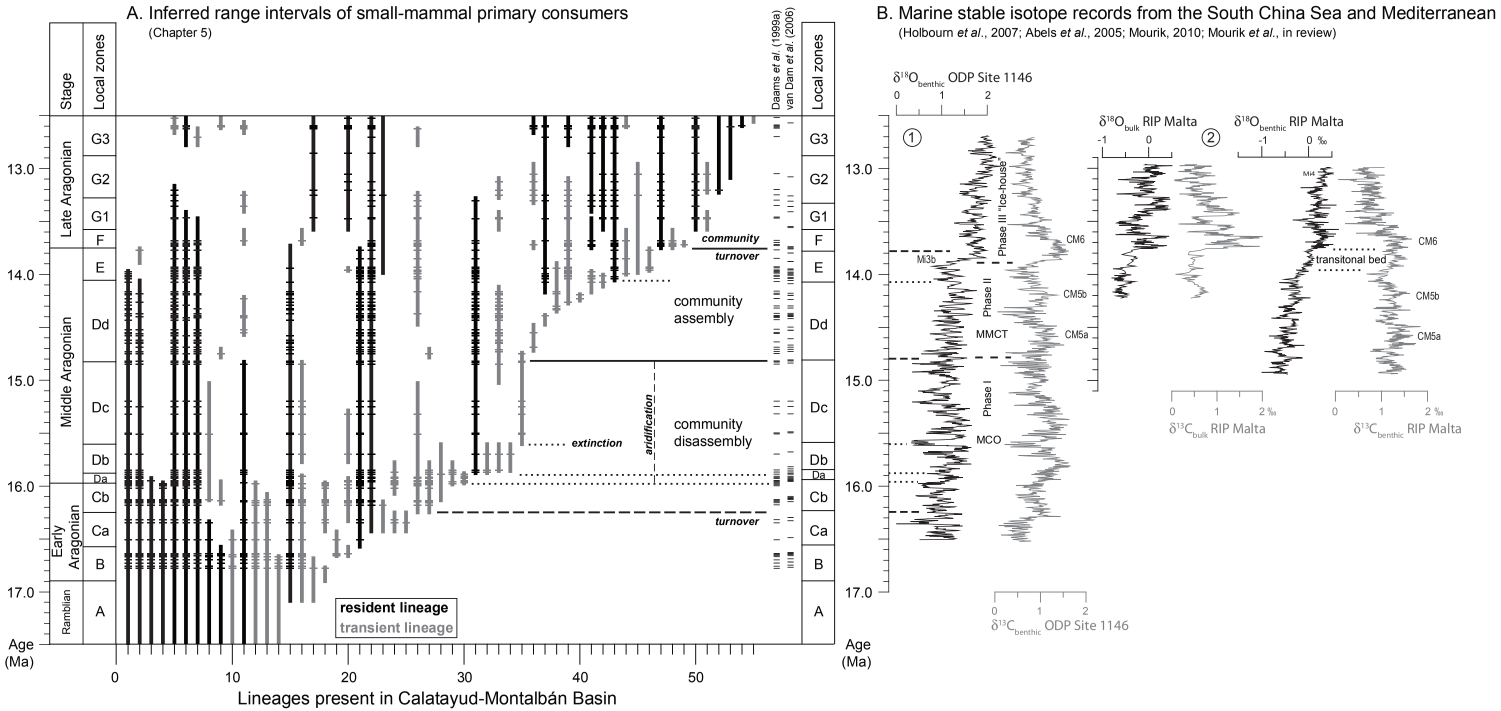
Holbourn *et al.* (2007) identified three distinct climate phases in the stable oxygen and carbon isotope record of ODP Site 1146 (Figure 6.2B). Their "Phase I" is associated with the Miocene Climate Optimum and is characterized by high-amplitude 100-kyr eccentricity variability in oxygen isotopes showing peak light values indicating minimum ice volume and by prominent 400-kyr oscillations in carbon isotopes. "Phase II" on the other hand is characterized by a long-term cooling trend inferred from heavier $\delta^{18}O$ values is modulated by obliquity, while $\delta^{13}C$ continues to show prominent 400-kyr eccentricity cycles. The series of positive 400-kyr excursions in these first two phases are part of the long lasting "Monterey" carbon excursion (Vincent & Berger, 1985; Woodruff & Savin, 1991; Holbourn *et al.*, 2007, 2010). Holbourn *et al.* (2010) have drawn the base of Phase II at a slightly younger level, but the essence of the interval remains unchanged. The significant shift to heavier $\delta^{18}O$ values at the end of Phase II marks the onset of the "Ice-house", which is characterized by ice-volume expansion on East Antarctica. Abrupt Antarctic cooling has been inferred to have initiated at around 14.07 Ma, prior to the main oxygen isotope shift (Lewis *et al.*, 2008). This polar cooling episode appears to occur within with the brief warmer phase at the end of Phase II in the Northern Hemisphere tropical-subtropical belt and illustrates the stepwise character of high-latitude and subsequently deep ocean cooling that led to Antarctic ice-sheet expansion (Lewis *et al.*, 2007; Holbourn *et al.*, 2010). "Phase III" represents the "Ice-house" phase during which the prominent 100 kyr variability in $\delta^{18}O$ has returned, modulating a long-term trend to heavier values. The $\delta^{13}C$ trend initially shows heavy values (CM6), but subsequently shows a long-term declining trend to lighter values and significantly reduced amplitude variations.

