

Biostratigraphical and palaeoecological implications of the small mammal assemblage from the late early Miocene of Montalvos2, Teruel Basin, Spain

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Abstract The rich early Miocene small mammal assemblage from Montalvos2, collected from lacustrine deposits directly overlying the basement, is unique within the Teruel Basin, a basin that is otherwise well known for its late Miocene/Pliocene mammal faunas. The presence of *Democricetodon decipiens*, *Megacricetodon primitivus*, *Eumyarion* and *Ligerimys ellipticus* enables correlation with the local biozone Ca (approx. 16.3 Ma, MN4). The high percentage of ochotonids in Montalvos2 is remarkable, a phenomenon that is known to occur in older assemblages from the adjacent Calatayud-Montalbán Basin. The association in Montalvos2 includes species indicative of an arid biotope, such as the ochotonid *Lagopsis penai* and the rodents *Simplomys simplicidens*, *Armantomys aragonensis*, *Melissiodon dominans* and the xerine squirrel *Heteroxerus*, and species that are supposed to have lived in a more humid forested biotope, such as the Talpidae and the flying squirrel *Albanensia*. This wide range of species indicates that the en-

vironment in the Teruel Basin was highly diverse during the early Miocene.

Keywords Early Miocene · Aragonian · Spain · Small mammals · Biostratigraphy · Palaeoecology

Introduction

Spain is well known for its continental sedimentary basins with rich fossil faunas of vertebrates, particularly smaller mammals (rodents, insectivores and lagomorphs). One of these basins is the Teruel Basin, from which numerous mammal assemblages, mostly of late Miocene age, have been recovered (Van de Weerd 1976; Van Dam et al. 2001). The small mammal assemblage of Montalvos2 represents the only known find in the Teruel Basin of a late early Miocene age, and it is therefore of great interest.

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The locality Montalvos2 is situated in the northern part of the Teruel Basin, 3 km ESE of the village of Cuevas Labradas (Fig. 1) and has yielded a rich small mammal assemblage, which we here summarily describe and place within a stratigraphical and palaeoecological framework. It contains 775 dental elements of small mammals: rodents, lagomorphs, insectivores and marsupials. The assemblage has already been given an estimated age of approximately 16.4 Ma by Van der Meulen et al. (2012), based on the interpolation of two comparable assemblages from the Aragonian type area in the nearby Calatayud-Montalbán Basin (Artesilla, dated 16.49 Ma; San Roque 3, dated 16.33 Ma).

Sediments of the Calatayud-Montalbán Basin (Fig. 1) have provided the data needed to define both the Aragonian and Ramblian stages and their associated small mammal biozones (Daams et al. 1977; Daams et al. 1987). The Aragonian stage and the included biozones have undergone significant revisions and updates since their original definition (Daams and Freudenthal 1981; Freudenthal and Daams 1988; Daams et al. 1999a, b; Van der Meulen et al. 2012). The combination of the Aragonian biozones, based on a densely sampled record of, in many cases, superposed localities with high-resolution magnetostratigraphical data, has resulted in a well-established chronological framework for this time slice and region (Krijgsman et al. 1994, 1996; Daams et al. 1999a; Alcalá et al. 2000; Van der Meulen et al. 2012). However, in the absence of magnetostratigraphical data from the Olmo-Redondo-San Roque sections, the dating of the early Aragonian (late early Miocene) mammal faunas in the type area, which includes zone A to Ca assemblages, is inferred from assumed sedimentary rates (Daams et al. 1999a; Van Dam et al. 2006).

The late early Aragonian is characterised by a mild turnover and species enrichment phase in the mammal succession from the Calatayud-Montalbán Basin (Van der Meulen et al. 2005; Hordijk 2010). The mammal assemblage from Montalvos2 is located outside this basin, and its mammal assemblage comprises an uncommon combination of species. We used the presence of species, taxon-free characteristics (i.e. a ridge index), relative abundances and a method to estimate mean annual precipitation to interpret the Montalvos2 assemblage and thereby provide additional and new insights in the biostratigraphy and palaeoecology of the region.

Locality, material and methods

The geological and stratigraphical position of Montalvos2 is special, as it is situated precisely at the northernmost extension of the NNE–SSW-running fault bordering the basin. The small lacustrine unit that contains the site of Montalvos2 directly overlies the Jurassic limestone that constitutes the local basement (approx. 1 m below the site). The fossiliferous bed

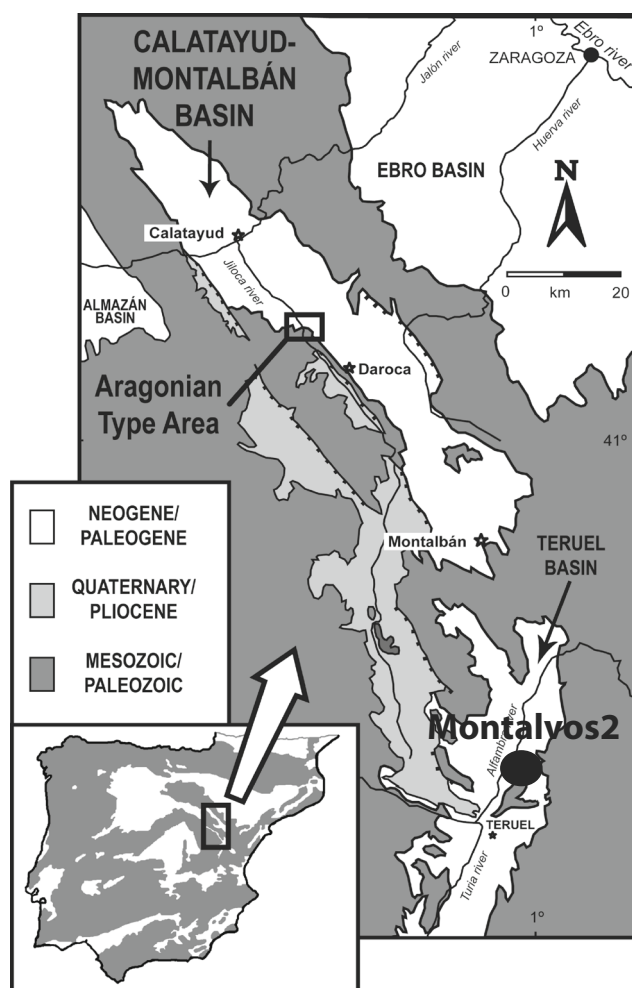


Fig. 1 Location of the Calatayud-Montalbán Basin and the Teruel Basin in Spain (Modified from García-Paredes et al. 2010); Montalvos2 is situated in the Teruel Basin

consists of grey marl and is situated between limestone beds. Higher up in the sequence, lacustrine deposits are replaced by reddish clastic sediments. A thick series of dominantly conglomeratic sediments represents the proximal basin infill that is ultimately overlain by the “classical” late Miocene distal fluvio-lacustrine sediments that are well-known for their rich mammal record of the Teruel Basin (Van de Weerd 1976; Van Dam et al. 2001).

Montalvos2 contains four mammalian orders, as represented by 490 dental elements of rodents, 247 elements of lagomorphs, 37 elements of insectivores and one tooth of a marsupial (numbers excluding the incisors). The material was collected by the late Remmert Daams, and Albert van der Meulen, and the sediments were wet-screened by using a set of screens, the finest of which had a 0.5-mm mesh. The fossils are stored in the collection of the National Museum of Natural History Madrid (Spain).

The measurements of the dental elements were taken with a reflex microscope (Prior S2000, ocular 25×; Prior Scientific,

Cambridge, UK) and with the Leitz Ortholux measuring microscope equipped with mechanical stage and measuring clocks (Esselte Leitz GmbH & Co KG). All measurements (Appendix 1) are given in millimetres. Tooth size measurements and morphology of the ochotonids were taken following the procedure of Hordijk (2010).

The Lagomorpha are described here in detail because lagomorphs have received considerable less attention in the literature. *Prolagus lopezmartinezae* is only known from a few localities and is not abundant in fossil assemblages. For the following reasons there is a strong focus on the p3, P2 and P3 in the descriptions, elements which are usually the most distinctive in pika taxonomy. First, the other cheek teeth, the p4–m1 in particular, are generally less informative in taxon identifications, although these elements may possess taxon specific traits. Secondly, many specimens in the available pika material of Montalvos2 are damaged to a variable degree. The P4–M2 and p4–m2–3 are very poorly preserved, if at all. Thirdly, the available D3 and D4 material in the Montalvos2 assemblage is fragmentary and is very likely a mix of both species. Both the level of damage and the worn state of the specimens prevent reliable identification of these elements.

We follow the taxonomic interpretation of Van der Meulen et al. (2003) and consider *Fahlbuschia*, *Pseudofahlbuschia* and *Renzimys* to be synonyms of *Democricetodon*. In the family assignment of the genus *Prolagus*, we prefer the use of the family name Ochotonidae over the family name Prolagidae Gureev, 1960, as has been proposed by Erbajeva (1988, 1994) and endorsed by Hoffmann and Smith (2005), following the argumentation of Hordijk (2010) and Angelone et al. (2014).

The nomenclature of the tooth morphology used is that of Rössner and Heissig (1999) for the Rodentia, Van den Hoek Ostende (2003) for the Eulipotyphla and Hordijk (2010; which is generally in line with López-Martínez 1974; 1989) for the Lagomorpha. Assuming that similarity in dental morphology indicates similarity in diet (Mayr 1979), the dentition types of extinct and extant glirid genera can be grouped, assuming that the diet of the genera within each group was similar to that of the extant member of that group (Van der Meulen and De Bruijn 1982; Daams et al. 1984). Since the extant dormice are a relict showing very specialised traits, such as hibernation (an adaptation to seasonality), the loss of the caecum (an adaptation to a protein-rich diet) and arboreal life style (except for *Myomimus*), it seems most unlikely that all were shared by the diverse array of extinct genera. This means that the actualistic approach may have a limited result for the Gliridae.

In order to avoid the effect caused by over-splitting on the generic level, as well as the difficulty of allocating extinct genera to a specific type of dentition, we use here the method of De Bruijn (1998), who introduced a ridge index that is based on the total number of ridges counted on all upper and lower first and second molars in an association divided by the number specimens. This method has the disadvantage that it

disguises the distribution over the various taxonomic classes because the number of ridges on the molars of different species within the same genus may vary (García-Paredes 2006).

Quantitative data in fossil assemblages provide a valuable source of information. Relative abundances of species in fossil mammal assemblages can be determined in various ways. For quantitative analysis of the Montalvos2 material, we follow the method adopted in several previous studies (e.g. Daams et al. 1988; Van Dam and Weltje 1999; Van der Meulen et al. 2005) and base relative abundance estimates of rodent and insectivore species on the sum of the first two upper and lower molars. In the Gliridae and Sciuridae, the M1 and M2 are not separated. Because of the high diagnostic value of ochotonid premolars in taxonomy and the lack of properly preserved ochotonid molars in the Montalvos2 assemblage, the relative abundance of ochotonid species is determined by the number of upper and lower third premolars multiplied by two, following Hordijk (2010). Although based on different elements, this relative abundance value for ochotonids is equivalent to that used for the rodents. Specifications on number of elements, measurement and collection numbers are provided in Appendix 1.

To estimate mean annual precipitation (MAP) we used a method based on the percentages of invertivore species (PI) and arboreal species (PA) in the total fauna of Rodentia, Eulipotyphla and Lagomorpha [Van Dam 2006; MAP for the NW Old World (i.e. Europe, Middle East and North Africa)]. The formula employed is $MAP (mm) = 0.179 + 14.134 PI + 18.066 PA$ ($R^2 = 0.69$), where $PI = 100 \times NI/N$ (with NI being the number of invertivore species and N being the total number of species) and $PA = 100 \times NA/N$ (with NA being the number of arboreal species).

