



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

The Aragonian and Vallesian high-resolution micromammal succession from the Calatayud-Montalbán Basin (Aragón, Spain)



Succession haute résolution des micromammifères de l'Aragonien et du Vallésien dans le bassin de Calatayud-Montalbán (Aragon, Espagne)

Israel García-Paredes^{a,b}, María Ángeles Álvarez-Sierra^{a,b},
Lars W. Van den Hoek Ostende^c, Verónica Hernández-Ballarín^d, Kees Hordijk^e,
Paloma López-Guerrero^{a,f}, Adriana Oliver^d, Pablo Peláez-Campomanes^{d,*}

^a Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/José Antonio Novais 2, 28040 Madrid, Spain

^b Departamento de Geología Sedimentaria y Cambio Medioambiental, Instituto de Geociencias IGEO (CSIC, UCM), C/José Antonio Novais 2, 28040 Madrid, Spain

^c Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands

^d Departamento de Paleobiología, Museo Nacional de Ciencias Naturales (MNCN-CSIC), C/José Gutiérrez Abascal 2, 28006 Madrid, Spain

^e Department of Earth Sciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands

^f Geologisch-Paläontologische Abteilung, Naturhistorisches Museum Wien, Burgring 7, 1010 Vienna, Austria

ARTICLE INFO

Article history:

Received 23 April 2015

Accepted after revision 15 September 2015

Available online 4 February 2016

Handled by Isaac Casanova-Vi

Keywords:

Neogene

Miocene

Faunal turnover

Global climatic events

Biodiversity

Mots clés :

Néogène

Miocène

Renouvellements fauniques

Événements climatiques globaux

Biodiversité

ABSTRACT

We present an updated taxonomy and faunal distribution of the micromammal fossil record from the Aragonian and Lower Vallesian of the Calatayud-Montalbán Basin. The analysed record includes the orders Rodentia, Eulipotyphla, and Lagomorpha. The pattern of species turnover shows seven major faunal events, which are correlated with major climate changes based on marine stable oxygen and carbon isotope records. Episodes $\delta^{18}\text{O}$ Mi-2 and Mi-3 are significantly correlated with major micromammal turnover at the boundaries between the Lower and Middle Aragonian and the Middle and Upper Aragonian, respectively. Our results support the existence of a selective turnover during the Aragonian and Lower Vallesian.

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Ce travail actualise la taxonomie et la distribution faunique du registre fossile des petits mammifères du bassin de Calatayud-Montalbán de l'Aragonien au Vallésien inférieur. Les ordres Rodentia, Eulipotyphla et Lagomorpha sont inclus dans l'étude. Le modèle de renouvellement faunique est analysé et expliqué en relation avec les changements climatiques globaux. Sept événements fauniques principaux ont été reconnus et corrélés

* Corresponding author.

E-mail address: pablopelaez@mncn.csic.es (P. Peláez-Campomanes).

aux changements climatiques majeurs, grâce aux enregistrements isotopiques marins (oxygène et carbone). Les événements $\delta^{18}\text{O}$ Mi-2 et Mi-3 sont significativement corrélés aux renouvellements fauniques qui touchent les micromammifères, respectivement aux limites de l'Aragonien inférieur/moyen et moyen/terminal. La présente analyse corrobore l'existence d'un renouvellement faunique sélectif au cours de l'Aragonien et du Vallesien inférieur.