6.4.3 Comparison between the mammal record and the marine realm

The boundary level between Ca and Cb marks the immigration of the cricetids *Democricetodon franconicus* Fahlbusch, 1966 and *Eumyarion* Thaler, 1966 from the north, both of which are widely regarded to be of significant biostratigraphic value (van der Meulen *et al.*, in review). *Prolagus vargasensis* n. sp., Chapter 3 represents another coeval invader originating from a northern stock (Chapters 3 & 4). Van Dam *et al.* (2006) have correlated this interval of community reorganization to a phase during a minimum in the long period (~2.37 Myr) eccentricity cycle and a minimum in the 400 kyr eccentricity cycle. The mammal fauna composition indicates somewhat wetter local environmental conditions during this cooling phase (Daams *et al.*, 1988; van der Meulen & Daams, 1992; van Dam *et al.*, 2006). The stable isotope record of ODP Site 1146 shows a maximum in the $\delta^{18}O$ record within zone Cb, while its amplitude variability is relatively reduced (Figure 6.2). Similarly, the $\delta^{13}C$ record in this interval shows distinctly heavier values that are related to a pronounced positive 400-kyr excursion that initiated slightly below the boundary interval. The somewhat dryer preceding interval, zone Ca, may possibly correspond to the warmer phase evident in the oxygen isotopes between 16.3 and 16.4 Ma.

The minimum in the long-period eccentricity cycle is closely followed by a node in the long period obliquity amplitude (~1.2 Myr), which is also associated with cooling (Lourens & Hilgen, 1997). Van Dam *et al.* (2006) have correlated this interval with the pronounced extinction phase in the Spanish small-mammal record, which had a significant effect on the local community richness in the Calatayud-Montalbán Basin (Figure 6.2). Zone Da comprises a short (~100 kyr) interval with a good small-mammal record and time control. The faunal change, both in terms of composition and diversity, is associated with the onset of enhanced aridification (Daams *et al.*, 1988; Daams *et al.*, 1999b; van der Meulen *et al.*, 2005; Van Dam *et al.*, 2006). The duration of this mammal zone strongly suggests the possibility that it is equivalent to a 100-kyr eccentricity cycle. The $\delta^{18}O$ record of ODP Site 1146 shows fairly pronounced 100-kyr cycles in the contemporary interval. We hypothesize therefore that zone Da likely corresponds to a 100-kyr shift to heavier values in the marine record and to the node in obliquity amplitude which is associated with marked aridification in Spain. However, given the current age calibration uncertainty between the two records this remains tentative.

The following time interval, which roughly spans the first half of the Middle Aragonian, represents the main part of the Miocene Climate Optimum. The stable isotope record at ODP Site 1146, i.e. Phase I, shows major fluctuations with a 100-kyr periodicity in both the O and C stable isotope records. The light value extremes in the oxygen isotopes represent phases of minimum ice volume (Holbourn *et al.*, 2007). The large contrasts in the eccentricity-paced stable oxygen isotope variability suggest considerable shifts in climate conditions, although the recorded contrast also depends on local or regional effects in the oceanic depositional environment. The very light oxygen isotope values may correspond to very dry or seasonally very dry conditions in Spain.



A. Inferred range intervals of small-mammal primary consumers
(Chapter 5)

B. Marine stable isotope records from the South China Sea and Mediterranean
(Holbourn *et al.*, 2007; Abels *et al.*, 2005; Mourik, 2010; Mourik *et al.*, in review)

Figure 6.2: Comparative overview of events and large scale changes during the middle Miocene in the small-mammal primary consumer community composition from the Villafeliche-Daroca succession and in global climate as recorded in marine stable isotope records. (A) Inferred range intervals of small-mammal primary consumer lineages from the Villafeliche-Daroca succession (Chapter 5). Horizontal dashes on the right-hand side represent locality ages of Daams *et al.* (1999a) and their recalibrated ages after van Dam *et al.* (2006). (B) Marine stable oxygen and carbon isotope records from 1) benthic foraminifera from ODP site 1146 in the South China Sea (Holbourn *et al.*, 2005, 2007) after the revised age model of Mourik (2010; *et al.*, in review); 2) the land based Ras il Pellegrin section (RIP) on Malta showing bulk carbonate (Abels *et al.*, 2005; Hilgen *et al.*, 2009) and benthic foraminifera records (Mourik, 2010; *et al.*, in review).