Systematic palaeontology

In the faunal list (Table 1) all species are listed, including their taxonomic placement and authorities. Here we briefly introduce the most important taxa.

Order Rodentia Bowdich, 1821

The order Rodentia is represented by 15 species from four families, of which the Muridae is quantitatively the best represented. Here we also report on species of the Gliridae, Sciuridae and Eomyidae families.

Family Muridae Illiger, 1811

Subfamily Melissiodontinae Schaub, 1920

Melissiodon dominans (Fig. 2) has teeth that fall in size and morphology within the range of the type material (Wintershof-West, Germany; MN3); however, apart from the m2 and m3, the molars are distinctly larger than those from the localities

Table 1 Faunal list of Montalvos2 (Teruel Basin, Spain)

Rodentia	
Muridae Illiger, 1811	
Melissiodontinae Schaub, 1920	
	<i>Melissiodon dominans</i> (Dehm, 1950)
Cricetinae Fischer, 1817	
	<i>Democricetodon decipiens</i> (Freudenthal and Daams, 1988)
	<i>Megacricetodon primitivus</i> (Freudenthal, 1963)
	<i>Eumyarion weinfurteri</i> (Schaub and Zapfe, 1953)
Gliridae Muirhead, 1819	
	<i>Pseudodryomys ibericus</i> De Bruijn, 1966
	<i>Simplomys simplicidens</i> (De Bruijn, 1967)
	<i>Simplomys julii</i> (Daams, 1989)
	<i>Simplomys</i> sp.
	<i>Microdryomys legidensis</i> Daams, 1981
	<i>Glirudinus gracilis</i> (Dehm, 1950)
	<i>Armantomys aragonensis</i> De Bruijn, 1966
Eomyidae Winge, 1887	
	<i>Ligerimys ellipticus</i> Daams, 1976
Sciuridae Fischer, 1817	
Sciurinae Fischer, 1817	
	<i>Heteroxerus rubricati</i> Crusafont, de Villata and Truloys, 1955
	<i>Heteroxerus</i> cf. <i>grivensis</i> (Major, 1893)
Pteromyinae Brandt, 1855	
	<i>Albanensia</i> cf. <i>sansaniensis</i> (Lartet, 1851)
Lagomorpha	
Ochotonidae Thomas, 1897	
	<i>Lagopsis penai</i> (Royo, 1928)
	<i>Prolagus lopezmartinezae</i> Hordijk and Van der Meulen, 2010a
Eulipotyphla	
Erinacidae Fisher, 1814	
Galericinae Pomel, 1848	
	<i>Galerix symeonidisi</i> Doukas, 1986
Talpidae Fischer, 1817	
Uropsilinae Dobson, 1883	
	cf. <i>Desmanella</i> sp.
Talpinae Fischer, 1817	
	<i>Desmanodon</i> sp.
Heterosoricidae Viret and Zapfe, 1951	
	<i>Heterosorex</i> cf. <i>neumayrianus</i> Schlosser, 1887
Soricidae Fischer, 1817	
	Soricid gen. et sp. indet.
Didelphimorphia Gill, 1872	
Didelphidae Gray, 1821	
	Herpetotheriinae Trouessart, 1879
	<i>Amphiperatherium</i> sp.

Forsthart and Rembach in the lower part of the Freshwater Molasse of Bavaria (Germany) that otherwise contain the

same murid association (Ziegler and Fahlbusch 1986). *Melissiodon* is known from two localities in the Calatayud-Montalbán Basin (biozone A, approx. 17 Ma), from Buñol (MN4; Prov. Valencia; Daams 1976) and from a MN4 locality in the Ribesalbes-Alcora Basin (Crespo et al. 2014).

Subfamily Cricetinae Fischer, 1817

Democricetodon decipiens from Montalvos2 is of the same size as *D. decipiens* from Buñol (Freudenthal and Daams 1988) and *D. decipiens* from several other localities in the Aragonian type area (Calatayud-Montalbán Basin, OR4A, SR3, ART1; in Van der Meulen et al. 2003). An exception is the M2, which is slightly shorter and overlaps the size range of *D. hispanicus* Freudenthal, 1967. The mesoloph and mesolophids are never long, and the metalophule is always directed forwards.

Megacricetodon primitivus from Montalvos2 is of about the same size as the material from the type-locality, Valtorres (early Aragonian, zones C and D; Freudenthal 1963). The m1s from Valtorres, however, are more elongate than our m1s (L/W ratio is 1.49 in Montalvos2 and 1.56 in Valtorres), and the width of the M1 from Montalvos2 is slightly larger.

Eumyarion weinfurteri from Montalvos2 has somewhat larger teeth than *E. weinfurteri* from Dolnice 1–3 and Orechov (Czechoslovakia; Fejfar 1974). They are about the same size as *E. weinfurteri* molars from Aliveri (Greece; Klein Hofmeijer and De Bruijn 1988), although in Montalvos2 the teeth are slightly wider. A simple anterocone, no mesostyl and a poorly developed or absent anterolophulid of the m1 are all characteristics of *E. weinfurteri*.

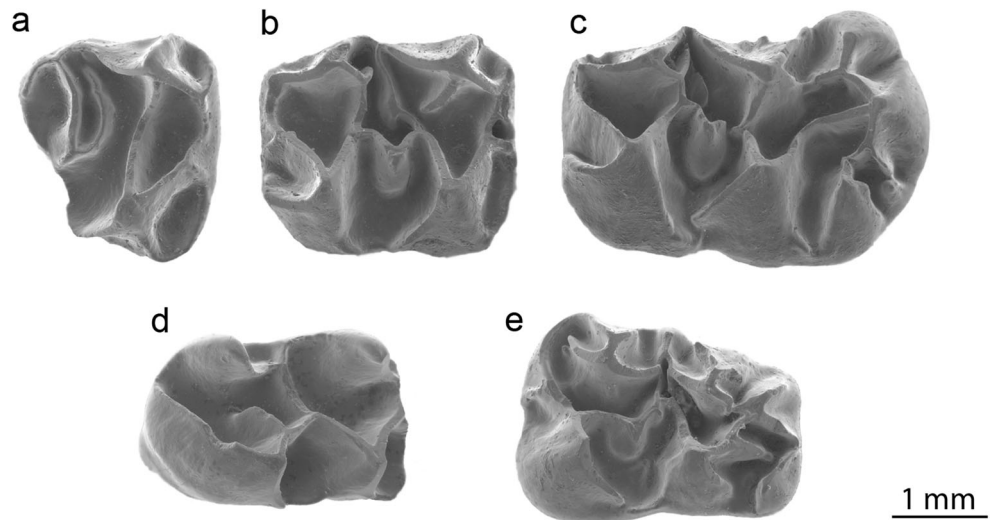
Family Gliridae Muirhead, 1819

The family Gliridae is represented in Montalvos2 by five species groups, differentiated by their dental morphology.

The *Peridyromys/Pseudodryomys* group: In the *Peridyromys/Pseudodryomys* group the genera share the basic glirid pattern, consisting of the four main ridges plus the two centrolophs and sometimes an extra ridge between the protoloph and the anterior centroloph in the upper molars (M1-2), and the four main ridges plus a centrolophid of medium length and sometimes an extra ridge in the valley between the mesolophid and the posterolophid in the lower molars (m1-2).

In this group, a larger part of the ‘genera’ is included in the ‘subfamily’ Myomiminae sensu Daams and De Bruijn (1995). However, disregarding endemic island forms, the group contains *Peridyromys*, *Pseudodryomys*, *Myomimus*, *Miodryomys*, *Prodryomys* and *Ramys*. The differences in dental pattern shown by these ‘genera’ are recognised as being very subtle due to descriptions of generic type species that are intermediate in size

Fig. 2 *Melissiodon dominans*. **a** M3 dex (MNT2 354), **b** M2 dex (MNT2 351), **c** M1 dex (MNT2 346), **d** m3 dex (MNT2 361), **e** m1 dex (MNT2 357). Scale bar: 1 mm



and morphology. This phenomenon is especially obvious in the case of *Pseudodryomys* and *Peridyromys*. When one of us (HdB) first defined the genus *Pseudodryomys* (type *P. ibericus*), it included the species that are now correctly separated into the genus *Simplomys* García-Paredes, 2009 (in García-Paredes et al. 2009). Moreover, *Peridyromys* was at the time known by its type species only, *P. murinus*, a small animal with a simple basic glirid dental pattern, which is clearly different from the much larger *Pseudodryomys ibericus* occurring in the same sites. With our present knowledge, separating the species *P. ibericus* from *P. murinus* on the generic level seems a case of over-splitting, so we believe it would be a good idea to synonymise these genera. Obviously, there is a need for a revision of this group, an action that is well beyond the scope of this paper.

The cheek teeth with a *Pseudodryomys*/*Peridyromys* morphology from Montalvos2 constitute a homogeneous sample (Fig. 3) and resemble those of *Pseudodryomys ibericus* and *Peridyromys darocensis*. However, they are intermediate in size between these species and have less frequently an extra ridge in the valley between the protoloph and anterior centroloph in the M1-2 (4/13) and between the mesolophid and the posterolophid (3/18) than in either of these species (García-Paredes 2006). Since our association contains specimens that are identical to ones from the type localities of these two species, we arbitrarily allocate the material from Montalvos2 to *Pseudodryomys* aff. *ibericus* De Bruijn, 1966.

The *Simplomys* group: In the *Simplomys* group the morphology of the M1-2 and the m1-2 consists of the four main ridges only. Other dental characteristics of the species included into the *Simplomys* group are the strong reduction of the P4/p4 and M3/m3.

The *Simplomys* group currently contains five species: *S. simplicidens* (type species), *S. robustus*, *S. julii*, *S. meulenorum* and *S. aljaphi*. These species have very similar dental morphologies and differ primarily in size and, in the

case of *S. meulenorum*, in the degree of reduction of the pre-molars and of the m3. The bulk of the material from Montalvos2 has the size of *S. simplicidens* (Fig. 3), but there are a few outliers, which are assigned to *S. julii* and *Simplomys* sp. (dental elements that differentiate between *S. meulenorum* and *S. robustus* are absent). The *S. simplicidens* teeth from localities assigned to the early/middle Aragonian (MN4) are somewhat narrower than the ones from the middle Miocene (García-Paredes 2006; García-Paredes et al. 2009).

The *Microdryomys* group: In the *Microdryomys* group, the M1-2 share the presence of a complete endoloph, a protoloph and metaloph that do not strongly converge lingually, while both centrolophs plus a species-specific number of extra

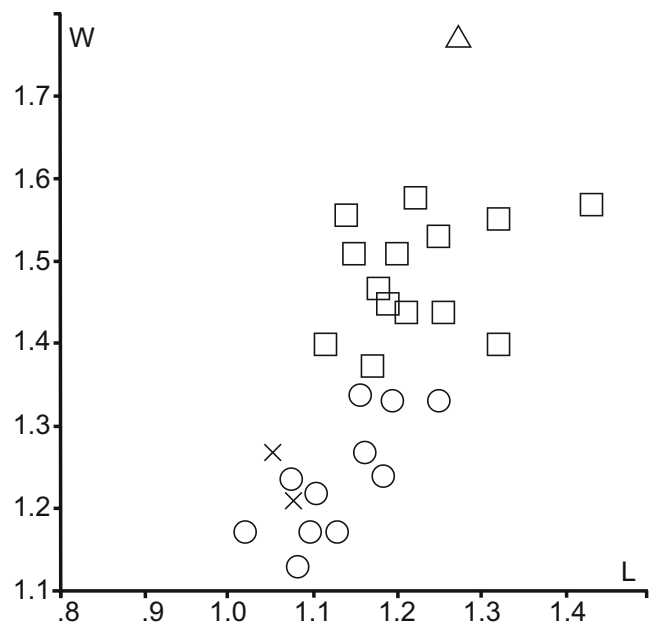


Fig. 3 Scatter plot of Gliridae (MNT2), M1-2. Open circle *Pseudodryomys ibericus*, X *Simplomys julii*, open triangle *Simplomys* sp., open square *Simplomys simplicidens*

ridges may be developed. The m1-2 of *Microdyromys* are not characteristic and may be easily confused with those of the smaller, more complex species of the *Peridyromys*/*Pseudodyromys* group (Daams and De Bruijn 1995).