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

The Calatayud-Montalbán Basin (North Central Spain; Fig. 1) has yielded a rich and comprehensive Lower to Upper Miocene mammal record which forms the basis of the Ramblian (Daams et al., 1987) and Aragonian (Daams et al., 1977) continental stages, and the widely used local zonation that has been defined in this basin (Daams et al., 1999a; Van der Meulen et al., 2012). The area owes its importance to a number of factors. First, there is the sheer multitude of small mammal localities. In the northern part of the basin, in the vicinity of the villages of Villafeliche, Daroca, and Nombrevilla, over 150 small mammal assemblages have been collected from alluvial fan and shallow-lake deposits. These localities have been found in superposition in a series of sections, allowing good stratigraphic control. The stratigraphic span of these localities ranges from the Uppermost Ramblian (~17 Ma) to the uppermost Lower Vallesian (~10 Ma) (Daams et al., 1999a; Van Dam et al., 2014). The second important characteristic of the area is its suitability for magnetostratigraphy, since most of the sections preserve a good palaeomagnetic signal (Garcés et al., 2003; Krijgsman et al., 1994, 1996; Van Dam et al., 2014). In combination with the superposition of localities and the biostratigraphy, the magnetostratigraphy provides excellent time control for the major part of the sequence. This allows straightforward correlations and the building of palaeobiogeographical hypotheses at the European scale (Álvarez-Sierra et al., 2013; Oliver and Peláez-Campomanes, 2013, 2014a; Van den Hoek Ostende et al., 2015; Van der Meulen et al., 2011).

The study of the basin also included analyses involving the long-term evolution of micromammal communities along wide temporal periods (e.g., Daams et al., 1999c; Van der Meulen and Daams, 1992), which have started to increase especially over the last decade (e.g., Hordijk, 2010; Peláez-Campomanes et al., 2015; Van Dam et al., 2006; Van der Meulen et al., 2005).

This brings us to the third important characteristic of the sequence, which is the homogeneity of depositional environments. Because all localities are from alluvial fan and shallow-lake deposits with similar sedimentation rates (see Daams et al., 1999a for details on the sedimentology of the studied area), the taphonomic bias is reduced to a minimum, allowing direct comparison of assemblages. Although a certain degree of bias cannot be excluded (e.g., accumulation by different types of raptors), we can safely assume that these will not influence the major patterns in community changes observed in the sequence (Van der Meulen et al., 2005). Additionally, the sampling coverage of the sequence was calculated by Van der Meulen et al.

(2005) using the number of upper and lower first and second molars of rodents from 96 localities of the studied area. The cumulative curve of sample sizes of the temporally ordered localities yields a good fit with the linear regression line ($R^2 = 0.98$), indicating that the sections have been sampled quite evenly (Van der Meulen et al., 2005: fig. A1).

Recent studies, dealing with different aspects of the Calatayud-Montalbán Basin, have resulted in the proposition of more refined biostratigraphic scale and new numerical ages for the succession of fossil localities (Van der Meulen et al., 2012; Fig. 2). All these new interpretations are based on an increased number of localities studied (Álvarez-Sierra et al., 2003; López-Guerrero et al., 2011), new magnetostratigraphic information (Garcés et al., 2003; Van Dam et al., 2014), and recent important revisions on micromammal groups recorded in the basin (García-Paredes, 2006; García-Paredes et al., 2009, 2010; Hordijk, 2010; López-Guerrero, 2014; López-Guerrero et al., 2008, 2013, 2014a, 2014b; Oliver, 2015; Oliver and Peláez-Campomanes, 2013, 2014b; Van den Hoek Ostende and Furió, 2005; Van den Hoek Ostende et al., 2009, 2012; Van der Meulen et al., 2003).

Here, we use all new information to present an updated framework for the evolution of the Aragonian and lower Vallesian faunas in the Calatayud-Montalbán Basin and to identify possible global environmental factors that may have triggered faunal changes.

2. The small mammal fossil record from the Aragonian and Vallesian of the Calatayud-Montalbán Basin

The fossiliferous localities included in this study come from three main areas (Fig. 1); starting from the north-western margin of the basin: the Armantes area (near Calatayud), the Villafeliche-Manchones area, and the Daroca-Nombrevilla area (Daams and Freudenthal, 1988; Daams et al., 1999a, 1999b; De Bruijn, 1967; López-Guerrero et al., 2011; Van Dam et al., 2014; Van der Meulen et al., 2012).