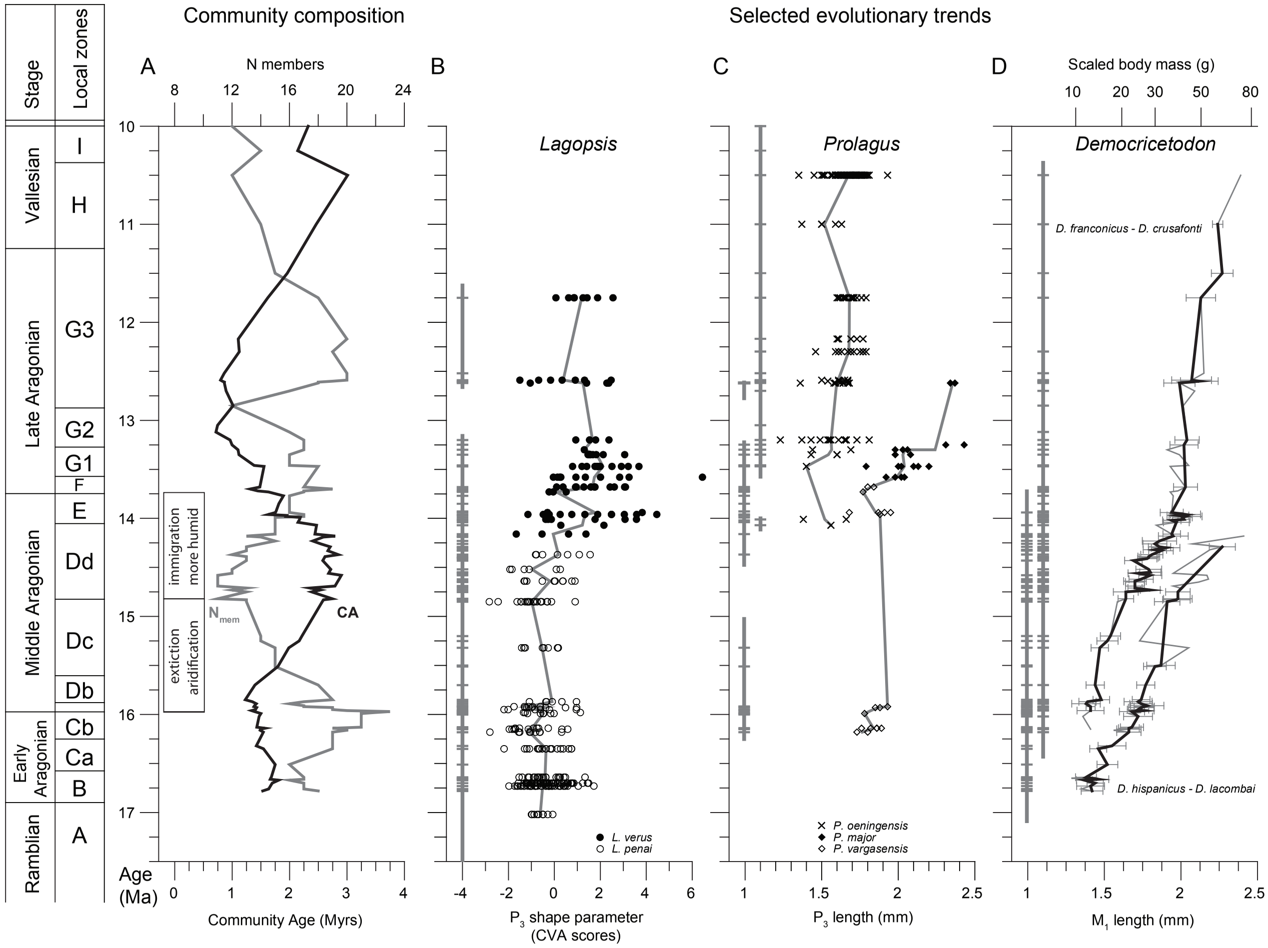
The inferred variable and regularly extreme environment appears to have imposed particularly harsh constraints on the fauna, which likely caused the stepwise decrease in the small-mammal primary consumer diversity during this interval. The extinctions characterizing the base of zone Dc in particular appear to be associated with the large and prolonged peak in light $\delta^{18}O$ values around 15.6 Ma. This shift is similarly evident in the herpetological community and its associated local paleoprecipitation estimate (Böhme *et al.*, accepted).

The series of arrivals of northern immigrants in zone Dd and E coincides neatly with Holbourn *et al.* (2007)'s Phase II. The distinct change in the climate variability, evident from the dominance of the obliquity signal, and the accompanying cooling trend visible in the oxygen isotope record of ODP Site1146 are a likely cause for the improvement of the local environment in the Calatayud-Montalbán Basin. These changes were probably beneficial for northern invaders, which were evidently able to migrate south again after a fairly long phase of non-invasibility in the study area during the Miocene Climate Optimum. The marked increase of the community richness during the initial immigration phase (zone Dd) illustrates the increase of local habitat variability that promoted the entrance of new taxa without replacing resident community members (Figure 6.3A; Chapter 5). Zone E represents a brief plateau in the community richness increase. Two long-term residents disappear from the local community and some recent arrivals temporarily disappear during this phase, while immigrations continue as well. This interval appears to coincide with a brief warming phase visible in the stable isotope record of ODP Site 1146. This warming phase is, however, less pronounced in the benthic oxygen isotope record of the Ras Il Pellegrin section. The distinct oxygen isotope shift (Mi3b) that is related to the major cryogenic expansion on Antarctica at the base of the Serravallian has been correlated to the turnover between the Early-Middle Aragonian community and the Late Aragonian community for a long time (van der Meulen & Daams, 1992; Krijgsman *et al.*, 1994; van der Meulen *et al.*, 2005; van Dam *et al.*, 2006). The turnover spans up to around ~1 Myr and is therefore in part slightly arbitrarily defined, but the E-F boundary interval is inferred to represent the main succession level of the two communities. The current zone boundary slightly postdates the Mi-3b event, which may be partly due to the choice of biozone boundary definitions. However, this difference may also reflect a real lag in the local response of the mammal community composition, since the scale of the community change is considerable. Persistence and succession of temporal small-mammal metacommunities occurs on a million year scale (van der Meulen et al., 2005).