In Montalvos2, the *Microdyromys* group is represented by a small species that may have an anterior extra ridge in the M1-2 and/or a posterior extra ridge in the m1-2. Four species with these dental characteristics have been formally named: *Microdyromys koenigswaldi*, *M. legidensis*, *M. monspeliensis* and *M. remmerti*. Among these, *M. remmerti* is the largest in comparison to the others (García-Paredes et al. 2010).

The type material of *M. koenigswaldi* is slightly larger than that of *M. legidensis*, and that of *M. legidensis* is slightly larger than that of *M. monspeliensis*. García-Paredes (2006), who studied the sequence of samples of the Gliridae from the type area of the Aragonian, suggested synonymising *M. legidensis* from the early Miocene with the somewhat larger *M. koenigswaldi* from the middle Miocene, whilst identifying the smaller specimens from the middle Miocene as *M. monspeliensis*. Van der Meulen et al. (2012) rehabilitate *M. legidensis* and include all in the lineage *M. legidensis-koenigswaldi*. The teeth of *Microdyromys legidensis* from Montalvos2 are identical to those of the type material of *M. legidensis* (= *M. koenigswaldi* sensu García-Paredes 2006).

The *Glirudinus* group: In the *Glirudinus* group, the occlusal surface of the cheek teeth is (almost) flat and bears a large number of very fine parallel ridges that make an angle with the longitudinal axis of the teeth. Records of the genus *Glirudinus* in Spain are known from late Oligocene until late Miocene, where species diversity is low and the number of specimens per locality is usually limited. Other than from Montalvos2, *G. gracilis* is known in Spain from the locality of Buñol (Province of Valencia; Daams 1976) and from the Vallès-Penedès Basin (Agustí et al. 1985; Casanovas-Vilar et al. 2010). Here, the material of this genus assigned to *Glirudinus gracilis* (Fig. 4) is also quite poor. Species

diversity in *Glirudinus* seems to have been largest in Anatolia and in Central Europe (Ünay et al. 2003).

The *Armantomys* (= *Quercomys*) group: Finally, in the *Armantomys* (= *Quercomys* sensu Daams 1991) group the dental pattern of the M1-2 and m1-2 consists of the four main ridges. Other than in *Simplomys*, these teeth show a tendency to develop a detached metaloph in the M1-2 and are hypsodont. In the Montalvos2 association, the *Armantomys* (= *Quercomys*) group is represented by very few and poorly preserved teeth. The genera *Armantomys* and *Praearmantomys* are unique within the family Gliridae in having cheek teeth with ridges that are high relative to the crown basis and in being geographically restricted to the Iberian peninsula. Two evolutionary lineages have been reconstructed within *Armantomys* (Daams 1991). The material from Montalvos2 represents one of the larger species, *Armantomys aragonensis*.

Family Eomyidae Winge, 1887

In Montalvos2, the Eomyidae are represented by a few teeth only, here assigned to *Ligerimys ellipticus*. These teeth are morphologically similar to those of *L. ellipticus* from Buñol (typelocality). Some of the M1-2, M3 and m3 from Montalvos2 are slightly wider than the molars from the typelocality, but they fall within the size ranges of *L. ellipticus* from Vargas 1A, Olmo Rodondo 8 and San Roque 3 (Álvarez-Sierra 1987).

Family Sciuridae Fischer, 1817

The Sciuridae are represented in Montalvos2 by two species of the subfamily Sciurinae Fischer de Waldheim, 1817 and one species of the subfamily Pteromyinae Brandt, 1855.

The *Heteroxerus rubricati* teeth correspond in size with teeth of *H. rubricati* from several Spanish localities (Cuenca Bescós 1988).

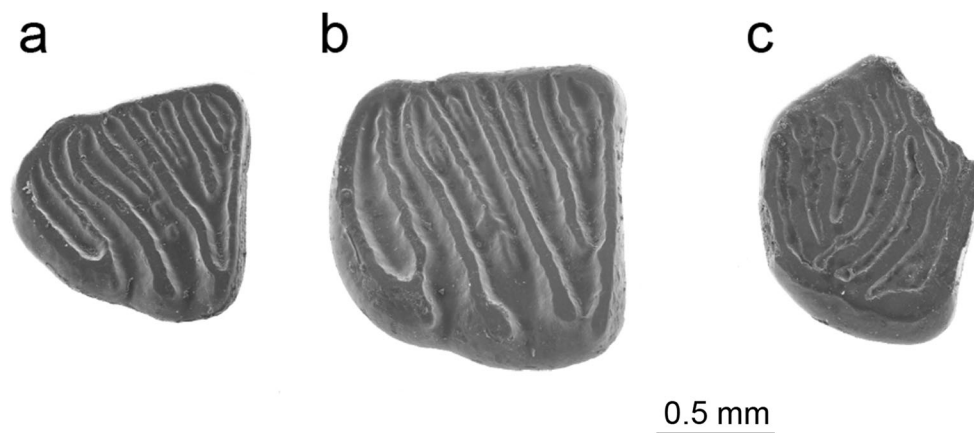


Fig. 4 *Glirudinus gracilis*. **a** M3 dex (MNT2 529), **b** M1-2 sin (MNT2 525 **c** m3 dex (MNT2 524). Scale bar: 0.5 mm. Underlined letter indicates inverse specimen

One xerine tooth, an m2 (Fig. 5a), is identified as *Heteroxerus* cf. *grivensis*. The tooth clearly exceeds the size of the *H. rubricati* teeth. In terms of size and morphology, it compares well with the m2 of *H. grivensis* from several Spanish localities (Cuenca Bescós 1988) and it is similar in morphology but smaller than m2 of *Atlantoxerus blacki* (De Bruijn 1967) from Spain (Peláez-Campomanes 2001). The presence of a species close to *H. grivensis* in the Montalvos2 fauna is unexpected because *H. grivensis* is only known from younger faunas (Van der Meulen et al. 2012). Van der Meulen et al. (2012) indicate two new but undescribed *Heteroxerus* species in their Figs. 2 and 6. Apparently, the development of *Heteroxerus* in early and middle Miocene times is more complex than has been thought earlier.

Albanensia sansaniensis is represented by an m3 (Fig. 5b). The tooth appears rather short, as compared with m3s from the type locality Sansan (France; Ginsburg and Mein 2012).

Order Lagomorpha Brandt, 1855

Family Ochotonidae Thomas, 1897

The ontogenetic stage of individual specimens plays a role in determining the presence or absence of particular morphological features. Chronospecies subdivisions in various ochotonid lineages are based on shifts in the occurrence frequency of particular tooth characteristics within an assemblage through time (López-Martínez 1984, 1988; Hordijk 2010).

Lagopsis penai

In the P2 the paraflexus and mesoflexus are narrow and oblique, with their apices oriented in postero-labial direction. The mesoflexus is mostly straight to lightly curved. The lagicone is well developed, usually intermediate in length and size between the smaller postlobus and larger hypercone.

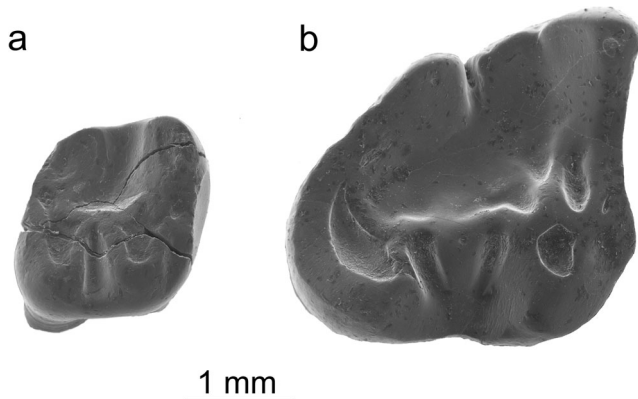


Fig. 5 *Heteroxerus* cf. *grivensis*. **a** m2 sin (MNT2 625), *Albanensia* cf. *sansaniensis*, **b** m3 dex (MNT2 623). Scale bar: 1 mm. Underlined letter indicates inverse specimen

A mesial hyperloph is absent. The lingual side of the hypercone is smooth in most specimens, but several show a weak to distinct indentation or incipient hypoflexus.

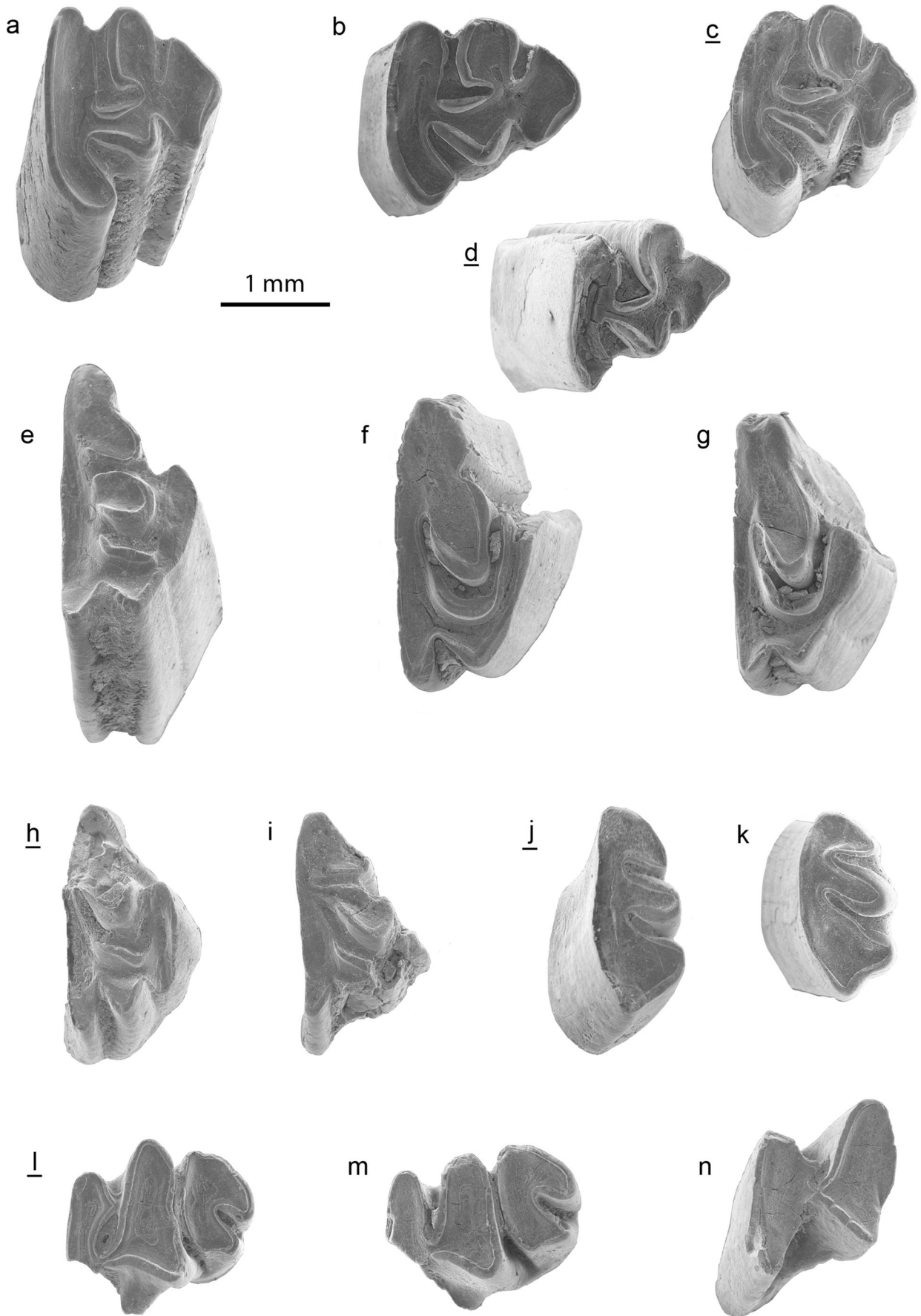
In general, the P3 has a trapezoidal-like shape in occlusal view, in which the mesial hyperloph lies almost parallel to the distal hyperloph and is usually thickest in its central part. The mesoloph length relative to the tooth width depends on the stage of wear. The postlobus usually extends widely on the labial side. The tip of the precone generally reaches to the position of the mesoflexus. The paraflexus has a distinct J-shape, which is narrowest at the anterior side of the lagicone. The lagicone is large and oval and is oriented in an antero-lingual direction. In ontogenetically younger specimens, a straight mesoflexus is present, which is distinctly more shallow or absent in more deeply worn specimens. A distinct shallow hypoflexus is visible in all specimens that have this part preserved.