Since the last synthesis by Daams et al. (1999a), which involved the rodents exclusively, the published information on the small mammals from the Aragonian and Lower Vallesian of the Calatayud-Montalbán Basin has increased considerably. In this way, Van der Meulen et al. (2012) provided an important update in the taxonomical information for the Lower and Middle Aragonian. Fig. 2 summarizes the most recent taxonomical and biostratigraphical information published on the Aragonian and Lower Vallesian from the Calatayud-Montalbán micromammal fossil record

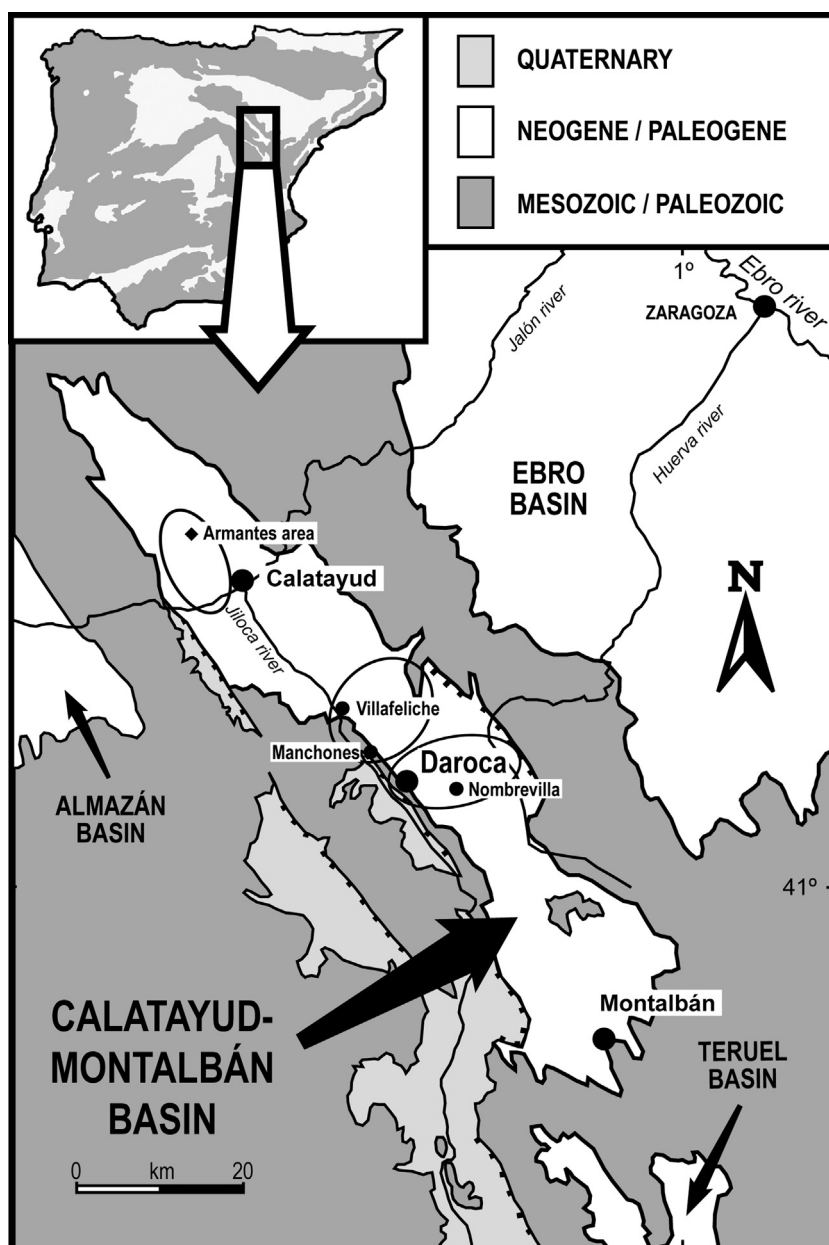


Fig. 1. Geographical situation and synthetic geology of the Calatayud-Montalbán Basin, indicating the main areas included in this study (Armantes, Villafeliche-Manchones, and Daroca-Nombrevilla).