Overall, the timing of the main changes in the composition of the small-mammal community from the Calatayud-Montalbán Basin corresponds well to the large trends global climate evident in marine benthic stable isotopes. The remarkable apparent coincidence of a series of events in the local small-mammal succession in the Calatayud-Montalbán Basin and main features in the stable oxygen and carbon isotope records of ODP site 1146 (Figure 6.2) suggests a close relationship between changes in global climate and changes in the composition and evolution of the local small-mammal community. This connection emphasizes that the local environment in Spain is highly sensitive to climatic changes on a continental or global scale, which is agreement with reconstructions of past bioprovinces and latitudinal ecological gradients and with modelling results of environmental tolerance (van Dam, 2006; Fauquette *et al.*, 2007; Maridet *et al.*, 2007; Bonebreak & Mastrandrea, 2010).

6.4.4 Lineage evolution in response to changes in past climate

Beside the construed effect of global climate change on the local small-mammal community composition, signs of climate influence are also found in the evolutionary trends of individual


Stage
Local zones
Vallesian
I
H
Late Aragonian
G3
G2
G1
F
Middle Aragonian
E
Dd
Dc
Db
Early Aragonian
Cb
Ca
B
Ramblian
A
Community composition
Selected evolutionary trends
A
N members
8
12
16
20
24
immigration more humid
extiction aridification
N_{mem}
CA
Age (Ma)
10
11
12
13
14
15
16
17
0
1
2
3
4
Community Age (Myrs)
B
Lagopsis
L. verus
L. penai
-4
-2
0
2
4
6
P_3 shape parameter (CVA scores)
C
Prolagus
P. oeningensis
P. major
P. vargasensis
1
1.5
2
2.5
P_3 length (mm)
D
Scaled body mass (g)
10
20
30
50
80
Democricetodon
D. franconicus - D. crusafonti
D. hispanicus - D. lacombai
1
1.5
2
2.5
M_1 length (mm)

lineages (Figure 6.3). Although many lineages are still (partly) under study, the fossil records of the pika lineages and some of the hamster lineages from the Calatayud-Montalbán Basin are currently known in great detail (van der Meulen *et al.*, 2003; Chapters 2, 3 & 4).

The *Lagopsis penai* – *Lagopsis verus* (Hensel, 1856) lineage represents a long-lived ochotonid lineage that is particularly abundant in Southwestern Europe, but has been documented in the region of Southern Germany and Switzerland as well (Hensel, 1856; López-Martínez, 1989, 2001; Kälin, 1997; Bolliger, 1997; Prieto, 2007, *et al.*, 2009; Angelone, 2009; Böttcher *et al.*, 2009; Kälin & Kempf, 2009). This lineage is characterized by anagenetic change during the middle Miocene. Although the transition of chronospecies *L. penai* and *L. verus* is well constrained to a narrow interval on the basis of the frequency of morphological features within assemblages (Chapter 2), the overall change in P_3 shape is fairly gradual (Figure 6.3B; Chapter 4). The interval of morphological change is coeval with the immigration phase preceding the community turnover and the obliquity-dominated cooling phase II in the Site 1146 oxygen isotope record (Holbourn *et al.*, 2007, 2010). It remains unclear whether the climate influence on the evolution of this lineage is primarily due to environmental change, in response to competition with new arrivals, or a combination of both.

The concurrent immigration and speciation of *Prolagus vargasensis* takes place during the community renewal phase in zone C (Figure 6.3C, Chapters 3 & 4), which appears to be approximately coeval with the shift to heavier O and C isotopes in ODP Site 1146 as is illustrated in Figure 6.2. During the Miocene Climate Optimum this lineage showed very little change and was also temporarily absent in the basin area. However, at the end of the community turnover phase shortly after the terminal cooling event of the Middle Miocene Climate Transition, *P. vargasensis* rapidly evolved to the distinctly larger *P. major* López, 1977. At that time the smaller but very similar and closely related species *P. oeningensis* (König, 1825) settled as a long-term inhabitant in the area after an earlier brief occurrence during the immigration phase prior to Mi-3b (Fig. 6.3C). The evolutionary pattern of the *P. vargasensis* – *P. major* lineage has therefore been related to both competition and climate change (Chapter 4).