In the p3, the anteroconid is generally triangular, wide and well developed. In a few specimens, however, a more simple and smaller diamond-shaped anteroconid is observed. The anteroconid is larger than the metaconid in all but two adult specimens. Proto- and paraflexid are always present, but may vary in depth. The metaflexid is distinctly developed toward the midsection of the occlusal surface of the tooth in all specimens, but its shape is variable. The majority of specimens (27) show a distinct anterior extension, while the outline of the rest (12) is more symmetrical. The shape of the mesial side of the anteroconid is variable. An anteroflexid is absent or incipient in the majority of specimens, while in a few, a more distinctly developed undulation is visible. Two specimens have crown cement preserved in the anteroflexid. The metaconid is relatively small and has a slightly oval to somewhat rounded rectangular shape. Its width is usually larger than its length, and this conid represents the most lingual extension of the tooth. The posterior lobe, formed by the entoconid and hypoconid has a more or equal thickness and is slightly curved labially, placing the hypoconid in a more anterior position.

The morphology of the D2 strongly resembles that of the P3 in having a very similarly shaped lagicone, postlobus and paraflexus. The paraflexus is deep and strongly curved, nearly reaching the posterior wall of the tooth. The mesoflexus is variably present and is usually straight. The mesial hypercone is distinctly more developed than the distal hypercone.

The d3s are slightly more robust and wider than the specimens provisionally assigned to *P. lopezmartinezae*.

All of the d4 specimens are provisionally assigned to *L. penai* on the basis of size, which fits that of the d3 assigned to this species. The tooth consists of two lobes that are isolated during most stages of wear but which are connecting in strongly worn specimens. The talonid lobe is wider than the trigonid lobe in relatively worn specimens. The general shape of the occlusal surface of the trigonid and talonid lobes strongly resembles that of the p4.



◀ **Fig. 6** *Lagopsis penai*, **a** p3 dex (MNT2 817B), **b** p3 dex (MNT2 812A), **c** p3 sin (MNT2 803A), **d** p3 sin (MNT2 804A), **e** P3 dex (MNT2 847B), **f** P3 dex (MNT2 851B), **g** P3 dex (MNT2 856A), **h** D2 sin (MNT2 932A), **i** D2 dex (MNT2 936A), **j** P2 sin (MNT2 892B), **k** P2 dex (MNT2 896B), **l** d3 sin (MNT2 922A), **m** d3 dex (MNT2 927A), **n** d4 dex (MNT2 928B). Scale bar: 1 mm. Underlined letter Inverse specimen

Prolagus lopezmartinezae

In the P2, the mesoflexus and paraflexus are straight and oriented in a posterior direction (Fig. 7). One slightly worn specimen shows an additional enamel loop and protrusions,

which would disappear with wear. The hypercone forms the largest cone of the tooth. The mesial hyperloph varies slightly in thickness and length, but is generally short. It does not cover the paraflexus in any of the specimens, but does represent the most anterior part of the tooth. The width of the distal hyperloph decreases from lingual to labial, which is primarily due to the mesoflexus almost reaching the posterior wall. A hypoflexus is absent (Fig. 7).

In the P3 specimens, the postlobus is well developed in specimens where it has been preserved, but represents a smaller portion of the width of the tooth in comparison to the width covered by the mesial hyperloph, which extends over 50 % of

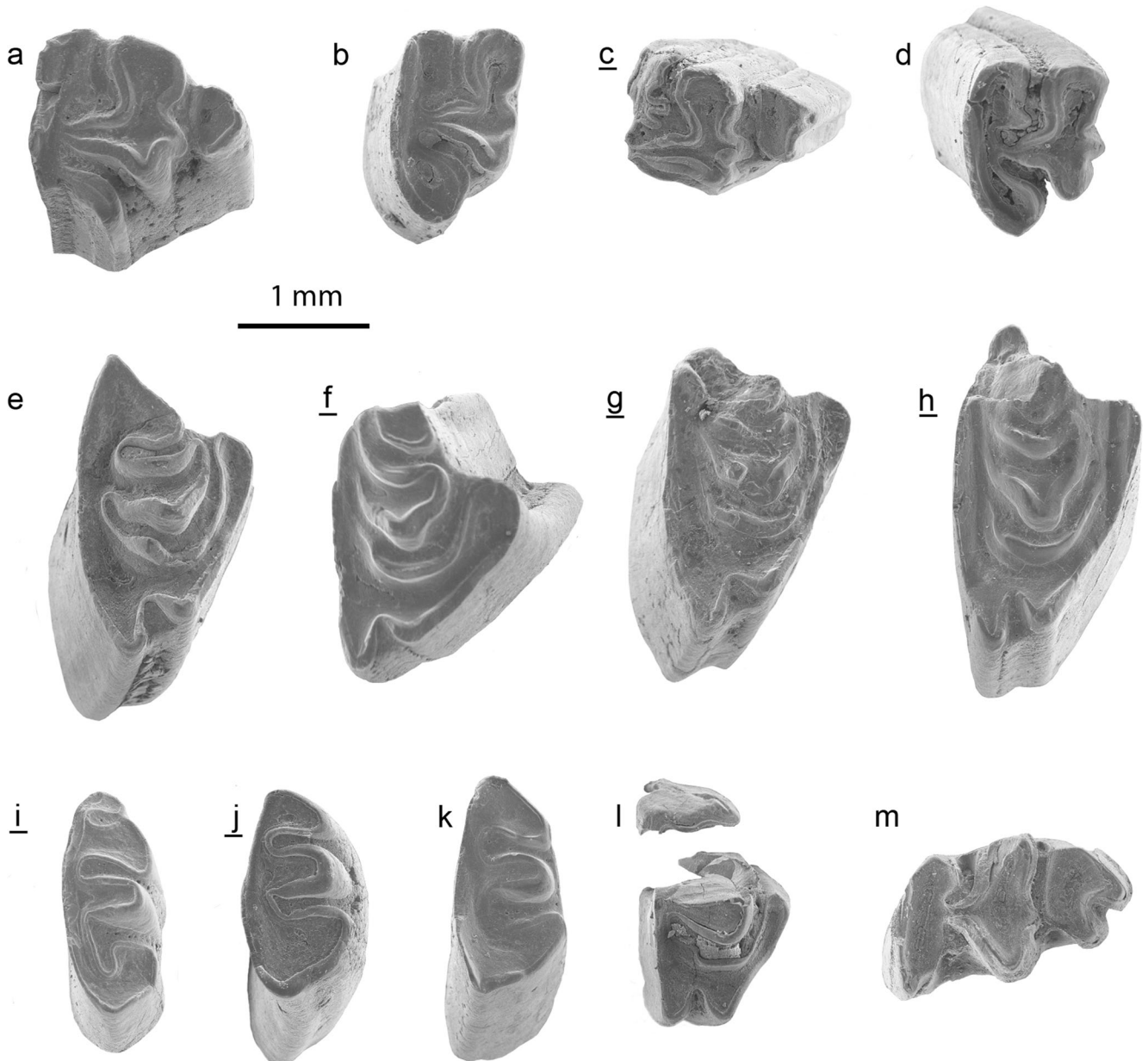


Fig. 7 *Prolagus lopezmartinezae*. **a** p3 dex (MNT2 837A), **b** p3 dex (MNT2 833A), **c** p3 sin (MNT2 826B), **d** p3 dex (MNT2 832A), **e** P3 dex (MNT2 878A), **f** P3 sin (MNT2 864B), **g** P3 sin (MNT2 862B), **h** P3

sin (MNT2 861B), **i** P2 sin (MNT2 913A), **j** P2 sin (MNT2 914A), **k** P2 dex (MNT2 917A), **l** D2 dex (MNT2 940A), **m** d3 dex (MNT2 921B). Scale bar: 1 mm. Underlined letter indicates inverse specimen

the tooth width. A precone is present in all but one specimen where this feature can be observed. The mesoflexus is deep and can vary in shape from being curved in various degrees to completely straight. In the latter case, the shape of the lagicone is somewhat triangular, and a lagiloph is lacking. In specimens with a curved mesoflexus, the lagicone usually has a short, but discernable lagiloph that does not reach the outline of the tooth. One incomplete specimen has a relatively long lagiloph, and the lagicone is compressed lingually, resulting in a lingual bulge. A shallow cement-filled hypoflexus is present in all specimens in which this part of the tooth has been preserved. The mesial hypercone tends to be less developed and placed more labially than the distal hypercone.

The P4-M2 are very fragmentary and poorly preserved. One fragment showing a hypoflexus that spans roughly one half to two thirds of the tooth width and has a small curved parafofsette which resembles the morphology of the M1 known from San Marcos (Hordijk 2010). A very small fragment containing only a parafofsette that is somewhat larger and placed more lingually than that of the surmised M1 is tentatively identified as a worn P4 fragment.

The p3 has a triangular outline of the occlusal surface. The anteroconid is somewhat sub-round to more or less ellipsoid in two specimens while being slightly anteriorly flattened on two sides, vaguely resembling a triangle. A third specimen shows a more clear triangular shape. The anteroconid is isolated in all specimens in which this feature can be verified. One of the anteroconids shows a weak anteroflexid along the crown. The protoistmid is present in all specimens, while a metaistmid is absent. A metaflexid is well developed and usually follows a path parallel to the width of the tooth, curving sharply toward the posterior side at the centre of the tooth. Three specimens also show a very shallow anterior extension. The entoconid shows one or more small ‘crochet’-like structures at, or close to, the curve of the metaflexid in half the number of the specimens. The protoconid and metaconid are broadly connected. A shallow centroflexid is present in all specimens, ranging from a very shallow indentation between the protoconid and metaconid to a distinct narrow short inflexion that is slightly narrowing the protoconid–metaconid connection. The protoconid is smaller than the metaconid; it is truly very small or incipient and clearly visible in all but two specimens. The entoconid has a relatively rectangular shape, while the hypoconid is more rounded and drop-like. The hypoflexid is deep, ending close to the posterior wall of the tooth, similar to the metaflexid.