Fig. 1. Situation géographique et géologie synthétique du bassin de Calatayud-Montalbán, avec les principales régions incluses dans cette étude (Armantes, Villafeliche-Manchones et Daroca-Nombrevilla).

(Álvarez-Sierra et al., 2003; García-Paredes, 2006; García-Paredes et al., 2009, 2010; Hordijk, 2010; López-Guerrero, 2014; López-Guerrero et al., 2011, 2013, 2014a, 2014b; Oliver, 2015; Oliver et al., 2009a, 2009b; Oliver Pérez et al., 2008; Van Dam et al., 2006, 2014; Van den Hoek Ostende and Furió, 2005; Van den Hoek Ostende et al., 2009, 2012; Van der Meulen et al., 2003).

The increase on the palaeontological information was accompanied by new magnetostratigraphical data, providing new numerical ages for this period (Garcés et al., 2003; Van Dam et al., 2014).

2.1. The Lower Aragonian

Since its redefinition by Daams et al. (1987), the Lower Aragonian includes the Biozones B and C (~17.00 Ma, ~15.93 Ma). It is characterized by high relative abundance and species richness of glirids combined with the presence of representatives of the eomyid genus *Ligerimys*. Compared to the previous stage, the Ramblian, there is not a strong faunal rupture; most of the rodent genera recorded from Ramblian localities persist in the lower Aragonian (only *Melissiodon* and *Palaeosciurus* are absent in the