The evolutionary patterns of the two closely related hamster lineages *Democricetodon hispanicus* Freudenthal, 1967 – *D. lacombai* (Freudenthal & Daams, 1988) and *D. franconicus* Fahlbusch, 1966 – *D. crusafonti* (Agustí, 1978) show a distinct size increase and parallel evolution during their stratigraphic ranges (Figure 6.3D; van der Meulen *et al.*, 2003). Both lineages show size increase from the time of their arrival in the basin onward, but the strongest growth is observed during the immigration phases, while during the Miocene Climate Optimum it is somewhat reduced. Similar to the *Lagopsis* Schlosser, 1884 lineage, a significant growth

← *Figure 6.3:* Comparative overview of evolutionary change in selected lineages from the Villafeliche-Daroca succession in relation to (Figure 6.2). (A) Community Age (CA) and the community species richness (N_{mem}) of small-mammal primary consumers (Chapter 5). Plots B-D include the inferred range intervals and observed occurrences of the respective lineages between 17 and 10 Ma (Chapter 5). (B) P_3 shape parameters expressed as CVA axis scores showing morphological change of the *Lagopsis penai* – *L. verus* lineage (Chapters 2 & 4). (C) P_3 length of the *Prolagus vargasensis* – *P. major* lineage and the closely related *P. oeningensis* lineage (Chapters 3 & 4). (D) M_1 length of the *Democricetodon hispanicus* Freudenthal, 1967 – *D. lacombai* (Freudenthal & Daams, 1988) lineage and the closely related *D. franconicus* Fahlbusch, 1966 – *D. crusafonti* (Agustí, 1978) lineage after van der Meulen *et al.* (2003). Black lines indicate localities with N>5 M_1 with standard deviations. Grey lines show all available M_1 lengths. The top axis denotes allometrically scaled body mass estimates using the equation of Martin (1986) (unpublished data).

phase of the two *Democricetodon* Fahlbusch, 1964 lineages is coeval with the cooling interval between ~14.8 and ~14 Ma and the associated small-mammal immigrations in the area. Although the evolutionary rate of the size increase is fairly low, the scale of the change in these cricetid lineages is significant as is evident from the body mass estimates on the basis of their M_1 length (Fig. 6.3D). An approximately five-fold increase of their body mass during the middle Miocene can be considered to affect their biology and life history significantly (unpublished data). The *D. hispanicus* – *D. lacombai* lineage disappeared from the record at the level of the main Mi-3b oxygen isotope shift in the middle Miocene. This lineage appears to have been at an evolutionary dead end, being stuck between the ongoing climate change of the MMCT pushing at the limits of its physiological comfort zone at one end and the presence of its potentially competitive sister lineage on the other.

6.4.5 Lattitudinal trends

Van der Meulen & Daams (1992) have related the major increase of aridity in Spain in the middle Aragonian to intensification of the subtropical climate belt. The vastly increased amount of data that is presently available confirms this hypothesis. The Miocene Climate Optimum represents the warmest time interval in the Neogene during which tropical to subtropical climate conditions existed across large parts of Europe (Utescher *et al.*, 2000, 2009; Mosbrugger *et al.*, 2005; Fauquette *et al.*, 2007; Jiménez-Moreno & Suc, 2007; Diester-Haass *et al.*, 2009; Kürschner *et al.*, 2008; Kürschner & Kvaček, 2009). The latitudinal temperature gradient was weak during this interval, which is also illustrated by the relatively warm conditions near both poles at this time (Williams *et al.*, 2008a; Williams *et al.*, 2008b). In contrast, a precipitation gradient across Western Europe is distinctly present during this phase (López-Martínez, 2001; Böhme, 2004; Fauquette *et al.*, 2007; Jiménez-Moreno & Suc, 2007; Costeur & Legendre, 2008; Furió *et al.*, 2010). Such a scenario is in agreement with recent observations on the current widening of the tropical belt due to global warming (Seidel *et al.*, 2008).

The reconstructed paleolatitude of the time-calibrated mammal record from the Calatayud-Montalbán Basin has been estimated at around 33.6° N on the basis of paleomagnetic inclination data from the same succession (Krijgsman & Tauxe, 2004). This paleolatitude corresponds to the present-day position of northern Morocco and lies within the outer interval of the arid subtropical high pressure zone at the polar side of Hadley cells, which suggests that the region was particularly sensitive to latitudinal shifts of the subtropical dry zone.

Climatic humidity has long been considered as one of the primary drivers for biotic change on the Iberian Peninsula (van der Meulen & Daams, 1992; van Dam & Weltje, 1999; van der Meulen *et al.*, 2005; van Dam, 2006; Furió *et al.*, 2010; Böhme *et al.*, accepted). The mammal succession is therefore likely to closely reflect the latitudinal shifts of the boundary zone between the subtropical dry and the temperate climate belts. This inference is further supported by the close correlation between the general trends visible in the small-mammal record and changes in high-resolution marine stable isotope records of ODP Site 1146.