The damaged D2 has a morphology which strongly resembles that of the P3 in terms of shape of the lagicone, metaflexus and parafofsette.

The three d3 have been provisionally assigned to *P. lopezmartinezae* because they are smaller than the specimens provisionally assigned to *L. penai*. The shape of these teeth is more slender and narrower than those assigned to *L. penai*. Unfortunately, two of the specimens show considerable damage.

The morphology and size of the material of *P. lopezmartinezae* strongly resembles that from the type locality (San Marcos) of the species with which it has been directly compared. The combination of the primitive and derived morphologies of P3, p3 and P2 as observed in *P. lopezmartinezae* represents an intermediate stage in the evolutionary lineage of *P. vasconiensis* Viret, 1930–*P. lopezmartinezae*–*P. tobiensis* López-Martínez, 1977 (Hordijk 2010).

Order Eulipotyphla Waddell, Okada and Hasegawa, 1999

The Eulipotyphla (formerly Insectivora) are represented by five species, belonging to four families.

Family Erinaceidae Fisher, 1814

According to Van den Hoek Ostende and Doukas (2003), two species of *Galerix* were identified in the Calatayud-Montalbán Basin in biozones B-Da. The small *Galerix symeonidisi* would have gradually been replaced by the middle-sized *G. exilis*. This assumption is based on the gradual decrease of P3 bearing a hypocone and the size variation that was too large for a single species. However, since the size ranges of the two species overlap, it is difficult to assign individual elements to the one or the other. The same problem arises in the small *Galerix* assemblage from Montalvos2. Here, we tentatively assign all elements to *G. symeonidisi*. The only P3 present bears a hypocone, which is indicative of *G. symeonidisi*. Furthermore, the elements from Montalvos2 fall within the lower part of the size ranges found for this species in the Calatayud-Montalbán Basin area. Other *symeonidisi*-like characters are the well-developed trigonid of the p4 and the absence of a protocone–metaconule connection in the M1 and M2. These characters are variable, however, and can only be used in large assemblages. Therefore, we can not entirely exclude the possibility that *G. exilis* was also present in Montalvos2.

Family Talpidae Fischer, 1817

The mole species cf. *Desmanella* sp., a representative of the Uropsilinae, has a symmetrical P4, which features a large paracone and a well-developed, conical protocone. This well-developed conical protocone of the P4 identifies this small talpid as an Uropsilinae. Van den Hoek Ostende (2001) showed that this subfamily was quite diverse in Europe during late Oligocene/early Miocene times, represented by such genera as *Asthenoscaptor*, *Desmanella* and *Mygatalpa*. Without the characteristic upper molars, the genus cannot be unequivocally determined. We tentatively assign the Montalvos2 material to *Desmanella*, which to date is the only uropsiline found in Iberia. The only early Miocene record of the genus is *D. fejfari* from Rubielos de Mora (Gibert 1975) and from Alto de Ballester (Van den Hoek Ostende et al. submitted). The

premolars are comparable in size to the material from these two MN3 localities, but the m3 are about 10 % shorter.

The second talpid species from Montalvos2 is *Desmanodon* sp. The upper molars of this species feature a relatively well-developed hypocone, particularly on the M2 and M3. These characters are in agreement with *Desmanodon* from the Daroca area (Van den Hoek Ostende 1997).

The presence of two talpid species in Montalvos2 is remarkable. In localities belonging to zones B and C in the Calatayud-Montalbán Basin only *Desmanodon* has been found.

Family Heterosoricidae Viret and Zapfe, 1951

The taxonomy of the Heterosoricidae is largely based on mandible characters (Engesser 1975; Ziegler 2009). However, there are also a number of useful characters to distinguish the various genera on the basis of dental characteristics (Engesser 1980; Ziegler 1998). One of the differences between the Miocene genera *Dinosorex* and *Heterosorex* is the weaker development of the lingual cusps of the upper molars in the latter. Since these cusps are weakly developed in Montalvos2 (the hypocone is not even discernible as a separate cusp), this heterosoricid is referable to *Heterosorex*. This is corroborated by the outline of the P4, which has a triangular shape and is not square as is usual in *Dinosorex*. The Montalvos2 material agrees in size and morphology well with *Heterosorex neumayrianus* from various German MN 3/ MN 4 localities (Doben-Florin 1964; Ziegler and Fahlbusch 1986; Ziegler 1989; Kliemann et al. 2014b).

Family Soricidae Fischer, 1814

The unidentifiable soricid (Soricid gen. et sp. indet.) has lower molars with a well-developed entoconid and which are entocristed, barring identification as *Paenelimnoecus*. The talonid of the only m3 is strongly reduced. The damaged M2 is characterised by a moderate posterior emargination and a ridge-shaped hypocone.

Order Didelphimorpha Gill, 1872

Family Didelphidae Gray, 1821

Subfamily Herpetotheriinae Trouessart, 1879

Marsupials are represented in Montalvos2 by a worn labial fragment of an upper molar only.

It cannot be further identified to the genus or species level and is assigned to *Amphiperatherium*, the only genus present at this time (Furió et al. 2012). The small marsupial *Amphiperatherium* is quite common in contemporary faunas from southern Germany (Ziegler and Fahlbusch 1986; Kliemann et al. 2014a). Marsupials have also been found in faunas from the Calatayud-

Montalbán Basin (L. van den Hoek Ostende, personal observation), but unfortunately, the material was lost.

Biostratigraphy

The presence of *Democricetodon decipiens* places Montalvos2 in local zone Ca, the *Megacricetodon primitivus*–*Democricetodon decipiens* zone, with an age of 16.6–16.2 Ma, as defined by Van der Meulen et al. (2012) in the neighbouring Calatayud-Montalbán Basin (Fig. 8). According to these authors, zone Ca (together with zones B and Cb) is correlated to the European MN4 (Fig. 8). In the Calatayud-Montalbán Basin, zone Ca is represented by three sites: Artesilla (16.49 Ma), San Roque 3 (16.33 Ma) and Olmo Redondo 4A (16.30 Ma). We regard the presence of *Ligerimys ellipticus* in Montalvos2 as an additional constraint, implying an age younger than that of Artesilla (16.49 Ma), which still contains *L. florancei*. This inference is further confirmed by the absence in Montalvos2 of *Praearmantomys crusafonti*, one of the most abundant forms (21 %) in the rodent fauna of Artesilla (Van der Meulen and Daams 1992).

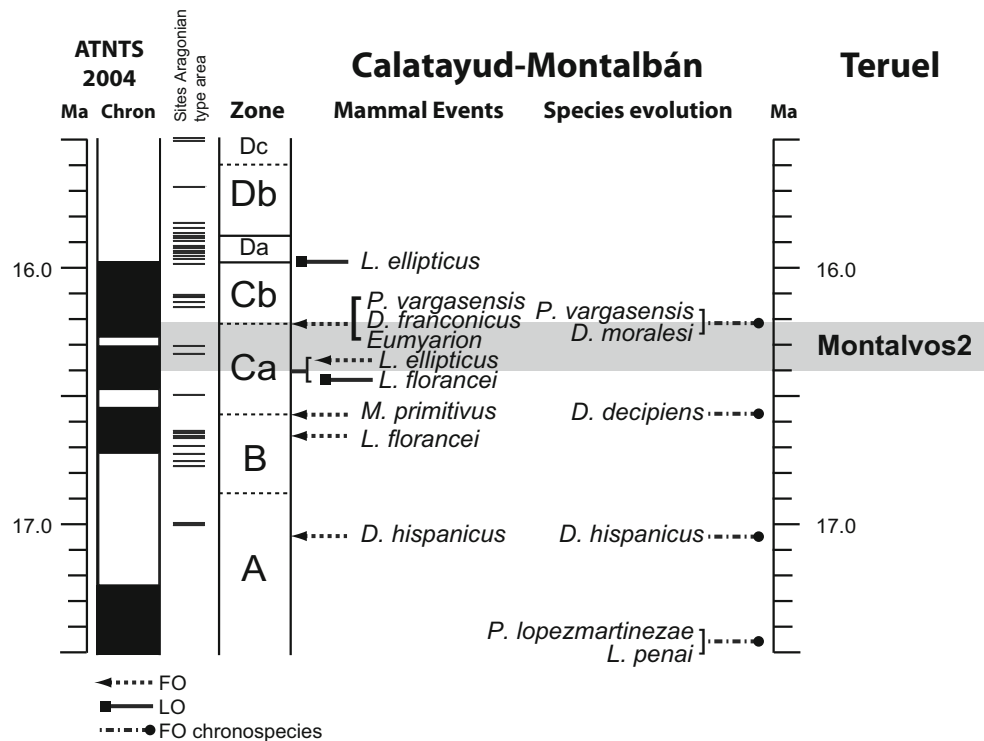
Furthermore, we note that San Roque 3 and Olmo Redondo 4A lack *Eumyarion*, a form present in Montalvos2 and in the next younger locality in the Calatayud-Montalbán sequence Vargas 4A, at the base of next zone Cb (16.15 Ma). Another similarity between Montalvos2 and Vargas 4A is the presence of Petauristinae, although these are very rare. Based on these similarities and differences, a placement of Montalvos2 between Olmo Redondo 4A and Vargas 4A seems probable (thus between 16.30 Ma and 16.15 Ma).

In terms of the most abundant family, the Gliridae, a placement of Montalvos2 in MN4 is not inconsistent with the stratigraphical ranges of the glirid species present. Although these are long and usually cover several MN-zones, the ages of three of seven type-localities of the species recognised in the assemblage from Montalvos2 correlate to MN4, whereas one correlates to MN2, two to MN3 and one to MN5. The concurrent range zone of *Simplomys simplicidens*, *S. robustus* and *S. julii* on the Iberian peninsula covers the local zones A, B and the lower part of C, which are correlated with the upper part of MN3 plus the lower part of MN4 (García-Paredes et al. 2009).

The ranges of the ochotonid species provide only limited biostratigraphical evidence for Montalvos2. Both *Lagopsis penai* (zone A–Dd) and *Prolagus lopezmartinezae* (zone A–Cb certain, Da–G1 lack of data) first appear in the Late Ramblian and continue into the middle Aragonian (MN3–5) (Hordijk 2010). Nevertheless, the available ochotonid material fits well with a correlation to MN4.

The *Lagopsis penai* from Montalvos2 is indistinguishable from *L. penai* from the nearby Calatayud-Montalbán Basin. *Lagopsis penai* is known to have a fairly stable size range through time, as well as a relatively high variability range in both size and

Fig. 8 The biostratigraphic position of Montalvos2. Indicated are a selection of key events of rodents and lagomorphs in the Calatayud-Montalbán Basin and the FO of several chronospecies in the time slice of interest. The correlation of Aragonian mammal sites to the Astronomically Tuned Neogenic Time Scale of Lourens et al. (2005) (ATNTS 2004) is after Van der Meulen et al. (2012). FO: First occurrence; LO: Last occurrence



morphology within assemblages (Hordijk 2010). Specific primitive or derived morphological features occur in assemblages throughout the *Lagopsis* lineage during the Miocene and thus do not provide a strong argument for precise biostratigraphical correlations. This is illustrated by the occurrence of two p3 with a cement-filled anteroflexid in the Montalvos2 assemblage, a feature that is associated with *Lagopsis verus* (Hensel 1856) when dominantly present in an assemblage (FO in zone Dd; Hordijk and Van der Meulen 2010a).