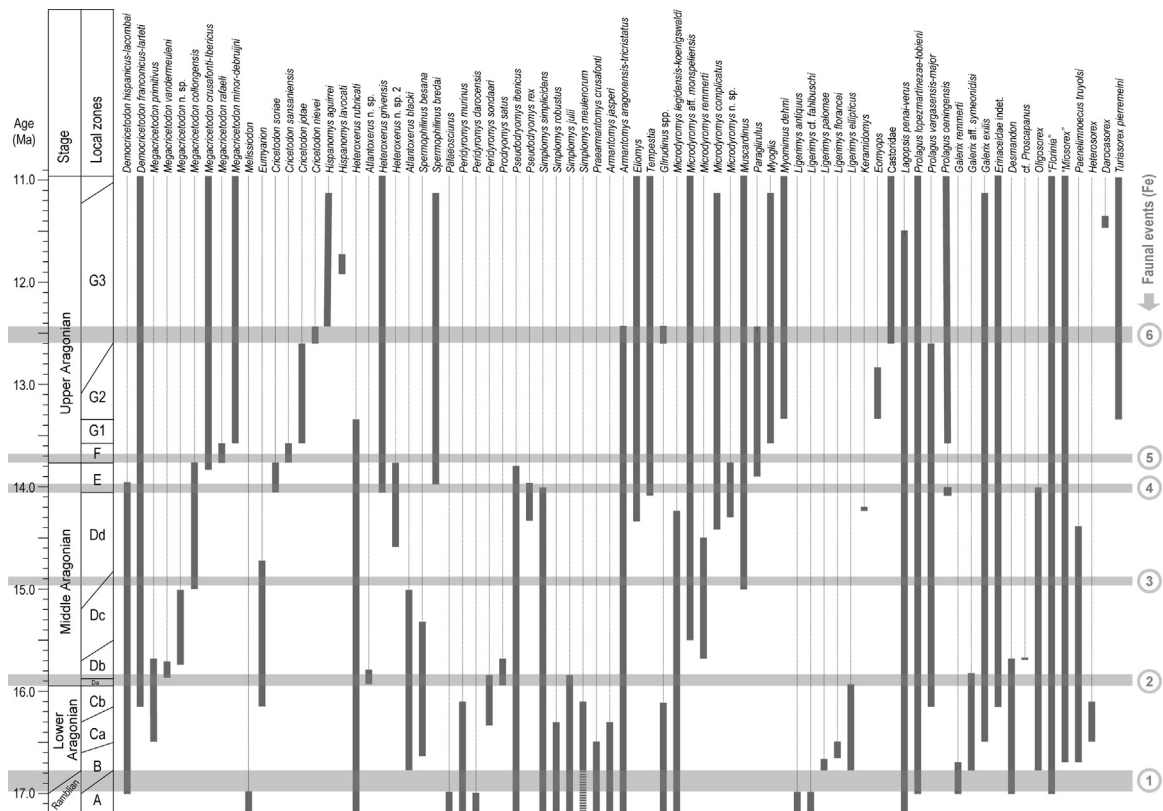


Fig. 2. Stratigraphic ranges of the most characteristic Upper Ramblian and Aragonian micromammal taxa from the Calatayud-Montalbán Basin, including rodents (Cricetidae, Sciuridae, Gliiridae, Eomyidae, and Castoridae), lagomorphs, and insectivores. Circles with numbers indicate main faunal events (Fe) discussed in the text.

Fig. 2. Distribution stratigraphique des taxa les plus caractéristiques du bassin de Calatayud-Montalbán pour le Ramblien terminal et l'Aragonien. Rongeurs (Cricetidae, Sciuridae, Gliiridae, Eomyidae et Castoridae), lagomorphes et insectivores sont pris en compte. Les cercles numérotés indiquent les principaux événements fauniques (Fe) discutés dans le texte.

Aragonian faunas from the Calatayud-Montalbán Basin). The main difference is the regular occurrence of the so-called “modern” cricetids in the Aragonian assemblages (Daams et al., 1998, 1999a; Van der Meulen et al., 2012).

Within the Lower Aragonian, three different migration events involving cricetids are clearly recognized and have been used to define its local biozonation (Van der Meulen et al., 2012). The first regular occurrence of *Democricetodon* is used to define the base of the Aragonian and its lowest biozone (Zone B). The Zone Ca is recognized by the presence of the genus *Megacricetodon* combined with *Democricetodon decipiens*. In this zone, the progressive depletion of gliroid species started, which continues across the Lower Aragonian (*Praearmantomys crusafonti*, *Armanatomyx jasperi*, and *Simplomys robustus*). Most of these taxa had survived the Ramblian-Aragonian boundary, and their association is typical for Iberian Early Miocene faunas. Across Zone Cb, the decrease in gliroid species continues. The cricetids increase in species richness with the entrance in the basin of a second lineage of *Democricetodon* of small size (*D. franconicus*) and the genus *Eumyarion*. The arrival of these cricetids, which present affinities with the central European representatives, co-occur with the first occurrence of a second *Prolagus* lineage (*P. vargasensis*). Across the zones Ca and Cb there is a momentary occurrence of

the heterosoricid shrew *Heterosorex*. For the first time during the Early Aragonian, the assemblages are dominated by eomyids (*Ligerimys ellipticus*) and cricetids instead of eomyids and gliroids.

2.2. The Middle Aragonian

The Middle Aragonian includes the Zones Da to E, from ~15.93 Ma to ~13.78 Ma, (Daams et al., 1999a; Van der Meulen et al., 2012). In central Spain, it represents a period of low richness in rodent species, with cricetids as the most abundant group, while the genus *Ligerimys*, dominant during the Ramblian and Lower Aragonian, went extinct. At the same time, the Talpidae, represented since the Ramblian by the genus *Desmanodon*, disappear from the area, as does the small gymnure *Galerix symeonidisi*. The gliroids show low relative abundances; *Microdyromys* increases in relative abundances compared to the gliroids of simpler dental pattern, which were dominant through the Early Miocene in the Iberian Peninsula. The beginning of the Middle Aragonian includes a period of high turnover with quick replacement of species, some of them with very short distributions. This rapid substitution of species is reflected in the short duration of the two first biozones, Da and Db, from ~15.93 Ma to ~15.60 Ma