The aridification phase in Spain, evidenced by the profound community disassembly, reflects the northward shift of the subtropical dry zone during the height of the Miocene Climate Optimum. The enhanced tropical influence is also evident at more northern latitudes in Europe. The locality of Sandelzhausen in Southern Germany, which can be dated to ~15.1 Ma (Chapter 4), is characterized by a humid warm-temperate to subtropical environment (Tütken & Vennemann., 2009; Böhme, 2010; Rössner, 2010). The contrast between the local environments of Spain and the Swiss-German region is clearly reflected in the mammal biostratigraphy. The diachrony between the first and last occurrences of taxa shared by both regions is significantly enlarged by the pronounced arid phase in Spain during which northern immigrants were unable to reach the peninsula and the Iberian faunas were highly endemic (van der Meulen *et al*. in review). The marked diachrony of entries and exits of up to ~2 Myr are thus a direct consequence of the environmental conditions imposed by the MCO.

The MMCT has resulted in the contraction of the tropical zone and the subsequent strengthening of the latitudinal temperature gradient (Flower & Kennett, 1994). The cooling and associated ice-sheet expansion has primarily been attributed to Antarctica, although the Northern Hemisphere may also play a role (Moran *et al*., 2006). Holbourn *et al*. (2010) postulate that the ITCZ in Southeast Asia shifted northward due to the asymmetric polar cooling. This view is in agreement with the interpretation by John *et al*. (2003) for the Miocene record on the Maltese islands in the Mediterranean. However, Mourik (2010) concluded that this northward shift does not appear to be evident in the Mediterranean. Likewise, the contraction of the subtropical climate belt is clearly reflected in the Spanish small-mammal record by the immigration phase comprising species that are primarily associated with more humid conditions and which is coeval with the ongoing global cooling evident in the marine record (Fig. 6.2). A northward shift cannot be discerned in the available data, although this may be disguised within the local rate of the climate shift. The increase in the small-mammal immigration rate after ~14.5 Ma is likely related to the improvement of the local environment under the influence of ongoing global cooling and may possibly reflect a local response of the stepwise growth pulse of the Antarctic ice-sheet inferred by Holbourn *et al*. (2010) during the MMCT.

6.5 Conclusion

The magnetostratigraphically-dated rich and high-resolution small-mammal record from the Calatayud-Montalbán Basin between 17 and 13 Ma is compared with the high-resolution marine stable isotope record of ODP Site 1146. The timing and effect of the main changes in the community composition of the mammal succession compares well with the three main climate phases recognized by Holbourn *et al*. (2007) in the oxygen and carbon isotopes of deep marine benthic foraminifera.

The Miocene Climate Optimum is characterized as a particularly arid phase in the small-mammal record and is characterized by a marked stepwise decrease in the community richness and by distinct endemism that appear to be related to recurring pronounced eccentricity-paced shifts to light oxygen isotopes reflecting minima in global ice-volume. The fairly gradual cooling phase characterizing the subsequent MMCT is coeval with a prolonged immigration phase and associated community richness increase in the small-mammal record. The correlation of the large increase in the stable oxygen isotopes marking the Antarctic ice-sheet expansion with the mammal community turnover has been reconfirmed. After the cooling step, the newly established community reflects more varied and less water-stressed environment than the community which was replaced. The correspondence between the climate change in the isotope record and the changes in the mammal record confirm earlier hypotheses of van der Meulen & Daams (1992) on the expansion of the subtropical climate belt and the marked latitudinal humidity gradient in Europe during the climate optimum and its subsequent contraction during the MMCT on the basis of the local mammal record.

Similar to community composition, evolutionary trends of individual lineages also show good correspondence with the main climate trends. The gradual cooling phase of the MMCT is coeval with the anagenetic change in the *Lagopsis* lineage and with marked size increase in the two *Democricetodon* lineages in the community. The evolutionary change in the *Prolagus vargasensis-P. major* lineage appears to be more strongly associated with the invasion of a closely related competitor, *P. oeningensis* that is related to the marked climate cooling into the ice-house state. In any case, the small-mammal record in the Calatayud-Montalbán Basin appears to be highly sensitive to shifts in global climate, in particular in relation to humidity.

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Introductie & Samenvatting (in Dutch)

Introductie

De fluithazen vertegenwoordigen een familie van kleine herbivoren die sterk verwant is met de familie van de konijnen en hazen. Hoewel de fluithazen in Europa momenteel uitgestorven zijn, zijn ze frequent en geregeld talrijk aanwezig in assemblages van fossiele kleine zoogdieren uit het Mioceen. Ondanks hun reguliere voorkomen zijn fluithazen een relatief weinig bestudeerde zoogdiergroep, vooral in vergelijking met de knaagdieren. Tanden representeren de belangrijkste fossiele elementen van kleine zoogdieren vanwege hun zeer goede preservatiepotentieel in het geologisch archief en hoge diagnostische waarde voor taxonomie, die vaak onderscheidend is tot op soortniveau. Naast de fylogenetische waarde is tandvorm ook sterk gerelateerd aan dieet en is daarom een potentiele bron van informatie over milieucondities in het verleden.