The absence of *Prolagus vargasensis* Hordijk and Van der Meulen, 2010 (Hordijk and Van der Meulen 2010b) in Montalvos2, known in the Aragonian type area from the base of Cb and consistently present in mammal assemblages of this zone (Hordijk 2010), suggests the likelihood that the fauna from Montalvos2 is older than zone Cb.

Independent of the ranges of the ochotonid species, the relative high abundance of *Lagopsis penai* in the Montalvos2 assemblage is very similar to that of mammal assemblages in zone B known from the nearby Calatayud-Montalbán Basin (Hordijk 2010; Van der Meulen et al. 2012), suggesting a potentially similar age. However, this feature strongly depends on the local environment. The relatively close proximity of the Calatayud-Montalbán Basin and Teruel Basin does not guarantee similar environments and mammal abundance patterns at the scale of biozones.

The insectivore *Desmanella* has been found in biozone A localities from the Rubielos de Mora basin (Van den Hoek Ostende et al. submitted). *Desmanodon* is a quite common element in the late early/earliest middle Miocene faunas of

Spain. In terms of size and morphology, the Montalvos2 *Desmanodon* agrees well with the finds from the Calatayud-Montalbán Basin. *Heterosorex* is found in various zone C localities in the Aragonian of the Calatayud-Montalbán Basin (Van der Meulen et al. 2012), and fragments referable to *Heterosorex* are also known from the Ramblan (Ramblar 1; Van den Hoek Ostende 2003).

Some of the faunal elements of the Montalvos2 assemblage point to a correlation with biozone B (e.g. lagomorph abundance, petauristines, some glirids); however, the presence of these species could also be an indication of differences in environmental conditions. That such differences played a role is also evident from the presence of some faunal elements [e.g. *Heterosorex* (cf.) *grivensis*] that occur much later in the Calatayud-Montalbán Basin, although these latter species are usually present in low abundances which could have limited the chance of being found.

Here, we consider the presence of the cricetines *Democricetodon decipiens*, *Megacricetodon primitivus* and *Eumyarion*, combined with the presence of *Ligerimys ellipticus*, as the key stratigraphical information and constrict the biostratigraphical position of Montalvos2 to biozone Ca. Thus, the best estimate of the age of Montalvos2 lies between 16.4 and 16.2 Ma (Fig. 8).

It is also interesting to compare the fauna of Montalvos2 to that of Buñol in the Province of Valencia (Daams 1976; Robles et al. 1991; Hoek et al. 2005). Both faunas are time-equivalent and can be correlated to zone Ca, as defined in the Calatayud-Montalbán Basin. Assuming an isochronous presence of *Ligerimys ellipticus*, the age of Buñol can be estimated to lie

between approximately 16.4 Ma (entry between Artesilla and San Roque 3), and 15.94 (Cb-D boundary). A specific parallel with Montalvos2 constitutes the presence of *Melissiodon*.

Palaeoecology and palaeoclimate

The relative abundances of the various small mammal species in Montalvos2 (Fig. 9; Table 2) show that rodents, despite comprising 15 species, are only slightly more abundant than the lagomorphs, represented by only two taxa (53 vs. 43 %, respectively). Two species are quite dominant, *Lagopsis penai* by approximately 32 % and *Megacricetodon primitivus* by approximately 22 %, followed by *Prolagus lopezmartinez* (approx. 11 %). The relative abundance of the small mammals in Montalvos2 is very similar to the abundance pattern in biozone B in the Calatayud-Montalbán Basin and differs from the abundances in biozones Ca and Cb.

The relative abundance of ochotonids in the Calatayud-Montalbán Basin is highly variable in the time interval between zone B and H (MN4–9), comprising on average 19 % of the small mammal primary consumers in fossil assemblages (Hordijk 2010). Despite the overall variability, the relative abundances observed in zones B to Cb are fairly consistent within these zones, where those of zone B are clearly different from those of Ca and Cb. The average abundance of ochotonids in zone B is particularly high relative to that of the rodents, ranging between 22 and 57 % (average approx. 44 %), while there is a distinct decrease in ochotonid abundance going into zone Ca, ranging between 13 and 18 % (average approx. 16 %), as well as into zone Cb, ranging between 0 and 13 % (average approx. 7 %) (Hordijk 2010). The markedly high abundance of the ochotonids in the Montalvos2 assemblage, and of *Lagopsis penai* in particular, suggests similar environmental conditions as in zone B assemblages of the Calatayud-Montalbán Basin.

Despite the known environmental flexibility of *Lagopsis penai*, which was fairly widespread in Western Europe and has even been found in the context of a subtropical and fairly humid environment with a mix of open to more closely vegetated habitats (Angelone 2009; Tütken and Vennemann 2009), this species is usually associated with relatively warm and drier conditions (Mein 1984; López-Martínez et al. 1987; López-Martínez 1989, 2001). The high abundance of *Lagopsis penai* in particular and of the ochotonids in general suggest the availability of a relatively open and (semi)-arid landscape in the vicinity of the locality of Montalvos2.

The Eulipotyphla constitute 3.4 % of the smaller mammal assemblage from Montalvos2. This is comparable with the relative abundance of the insectivores in biozones A, B and C in the Calatayud-Montalbán Basin, where they usually make up less than 5 % of the total assemblage. Only in the top of zone Cb (Vargas 2A) is the insectivore percentage around 8 %.

A reconstruction of the diet and biotope requirements of the various Gliridae is necessarily based on tooth morphology; therefore, we use the ridge index of De Bruijn (1998).

The percentages of glirid genera from five MN4 assemblages from Greece (Aliveri, Karydia), Austria (Oberdorf) and Spain (Villafeliche 2A, Montalvos2) and the distribution of the classes of the number of ridges on the M1-2 and m1-2 are given in Table 3. The choice of the localities used for comparison is largely the result of availability in the Utrecht University collection. To ensure a degree of uniformity within this comparison, endemic genera have been omitted (*Armantomys* and *Seorsumuscardinus*; De Bruijn 1998; García-Paredes 2006). We realise that results based on such limited material from insufficiently calibrated localities can, at best, only roughly suggest whether this approach has potential. Moreover, the dental pattern of *Peridyromys* and *Pseudodryomys* is basically the same, and here we combine the count of ridges for these two genera.

The differences in taxon composition, as well as in the distribution of the ridge-classes (Table 3) between the glirid associations analysed suggest differences in habitat. Remarkably, the generally common genus *Microdyromys* is absent or rare in the Greek localities (Karydia and Aliveri respectively), and *Peridyromys* is absent in the association from Montalvos2, while the Spanish associations (Villafeliche 2A and Montalvos2) are very similar otherwise. We believe that these differences may well have a different origin. The absence of *Microdyromys* in Karydia could be due to unfavourable circumstances, while the absence of *Peridyromys* in Montalvos2 may be either due to the unfavourable circumstances or to over-splitting on the generic level.

The data on the classes of ridge numbers suggest that within the range of ridge numbers chosen for study, there is a shift towards species with fewer ridges from SE to SW Europe. Van der Meulen and De Bruijn (1982) and Daams and Van der Meulen (1984) concluded that a vegetarian diet constitutes a smaller portion of the total diet of species with a limited number of ridges compared to those with many ridges. Moreover, these authors concluded that *Microdyromys* has a preference for a warm climate (and wet), whereas *Peridyromys* prefers a cool climate (and dry). Following these suggestions, it seems that the conditions may have been wetter in SE Europe than in SW Europe in the early part of MN4. The glirids from Montalvos2 thus suggest a semi-arid warm biotope.

The highly aberrant shape of the weak and slender mandible of *Melissiodon* was already noted by Schaub (1920) when he defined the genus. Subsequent workers in the field have commented on its unusual long tubular diastema with weak lower incisors that end below the m2 in combination with the complex fragile high-crested cheek teeth. In this context, it is of interest that the extant endemic shrew rats from Sulawesi and the Philippines which feed on soft-bodied invertebrates have mandibles that are very similar to those of

Fig. 9 The abundance distribution of the main small mammal orders present in Montalvos2 (Teruel Basin) compared to small mammal faunas of the Calatayud-Montalbán Basin

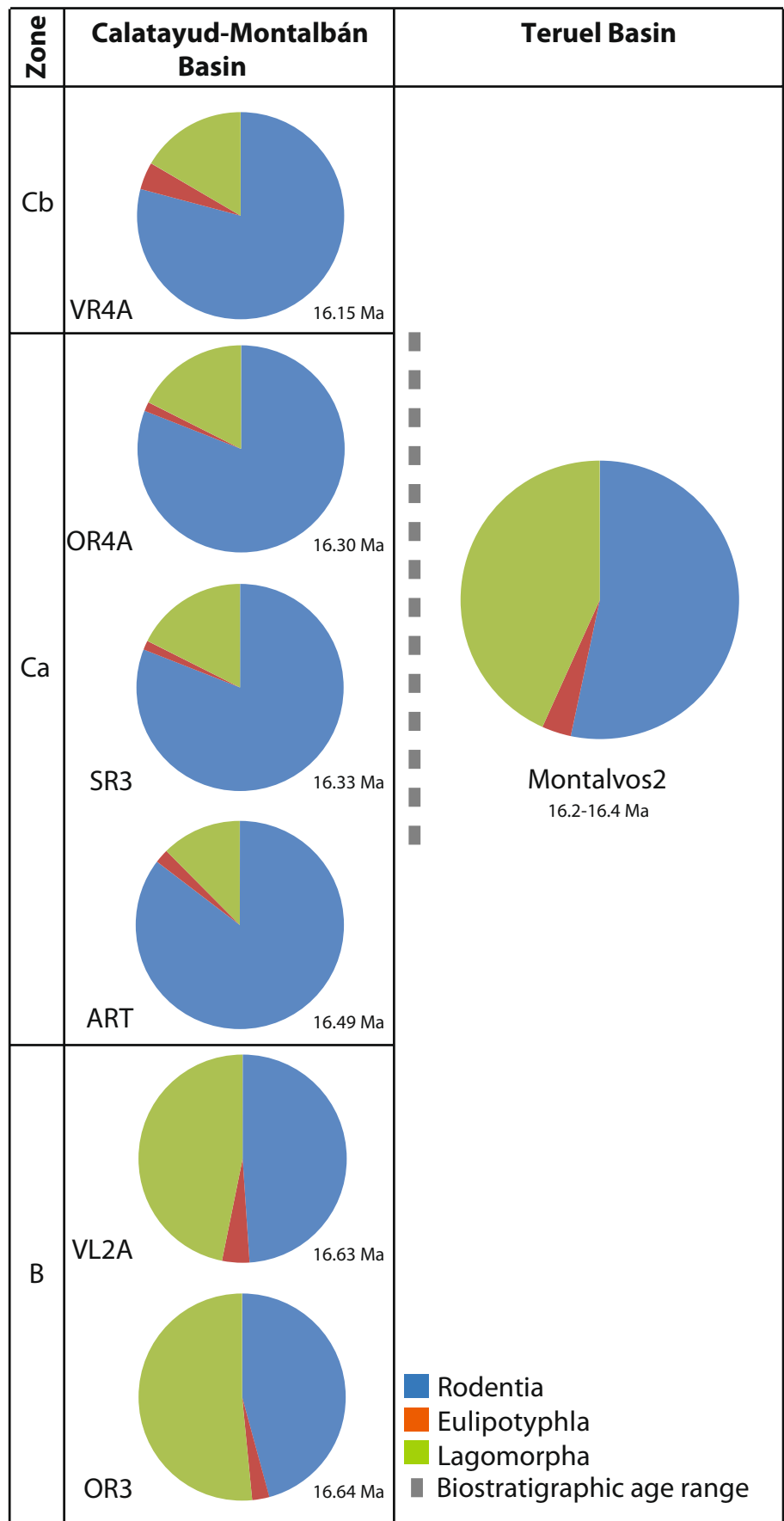


Table 2 Number of specimens and percentage of each species and of each of the orders Rodentia, Eulipotyphla and Lagomorpha in the small mammal assemblage of Montalvos2