(Van der Meulen et al., 2012). Both, and especially Zone Db (~15.85 Ma, ~15.60 Ma), include rodent species with affinities with central European taxa, such as *Megacricetodon vandermeuleni* or *Prodryomys* (Oliver and Peláez-Campomanes, 2013 and García-Paredes, 2006, respectively). Zone Dc (~15.60 Ma, ~14.82 Ma) includes the last occurrence of *Atlantoxerus blacki* and *Spermophilinus besanus*. *Microdryomys* is for the first time represented by three species in the area (García-Paredes et al., 2010). Zone Dd (~14.81 Ma, ~14.75 Ma) contains impoverished faunas with a strong dominance of cricetids. Across all Zone Dd, there are three species of *Microdryomys*, although the species changed through time, leading to a more-complex dental pattern at the end of the biozone (García-Paredes et al., 2010). The upper part of Zone Dd is also characterized by an increase in the diversity of glirids with the first occurrence of *Pseudodyromys rex*, *Tempestia ovis* and *Muscardinus thaleri*. For a short period of time, *Keramidomys* is recorded in the basin. This genus was a common representative in Middle Aragonian faunas from central Europe (Kälin and Kempf, 2009; Van der Meulen et al., 2011). The end of the Middle Aragonian includes the extinction of a high proportion of the most characteristic taxa for the Early and Middle Aragonian. In this way, during the Zone E (~14.75 Ma, ~13.78 Ma), *Pseudodyromys ibericus*, *Simplomys simplicidens*, *Microdryomys legidensis-koenigswaldi*, and the lineage *Democricetodon hispanicus-D. lacombai* have their last occurrences in the basin. The biozone includes the first occurrence of *Cricetodon* (*Cricetodon soriae*) and *Heteroxerus grivensis*, which represents the third *Heteroxerus* species co-occurring in this biozone.

2.3. The Upper Aragonian

As pointed out by Van der Meulen et al. (2005), the rodent faunas from the Upper Aragonian represent a different community to that previously recorded in the area. There are new important taxa that characterize this time interval and have their first occurrences. The cricetids are still the dominant group with relative abundances usually higher than 75%. Across the Upper Aragonian, the species richness of glirids increases, although their relative abundance remained low. The biostratigraphy of this period is mainly based on the evolutionary degree of the *Megacricetodon ibericus* lineage combined with the presence of representatives of small-sized *Megacricetodon*. In addition to the *Megacricetodon* evolution, López-Guerrero et al. (2013, 2014a, 2014b) have recently showed the importance of the evolution of the representatives of the tribe Cricetodontini for the biostratigraphy. In this way, the Zone F (~13.78 Ma, ~13.62 Ma) can be recognized by the presence of *Megacricetodon rafaeli* and *Cricetodon sansaniensis*. The representatives of the *M. ibericus* lineage in Zone G1 show the same evolutionary degree than in the previous zone. However, Zone G1 (~13.62 Ma, ~13.27 Ma) can be easily recognized by the presence of *Megacricetodon minor* and *Cricetodon jotae*, a smaller and more advanced Cricetodontini (López-Guerrero et al., 2014b). The next local biozone, Zone G2 (~13.27 Ma, ~13.00 Ma), maintains the same micromammal structure as the previous one, continuing the increase of species of glirids present and the

sporadic presence of the eomyid *Eomyops*. The first occurrence of the insectivore *Turiasorex pierremeini* is within this zone. The cricetids are very abundant, with *Megacricetodon crusafonti* as the most characteristic and abundant taxon.