De sedimentaire successie in de buurt van Villafeliche in het Calatayud-Montalbán bekken (Fig. 1.1) staat bekend om zijn rijke opeenvolging van Miocene fossiele zoogdieren. Intensief onderzoek gedurende de laatste 50 jaar gericht op de Neogene zoogdierpaleontologie in het gebied heeft geresulteerd in een database met tienduizenden zoogdiertanden die zijn verzameld op meer dan 100 vindplaatsen in de successie. Dit zoogdier archief omvat de periode tussen ~17-10 miljoen jaar geleden en is voor een groot deel gedateerd aan de hand van paleomagnetisme (Krijgsman et al., 1994, 1996; Daams et al., 1999a).

Het tijdsinterval dat deze zoogdieropeenvolging beslaat wordt gekenmerkt door opvallende fasen en veranderingen in het mondiale klimaat. Het Miocene Klimaat Optimum vertegenwoordigt de warmste fase van het Neogeen en de daaropvolgende Midden Miocene Klimaat Transitie omvat een van de grote verkoelingsfasen van het Cenozoicum (Flower & Kennett, 1994; Zachos et al., 2001).

De combinatie van een rijke en dicht bemonsterde zoogdiersuccessie met een zeer goede tijdcontrole geven een ideaal uitgangspunt voor de bestudering van de biostratigrafie, de evolutionaire trends en veranderingen in de faunasamenstelling onder invloed van grootschalige klimaatveranderingen. Recentelijk hebben studies gericht op fossiele knaagdieren geleid tot diverse nieuwe inzichten in de dynamiek en struktuur van de faunasamenstelling van kleine zoogdieren (van der Meulen et al., 2005; van Dam et al., 2006). De rol van de fluithazen is in deze context top op heden nog buiten beschouwing gebleven.

De taxonomie van fossiele fluithazen is niet eenvoudig. Dit hangt in hoge mate samen met o.a. mozaiek evolutie, convergente en parallele evolutionaire trends en over het algemeen relatief geringe aanpassingen, terwijl de intraspecifieke en ontogenetische variatie binnen soorten relatief groot zijn. Het uitvoerige werk van López-Martínez (1989) omvat een helder taxonomisch model voor de Spaanse Miocene fluithazen en verschaft een rijkdom aan informatie met betrekking tot de evolutie van deze groep. Dit werk vormt een belangrijke basis en dient als startpunt voor de analyse van enige duizenden fluithaaskiezen afkomstig uit de opeenvolging bij Villafeliche.

Het doel van dit proefschrift is vierledig en omvat:

1) Een gedetailleerde analyse en beschrijving van het uitgebreide nieuwe fluithazenmateriaal uit de zoogdieropeenvolging bij Daroca-Villafeliche en een herevaluatie van de bestaande taxonomie en biostratigrafie. (Hoofdstuk 2 & 3);
2) Een analyse van de belangrijkste evolutionaire trends in de aanwezige evolutielijnen met speciale aandacht voor speciatie en competitie. (Hoofdstuk 4);
3) Een analyse van de rol van fluithazen in de groep van primaire consumenten in faunas van kleine zoogdieren en een analyse van de faunastructuur in termen van de duur van hun deelname in de fauna. Daarnaast worden patronen tussen persistentie en abundantie bestudeerd. (Hoofdstuk 5);
4) De bestudering van de invloed en het effect van klimaatveranderingen op de lange termijn op de samenstelling van faunas en de evolutie van individuele lijnen. Hiervoor wordt de zoogdiersuccessie vergeleken met gedetailleerde stabiele zuurstof- en koolstofisotopenreeksen uit het mariene bereik, die dienen als proxy voor veranderingen in mondiaal klimaat. (Hoofdstuk 6).

Samenvatting

De hoge resolutie van de opeenvolging van zoogdierfaunas in het Calatayud-Montalbán bekken geeft een ideale mogelijkheid voor het verifiëren en specificeren van de bestaande taxonomie en biostratigrafie van midden Miocene fluithazen. Hoofdstuk 2 beschrijft het materiaal en behandelt de taxonomische systematiek van de evolutielijnen die gedurende het vroege Mioceen in het gebied aanwezig waren: de *Lagopsis penai – L. verus* lijn en de *Prolagus lopezmartinezae* n. sp. – *P. tobieni* lijn. De definitie van de chronospecies is aangepast, zowel op het gebied van de morfologische karakteristieken als in het temporele bereik van de soorten. De anagenetische transitie in de Lagopsis lijn is op een 400.000 jaar ouder niveau gelegd dan voorheen het geval was. De aanwezigheid van *P. lopezmartinezae* markeert het begin van endemische evolutie van deze lijn en representeert een afzonderlijk evolutiestadium voorafgaand aan *P. tobieni*.