Small mammal assemblage at Montalvos2	All elements	m1m2/M1M2 or 2 (P3 + p3)	
	<i>N</i>	<i>N</i>	%
Total rodents	490	348	53.3
<i>Melissiodon dominans</i> (Dehm, 1950)	18	13	2.0
<i>Democricetodon decipiens</i> (Freudenthal and Daams, 1988)	48	40	6.1
<i>Megacricetodon primitivus</i> (Freudenthal, 1963)	154	143	21.9
<i>Eumyarion weinfurteri</i> (Schaub and Zapfe, 1953)	33	27	4.1
<i>Pseudodryomys</i> aff. <i>ibericus</i> De Bruijn, 1966	58	30	4.6
<i>Simplomys simplicidens</i> Garcia-Paredes, 2009	88	45	6.9
<i>Simplomys</i> sp.	1	1	0.2
<i>Simplomys julii</i> Daams, 1989	2	2	0.3
<i>Armantomys aragonensis</i> De Bruijn, 1966	14	0.5	0.1
<i>Microdyromys legidensis</i> Daams, 1981	19	16	2.5
<i>Glirudinus gracilis</i> Mayr, 1979	7	2	0.3
<i>Ligerimys ellipticus</i> Daams, 1976	26	20	3.1
<i>Heteroxerus rubricati</i> Crusafont, 1955	20	7	1.1
<i>Heteroxerus</i> cf. <i>grivensis</i> (Major, 1893)	1	1	0.2
<i>Albanensia</i> cf. <i>sansaniensis</i> (Lartet, 1851)	1	0.5	0.1
Total lagomorphs	247	282	43.2
<i>Lagopsis penai</i> (Royo, 1928)	210	208	31.9
<i>Prolagus lopezmartinezae</i> Hordijk and Van der Meulen, 2010	37	74	11.3
Total insectivores	37	22.5	3.4
<i>Galerix symeonidisi</i> Doukas, 1986	14	7	1.1
cf. <i>Desmanella</i> sp.	4	0.5	0.1
<i>Desmanodon</i> sp.	9	7	1.1
<i>Heterosorex</i> cf. <i>neumayrianus</i> Schlosser, 1887	7	4	0.6
Soricid gen. et sp. indet.	5	4	0.6
Total marsupials	1	0.5	0.1
<i>Amphiperatherium</i> sp.	1	0.5	0.1
Total	775	653	

Melissiodon (Musser 1990; Esselstyn et al. 2012). The combination of a long and weak mandible and high-crested cheek teeth in *Melissiodon* suggests that these murids were also feeding on insects (beetles?), thus making the members of this taxon, ecologically speaking, an insectivore. The continuous availability of this very specific food source may well be the reason that these murids survived the decline of the family in Europe during the early Miocene. Since *Melissiodon* is invariably rare in lacustrine deposits and more common in fissure infills, we interpret *Melissiodon* species to be inhabitants of dry limestone plateaus.

The overall percentage of eulipotyphlan insectivores can be used as a crude indicator of humidity (Van den Hoek Ostende 2001) as the percentages of insectivores present in Montalvos2 are not much different from those in the Calatayud-Montalbán Basin, suggesting similar humidity conditions. However, the presence of a second talpid suggests

that the environment in Montalvos2 may have been somewhat more humid than in contemporaneous localities in the Calatayud-Montalbán Basin.

To estimate mean annual precipitation (MAP), the method of Van Dam (2006) is used, where $MAP = 0.179 + 14.134 PI + 18.066 PA$ ($R^2 = 0.69$). The percentages of insectivore species (PI) and arboreal species (PA) are based on the fauna of Rodentia, Eulipotyphla and Lagomorpha (the marsupial *Amphiperatherium* was not included in the calculations), and thus the total number of species considered (*N*) amounts to 22. The large majority of the species recorded are considered to be ground-dwelling. The glirid *Glirudinus* and the flying squirrel *Albanensia*, however, can be considered to have had an arboreal life style (NA=2). *Melissiodon* and all Eulipotyphla are assumed to have been insectivorous (NI=6). PA and PI have respective values of 9.1 and 27.3 %, and the resulting best estimate for MAP is 550 mm/year. The 95 % prediction interval, which is

Table 3 Number of gliroid genera from five MN4 assemblages from Greece (Aliveri, Karydia), Austria (Oberdorf) and Spain (Villafeliche 2A, Montalvos2) and the distribution of the classes of the number of ridges on the M1-2 and m1, m2 of selected genera^a

Selected MN4 assemblages	Gliroid genera										Number of specimens (M1, M2, m1, m2)	Number of ridges	Number of ridges per molar	
	<i>Armantomys</i>	<i>Bransatoglis</i>	<i>Glirulus</i>	<i>Glirudinus</i>	<i>Glis</i>	<i>Microdryomys</i>	<i>Peridyromys</i> (<i>Pseudodryomys</i>)	<i>Simplomys</i>	<i>Scorsumuscardinus</i>	Number of species				Corrected number of species
Karydia2			3	1	1					5	5	46	440	9.6
Aliveri	1		2	1	1	1				6	6	135	1163	8.6
Oberdorf	2		2	1	1	2	1		1	10	9	101	853	8.4
Montalvos 2	1			1		1	1		3	7	6	83	446	5.4
Villafeliche 2A	1			1		1	2		3	8	7	209	1291	6.2
Selected MN4 assemblages	4	5	6	7	8	9	10	11	12	13	Total	Number of specimens	Number of ridges	Number of ridges per molar
Karydia2			4	17	3	8	6	3	2	3	46	46	440	9.6
Aliveri				20	18	91	6				135	135	1163	8.6
Oberdorf	1	5	9	11	7	45	13	6	3	100	101	101	853	8.4
Montalvos2	19	33	17	12	1	1				83	83	83	446	5.4
Villafeliche 2A	22	71	68	40	9	2	7			219	219	219	1291	5.9

^a Excluded from the latter analysis are *Armantomys* and *Scorsumuscardinus*

^b The ridge index is based on the total number of ridges counted on all upper and lower first and second molars in an association divided by the number of specimens

a combination of the both uncertainty in the regression parameters and individual variation (i.e. the residuals), is 204–897 mm/year. Estimates for the MAP from time-equivalent (zone Ca) sites in the Calatayud-Montalbán Basin are lower at 283 mm/year (Artesilla), 404 mm/year (San Roque 3) and 250 mm/year (Olmo Redondo 4A); this decrease is caused by the lower number of arboreal (0–1) and/or invertivore species (3–5). It is therefore likely that annual rainfall levels could have been some 150–300 mm/year lower at these three sites than at Montalvos2. The next younger locality Vargas 4A (base zone Cb, NI=8, NA=1) would have had a MAP value only somewhat lower than that of Montalvos2 (estimated at 505 mm/year). The precipitation (MAP) estimate for Buñol amounts to 875 mm/year, i.e. much higher than that of Montalvos2 and sites near Daroca. This is mainly due to a

much higher number of arboreal species (NA=7, PA=24 %, both dormice and flying squirrel species), pointing to a more closed environment. It is possible that both geographic and small temporal differences in climate can explain the differences in relative abundances, composition and relative humidity between Montalvos2 fauna in the Teruel Basin and the time-equivalent faunas from the more NNW-situated Calatayud-Montalbán Basin.

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Appendix

Material and measurements of all the Montalvos2 small mammal cheek teeth elements, including collection numbers

Element	Length (mm)				Width (mm)			Collection number	
	Mean	Range	SD	<i>N</i>	Mean	Range	SD	Locality code	Number
<i>Melissiodon dominans</i>									
m1	2.68			1	1.94			MNT2	356–357
m2	2.50			1	2.09			MNT2	358–360
m3	2.37	2.29–2.44		2/1	1.67			MNT2	361–362
M1	3.49	3.37–3.56		3	2.27	2.25–2.28		MNT2	344–348, 350
M2	2.35	2.33–2.37		2	1.99	1.98–2.00		MNT2	349, 351
M3	1.78	1.68–1.86		2/1	2.11			MNT2	352–354
<i>Democricetodon decipiens</i>									
m1	1.50	1.31–1.67	0.099	12	1.06	0.96–1.16	0.061	MNT2	126–139
m2	1.37	1.31–1.40	0.035	8	1.12	1.01–1.17	0.057	MNT2	140–148
m3	1.18	1.13–1.23		2	0.96	0.87–1.04		MNT2	149–150
M1	1.76	1.68–1.80	0.050	12	1.20	1.15–1.25	0.036	MNT2	101–107
M2	1.25	1.20–1.30	0.037	9	1.17	1.13–1.26	0.042	MNT2	108–116
M3	0.91	0.87–0.97	0.041	5	1.00	0.96–1.06	0.037	MNT2	118–123
<i>Megacricetodon primitivus</i>									
m1	1.30	1.19–1.37	0.052	22	0.87	0.77–0.93	0.055	MNT2	241–270
m2	1.37	1.31–1.40	0.035	33	1.12	1.01–1.17	0.057	MNT2	271–288, 290–304
m3	1.07	0.97–1.15	0.046	6	0.90	0.77–0.99	0.055	MNT2	306–310
M1	1.47	1.37–1.60	0.055	26	0.97	0.90–1.03	0.032	MNT2	151–186
M2	1.01	0.91–1.09	0.040	41	0.93	0.82–1.02	0.047	MNT2	187–209, 211–231, 289
M3	0.88	0.85–0.92	0.038	5	0.77	0.74–0.82	0.036	MNT2	233–237
<i>Eumyarion weinfurteri</i>									
m1	1.73			2	1.13	1.13–1.13		MNT2	331–334
m2	1.48	1.47–1.49	0.008	4	1.28	1.24–1.31	0.034	MNT2	335–340
m3	1.45	1.37–1.54		3	1.14	1.13–1.16		MNT2	341–343
M1	1.96	1.84–2.03	0.072	7	1.34	1.21–1.40	0.069	MNT2	311–319
M2	1.39	1.33–1.46	0.043	5	1.4	1.34–1.48	0.056	MNT2	320–327
M3	1.10	1.02–1.16		3	1.18	1.13–1.23		MNT2	328–330