Approximately the second half of the Upper Aragonian corresponds to the Zone G3 (~13.00 Ma, ~11.26 Ma). This long zone represents a transition towards the Vallesian faunas. In the basin, common taxa such as *Armantomys*, *Paraglrulus*, *Lagopsis*, and *Galerix* went extinct during this biozone. There are noticeable morphological changes in the *Democricetodon* and *Megacricetodon* lineages that have been used to recognize different species. Also notable is the achievement of the 'Hispanomys evolutionary degree' in the representatives of the tribe Cricetodontini. Although this tribe is not very abundant across this biozone, its representatives had an important turnover involving four species (López-Guerrero, 2014; López-Guerrero et al., 2014a, 2014b). Zone G3 also includes the re-entry of the castorids in the Calatayud-Montalbán Basin, after a time interval of absence spanning ~7 Ma (Álvarez-Sierra et al., 2003; López-Guerrero et al., 2007), and the first appearance of the gymnure *Parasorex*. Álvarez-Sierra et al. (2003) pointed out that representatives from other northern Spanish basins enter in the upper half of the Zone G3. These results, indicating a decrease in isolation among different basins, have been further supported by López-Guerrero et al. (2008) studying the Cricetodontini and, also, by Abella et al. (2012) with carnivores.

2.4. The Lower Vallesian

Zone H was defined by Daams and Freudenthal (1988) based on the presence of *Megacricetodon ibericus*. Álvarez-Sierra et al. (2003) informally used the co-occurrence of latter species and *Hispanomys* to define Zone H. Nevertheless, López-Guerrero et al. (2008, 2014b), demonstrated the presence of *Hispanomys* representatives already in G3 localities. Therefore, Van Dam et al. (2014) implicitly modified that informal definition of the Zone H using, as lower boundary, the first occurrence of *Hispanomys nombrevillae*. According to Van Dam et al. (2014), the age of the lower boundary of Zone H could be older than 11.2 Ma, implying that it was about 500 ky before the first *Hippotherium* record in the basin at the Nombrevilla classic locality. This new way to define the Zone H therefore implies, as previously pointed out by Álvarez-Sierra et al. (2003), that the change towards 'Vallesian' micromammal faunas was already achieved in the upper part of the Aragonian.

The upper parts of the sections in the Daroca-Nombrevilla area correspond to the Zone I. The faunas of this period show strong differences with previous ones by the absence of members of the *Megacricetodon ibericus* lineage (the most abundant and characteristic lineage of the Upper Aragonian) and the presence of *Cricetulodon*. The glirid *Ramys* has also been considered as a typical genus for Zone I in the Calatayud-Montalbán Basin. However, after the study of the material available from the Cañada localities, a recently published stratigraphic section near the Carrilanga one, this taxon has been recorded associated with *H. nombrevillae*, indicating that its first occurrence in the basin predates the replacement of the *Hispanomys*

forms (López-Guerrero et al., 2011). Around the same time, moles, now represented by *Desmanella*, also return to the basin (Van den Hoek Ostende et al., 2012). The uppermost part of this biozone contains the first occurrence of the murid *Progonomys*, the regular presence of which defines the lower boundary of the Upper Vallesian (10 Ma, Van Dam et al., 2014).

3. Micromammal turnover in Miocene of the Calatayud-Montalbán Basin and their correlation to global climatic changes

3.1. Tripartite division of the Aragonian

An extensive discussion on the tripartite division of the Aragonian and the history of the different definitions were summarized by Daams et al. (1999a). These authors justified the division used till now by the short duration of some of the biozones, which indicated a high replacement of species. In this way, they placed the boundary between Lower and Middle Aragonian at the base of Zone Da (~16 Ma), and the boundary between Middle and Upper Aragonian at the base of Zone F (~13.8 Ma). Therefore, in the Calatayud-Montalbán Basin, the three important faunal intervals recognized (Fig. 2) are:

- the Early Aragonian, characterized by a high diversity and relative abundance of endemic Spanish glirids, combined with the progressive presence of modern cricetids coming from the east;
- the Middle Aragonian, characterized by the decline of glirids and the rise of cricetids, with communities that are relatively poor in micromammal species;
- the late Aragonian, characterized by an increase in species richness but still with a clear dominion of cricetids (Van der Meulen and Daams, 1992; Van der Meulen et al., 2005).