Hoofdstuk 3 is gericht op de taxonomie en beschrijving van de twee evolutionaire lijnen die gedurende het bestudeerde tijdinterval zijn geïmmigreerd in het gebied: de *Prolagus vargasensis* n. sp. – *P. major* lijn en de algemeen bekende Prolagus oeningensis lijn. Er wordt aangetoond dat de binnenkomst van *P. vargasensis* ~2 miljoen jaar voor die van *P. oeningensis* plaatsvond. Daarnaast wordt aangetoond dat *P. major* is ontstaan uit *P. vargasensis* in het vroege laat Aragonien, in tegenstelling tot eerdere hypothesen over de herkomst van *P. major*.

In hoofdstuk 4 worden de intraspecifieke variatie en de interspecifieke verschillen tussen de vier evolutielijnen uit hoofstukken 2 & 3 nader bestudeerd met behulp van multivariate analyse van de morfologische karakteristieken (grootte en vorm) van de P_3. Op basis van onze resultaten stellen we dat de combinatie van competitie en klimaat een rol heeft gespeeld in de evolutie en co-existentie patronen van de fluithaaslijnen in het Daroca-Villafeliche gebied. De eerste binnenkomst van *P. vargasensis* n. sp. wordt geïnterpreteerd als parapatrische speciatie uit een voorouder, *P. cf. oeningensis*, die afkomstig is uit een meer naar het noorden gelegen gebied. Uit de patronen van de gemodelleerde morfologische karakteristieken tussen de relatief gelijkvormige *P. vargasensis – P. major* en *P. oeningensis* lijnen blijkt dat naast klimaat, biotische mechanismen zoals competitieve exclusie van naburige niet co-existerende soorten en limiterende gelijkenis met co-existerende soorten waarschijnlijk van grote invloed zijn geweest op de evolutie en ontwikkeling van deze lijnen.

De faunastructuur van de lagomorfen en de knaagdieren uit het Calatayud-Montalbán bekken, de primaire consumenten onder de kleine zoogdieren, wordt geanalyseerd in hoofdstuk 5. Onze resultaten bevestigen de patronen die werden gevonden in eerdere studies waarbij alleen de knaagdieren in beschouwing werden genomen: 1) het onderscheiden van twee groepen op basis van verblijftijd, de "residents" en de "transients", waarbij de residents verder in een "resident" en een "long-term resident" groep kunnen worden onderverdeeld; 2) het preferentieel verdwijnen van de laatste binnenkomers gedurende fasen van sterke faunaverarming en 3) de herkenning van zoogdiergemeenschappen in tijd. Drie van de vier fluithaaslijnen zijn kernsoorten van de fauna in het bekken. De twee zeldzamere fluithaassoorten zijn endemisch op het Iberisch Schiereiland, terwijl de twee lokaal talrijke soorten wijd verspreid zijn in West Europa. De meest persistente soorten hebben tevens de hoogste maximum abundantie gedurende hun lokale verblijftijd. De persistentie-abundantie patronen suggereren een relatie met fylogenie.

In hoofdstuk 6 worden veranderingen in de faunasamenstelling en evolutionaire trends van individuele lijnen in het Calatayud-Montalbán bekken vergeleken met markante veranderingen en patronen in stabiele isotopenreeksen van ODP Site 1146 (Zuid-Chinese Zee) en de Ras Il Pellegrin sectie (Malta). De resultaten wijzen op een sterke connectie tussen klimaat en de veranderingen in de lokale Spaanse kleine zoogdierenopeenvolging. Het Miocene Klimaat Optimum valt samen met significante verdroging in Spanje die wordt gekarakteriseerd door markante verarming van de kleine zoogdierfaunasamenstelling en wordt geassocieerd met een toename van de invloed van de subtropische hoge druk zone in Spanje als gevolg van verbreding van de tropische klimaatzone. De Midden Miocene Klimaat Transitie is gecorreleerd met een langdurige immigratiefase, die wordt geïnterpreteerd als een gevolg van het krimpen van de tropische klimaatzone. Deze fase wordt daarnaast gekarakteriseerd door duidelijke anagenetische evolutie in meerdere lijnen. Uiteindelijk resulteert dit na het begin van de "ice-house" klimaattoestand in een grootschalige omslag in de faunasamenstelling van de kleine zoogdieren.

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Curriculum Vitae

Kees Hordijk was born on the 17th of December 1975 in Warnsveld. After graduating at the 'VWO'-level from the Isendoorn College in Warnsveld in 1994, he went to study Geology at Utrecht University in the same year. During his Master's research project on recent benthic foraminifera he was introduced to the world of mammal paleontology in the diverse research environment of the Stratigraphy & Paleontology group and started a second research project on Pliocene small-mammals from Greece under the guidance of Hans de Bruijn and Albert van der Meulen.

Following his graduation in Geology in 2000, he temporarily worked as teaching assistant and junior associate researcher at the department of Earth Sciences of Utrecht University during which period he assisted in developing and transforming courses to the Bachelor/Master system and worked on various research subjects on middle Miocene small mammals from Spain. In 2004 he started working as a PhD-student under the supervision of Albert van der Meulen, the results of which are described in this thesis.

After starting as trainee datamanager for a brief period in the fall of 2009, he is currently employed as subsurface datamanager for DataCo Ltd at Shell in Rijswijk.

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