Element	Length (mm)				Width (mm)			Collection number	
	Mean	Range	SD	<i>N</i>	Mean	Range	SD	Locality code	Number
<i>Pseudodryomys aff. ibericus</i>									
p4	0.82	0.80–0.92		4	0.89	0.69–1.06		MNT2	451–452, 464, 515
m1	1.16	1.07–1.32	0.070	11/12	1.06	0.98–1.20	0.059	MNT2	461–462, 484–493
m2	1.13	1.01–1.28		12	1.07	0.99–1.30		MNT2	463, 494–506
m3	0.97	0.77–1.07	0.108	7/8	0.93	0.87–1.00	0.050	MNT2	508–513, 521
P4	0.92	0.88–0.96		2	1.05	1.04–1.07		MNT2	466–467
M1-2	1.12	1.00–1.25		1/11	1.24	1.13–1.34	0.022	MNT2	454–458, 471–479
M3	0.89	0.74–0.98		3	1.10	0.96–1.19		MNT2	481–482, 522
<i>Simplomys simplicidens</i>									
m1	1.35	1.22–1.47		5/4	1.30	1.17–1.22		MNT2	415–420
m2	1.39	1.33–1.43		3/4	1.40	1.40–1.56		MNT2	421–432
m3	1.08	0.95–1.08	0.040	13	1.17	1.06–1.28	0.076	MNT2	434–448
D4	0.77	0.75–0.78		2	0.90	0.89–0.91		MNT2	652, 653
P4	0.82	0.72–0.92	0.027	10	0.97	0.83–1.12	0.065	MNT2	641–651
M1-2	1.22	1.12–1.43	0.083	16/22	1.49	1.36–1.57	0.066	MNT2	371–391, 93–398
M3	0.83	0.72–0.91	0.057	12	1.21	1.11–1.32	0.067	MNT2	399–413
<i>Simplomys sp.</i>									
	Length	Width	Collection number						
M1-2	1.27	1.77	MNT2	468					
<i>Simplomys julii</i>									
M1-2	1.05	1.27	MNT2	392					
M1-2	1.08	1.21	MNT2	470					
<i>Microdryomys legidensis</i>									
m1	0.93	0.87–0.96		5	0.89	0.77–0.97		MNT2	543–548
m2	1.08			1	1.04			MNT2	549–550
P4	0.72			1	0.70			MNT2	625
M1-2	0.91	0.84–1.00		10	1.01	0.94–1.00		MNT2	531–541
<i>Glirudinus gracilis</i>									
	Length	Width	Collection number						
m2	1.24	1.22	MNT2	525					
m2	1.21	1.19	MNT2	527					
m2	fragm.	fragm.	MNT2	528					
m3	1.03	0.94	MNT2	530					
m3	1.01	1.03	MNT2	529					
m3	fragm.	fragm.	MNT2	526					
M3	0.95	fragm.	MNT2	524					
<i>Armantomys aragonensis</i>									
P4	1.37	2.03	MNT2	556					
M2	1.27	1.99	MNT2	553					
M3	1.26	1.86	MNT2	554					
M3	1.12	1.81	MNT2	555					
10 fragments			MNT2	551–552, 558–567					

Element	Length (mm)				Width (mm)			Collection number	
	Mean	Range	SD	N	Mean	Range	SD	Locality code	Number
<i>Ligerimys ellipticus</i>									
D4	1.22	1.15–1.29		2	0.8	0.80–0.80		MNT2	595–596
P4	0.98	0.96–1.00		2	0.93	0.92–0.94		MNT2	597–598
M1-2	1.14	1.02–1.25	0.069	8/9	1.04	0.93–1.13	0.060	MNT2	581–591
M3	1.02	0.97–1.07		3	0.89	0.84–0.93		MNT2	593
M1-2	1.11	1.03–1.17	0.048	7	1.19	1.14–1.28	0.053	MNT2	571–579
M3	0.84			1	1.08			MNT2	580
<i>Heteroxerus rubricati</i>									
D4	1.23			1	0.94			MNT2	614–615
P4				0				MNT2	
M1-2	1.49	1.45–1.53		2	1.52	1.49–1.55		MNT2	616–617
m3	1.57			1	1.43			MNT2	618–620
D4	1.23	1.19–1.27		2	1.25	1.17–1.33		MNT2	611–612
P4	1.23	1.20–1.25		3/2	1.55	1.52–1.57		MNT2	603–604, 609
M1-2	1.41	1.40–1.42		3/5	1.63	1.60–1.68		MNT2	601–602, 605–608, 610
M3	1.45			1	1.52			MNT2	621
<i>Heteroxerus cf. grivensis</i>									
	Mean length	Mean width		Collection number					
m2	1.90	1.91		MNT2 625					
<i>Albanensia cf. sansaniensis</i>									
m3	3.20	3.08		MNT2 623					

Element	Length (mm)				Width (mm)			Collection number	
	Mean	Range	SD	N	Mean	Range	SD	Locality code	Number
<i>Lagopsis penai</i>									
d3	1.61			1/0				MNT2	921A–924A, 926A–928A
p3	1.56	1.25–1.74	0.13	21/19	1.65	1.44–1.86	0.12	MNT2	801A–810A, 801B–809B
								MNT2	811A–820A, 811B820B
								MNT2	821A–827A, 911B–913B
d4	1.20	1.14–1.28		3/1	1.54			MNT2	926B–928B
D2	1.04	0.96–1.10	0.05	6/1	1.81			MNT2	931A–939A
P2	0.80	0.69–0.99	0.07	35/29	1.53	1.29–1.78	0.13	MNT2	876B–880B, 881A–890A
								MNT2	881B–890B, 891A–900A
								MNT2	891B–892B, 896B–900B
								MNT2	901A–910A, 901B–904B
								MNT2	909B–910B
P3	1.24	1.07–1.39	0.07	43/9	2.46	2.32–2.64	0.11	MNT2	831B–840B, 841A–850A,
								MNT2	841B–850B, 851A–860A,
								MNT2	851B–860B, 861A–868A, 915B
<i>Prolagus lopezmartinezae</i>									
d3	1.63			1	1.27			MNT2	921B–923B
p3	1.47	1.47–1.48		2/9	1.41	1.21–1.59	0.12	MNT2	821B–829B, 831A–838A, 917B
D2	1.01			0				MNT2	940A
P2	0.78	0.69–0.88	0.07	5	1.53	1.40–1.61	0.08	MNT2	911A–919A
P3	1.35	1.31–1.42	0.04	8/2	2.24	2.22–2.25		MNT2	861B–870B, 871A–880A,
								MNT2	871B–872B, 918B, 919B

Species	Element	Length anteroconid (mm)				Width anteroconid (mm)			
		<i>N</i>	Mean	Range	SD	<i>N</i>	Mean	Range	SD
<i>L. penai</i>	p3	28	0.50	0.35–0.62	0.07	23	0.89	0.64–1.19	0.15
<i>P.lopezmartinezae</i>	p3	3	0.41	0.37–0.44		3	0.55	0.46–0.61	
<i>L. penai</i>	d3	3	0.66	0.64–0.71		2	0.91	0.90–0.92	
<i>P.lopezmartinezae</i>	d3	2	0.60	0.58–0.62		1	0.69		
		Length metaconid-entoconid (mm)				Width protoconid-metaconid (mm)			
<i>L. penai</i>	p3	22	1.10	1.01–1.18	0.05	28	1.19	0.89–1.41	0.12
<i>P.lopezmartinezae</i>	p3	10	0.95	0.85–1.03	0.06	14	0.95	0.69–1.22	0.13
		Length protoconulid-entoconid (mm)							
<i>P.lopezmartinezae</i>	p3	10	0.97	0.80–1.10	0.095				
		Width distal hyperloph (mm)				Length postlobe (mm)			
<i>L. penai</i>	P3	19	1.74	1.37–2.06	0.22	27	0.77	0.62–0.95	0.10
<i>P.lopezmartinezae</i>	P3	5	1.60	1.34–1.86	0.25	11	0.89	0.75–1.00	0.09
<i>L. penai</i>	P2	33	0.43	0.28–0.67	0.08	32	0.68	0.50–0.82	0.08
<i>P.lopezmartinezae</i>	P2	5	0.61	0.52–0.68	0.07	5	0.63	0.55–0.68	0.05
<i>L. penai</i>	D2	4	1.21	0.93–1.34		4	0.74	0.65–0.84	
<i>P.lopezmartinezae</i>	D2	1	0.93			1	0.74		
		Width mesial hyperloph (mm)				Width mesial hyperloph/width			
<i>L. penai</i>	P3	26	1.52	1.19–1.80	0.18	5	0.61	0.52–0.67	0.05
<i>P.lopezmartinezae</i>	P3	6	1.35	1.10–1.66	0.25	2	0.67	0.60	

p3 Species	Anteroconid			Anteroflexid			Protoconulid			Centroflexid				
	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
<i>L. penai</i>	43	0	0	28	5	2	8	23	0	0	0	43	0	0
<i>P.lopezmartinezae</i>	16	1	1	1	0	0	1	0	2	13	0	0	15	0
p3 Species	Ntotal (excl. juveniles)	Absent	Incipient/ small	Developed	Metaconid	Anterolophid	Metolophid	Protoisthmid present	Protoisthmid absent	Metaisthmid	Anteroisthmid	Anteroconid < metaconid	Anteroconid = metaconid	Anteroconid > metaconid
<i>L. penai</i>	43	41	0	0	0	43	43	43	0	0	0	0	2	41
<i>P.lopezmartinezae</i>	16	7	5	2	0	0	16	16	0	0	0	1	1	1
P3 Species	Ntotal (excl. juveniles)	absent	incipient	developed	Precone indistinct (mhl = pr)	distinct (precone thicker than mhl)	long	short	absent (only lagicone)	P2	Hypoflexus absent	incipient/ superficial	distinct	with cement
<i>L. penai</i>	57	7	16	7	40	5	0	1	56	52	32	9	1	2
<i>P.lopezmartinezae</i>	19	0	0	17	1	9	1	8	8	6	5	0	0	0

Element	Length (mm)	Width 1 (mm)	Width 2 (mm)	Collection number
<i>Amphiperatherium</i> sp.				
1 labial fragment of an upper molar				MNT2 1058
<i>Galerix symeonidisi</i>				
p4	1.76	1.18		MNT2 1001
m1	fragm.	fragm.		MNT2 1003
m2	fragm.	fragm.		MNT2 1004
m3	1.67	1.10	0.93	MNT2 1005
P3	1.88	1.57		MNT2 1007
P4	fragm.	fragm.		MNT2 1008
M1	fragm.	fragm.		MNT2 1009
M1	fragm.	fragm.		MNT2 1010
M2	1.88	2.46		MNT2 1011
M2	fragm.	fragm.		MNT2 1012
M3	1.17	1.75		MNT2 1014
M3	1.02	1.47		MNT2 1015
M3	1.07	1.00		MNT2 1016
cf. <i>Desmanella</i> sp.				
p4	0.93	0.64		MNT2 1021
m3	1.12	0.74	0.64	MNT2 1023
m3	1.05	0.78	0.64	MNT2 1024
P4	1.28	1.10		MNT2 1026

Element	Length (mm)	Width 1 (mm)	Width 2 (mm)	Collection number
<i>Desmanodon</i> sp.				
p4	1.21	0.78		MNT2 1028
m1	1.86	1.15	1.29	MNT2 1029
m1	2.04	1.18	1.34	MNT2 1030
m2	2.18	1.32	1.31	MNT2 1031
m3	1.63	1.10	0.96	MNT2 1033
M1	fragm.	fragm.		MNT2 1036
M1	2.54	1.57		MNT2 1035
M2	1.89	2.26		MNT2 1037
M2	fragm.	fragm.		MNT2 1038
M3	1.17	1.68		MNT2 1041
M3	1.06	1.59		MNT2 1043
M3	fragm.	fragm.		MNT2 1044
M3	fragm.	fragm.		MNT2 1042
<i>Heterosorex</i> cf. <i>neumayrianus</i>				
m1	fragm.	fragm.		MNT2 1046
m2	fragm.	fragm.		MNT2 1047
m3	1.39	0.95	0.91	MNT2 1048
P4	1.60	1.72		MNT2 1051
M1	1.79	1.94		MNT2 1053
M1	fragm.	fragm.		MNT2 1054
Soricid gen. et sp. indet.				
m1	1.15	0.70	0.80	MNT2 1061
m1	1.20	0.74	0.80	MNT2 1062
m2	1.21	0.74	0.74	MNT2 1064
m3	1.00	0.57	0.46	MNT2 1066
M2	1.13	1.41		MNT2 1068

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