Thus, the two limits on the Aragonian subdivisions correspond to two of the major changes. The first one corresponds to the start of the cricetid dominion over the glirids and eomyids (Fe 2 on Fig. 2), and the second one to the community reorganization (Fe 5 on Fig. 2) pointed out by Van der Meulen et al. (2005).

Three characteristic global climatic conditions, based on stable isotopes (Fig. 3), have been proposed for the period equivalents to Aragonian and Early Vallesian ages (Cramer et al., 2009; Miller et al., 1991, 1998; Zachos et al., 2001). The Miocene Climatic Optimum (MCO), an interval between 17 and 15–14.5 Ma (Mudelsee et al., 2014; Zachos et al., 2001) characterized by high temperatures and, in general, more humid environments (Zachos et al., 2001). The Middle Miocene Climate Transition (MMCT), between 15–14.5 Ma and ~13.8 Ma (Holbourn et al., 2007; Mourik, 2010; Mourik et al., 2011; Mudelsee et al., 2014), represents the beginning of the cooling trend of the Neogene (Mourik et al., 2011). The end of the MMCT marks the onset of the so-called “Icehouse”, a cold period during which an expansion of the Antarctic ice volume took place (Holbourn et al., 2007; Zachos et al., 2001).

The beginning of the Aragonian (Fig. 2, Fe 1) coincides with the onset of the MCO around 17 Ma (Mudelsee et al., 2014; Zachos et al., 2001). At that time, glirids were an important quantitative component of the rodent associations (García-Paredes, 2006; Van der Meulen et al., 2005). The components of these communities are residents, which appear to be predominantly open country dwellers (Daams et al., 1999c; Van der Meulen et al., 2005). Hordijk (2010) pointed out that, in the Calatayud-Montalbán Basin, Zone B is dominated by herbivores, especially *Lagopsis penai*. Their dominance could indicate the presence of open landscapes at that time, as was also noted by Van der Meulen and Daams (1992).

The faunal change that occurred between the Lower and Middle Aragonian (Fig. 2, Fe 2), involving the beginning of the dominion of cricetids over the eomyids and glirids, is included within the MCO and the Monterrey Carbon Excursion (Fig. 3). It corresponds approximately with the Mi2 Oxygen isotope zone of Miller et al. (1991) that represents a relative cooling period within the warm conditions of the MCO (Fig. 3).

The strongest taxonomical turnover is marked by the collapse of the Early and Middle Aragonian community (Fig. 2, Fe 5) and their replacement by a new community (Daams et al., 1999a, 1999c; Hordijk, 2010; Van der Meulen and Daams, 1992; Van der Meulen et al., 2005). In the general context, this corresponds approximately with the end of the MMCT (Fig. 3), marked by the Mi-3 of Miller et al. (1991), which is a major step in the Middle Miocene climatic cooling (Mi-3b in Abels et al., 2005). The new Upper Aragonian community is defined by the presence of a new set of sciurids and cricetids together with glirids associated to woodlands replacing the old resident open-land dwellers (Van der Meulen et al., 2005).

3.2. Correlation between climatic changes and local biozonation

Van Dam et al. (2006) studied this relationship between climate and rodent turnover, detecting turnover cycles of 2.4–2.5 and 1.0 over a long record of more than 20 Myr based on the rodent record from the Spanish central basins. They calculated the statistically significant rodent turnover peaks and related them to the major marine benthic stable oxygen isotope events and with the predicted time of rodent turnover based obliquity and eccentricity cycles. Hordijk (2010), at a lower scale and including lagomorphs in the analyses, explained changes in the structure of the small mammal community based on their relationship with the local effects of global changes in climate.

The refined taxonomic and stratigraphic information available allows us to propose the correlation of smaller faunal turnover corresponding to biostratigraphic zonal boundaries with several global climatic changes. The discussion is not only based on the quantitative aspects, number of originations and extinctions, of the micromammal turnover (Van Dam et al., 2006), but also on the qualitative ecological preferences of the taxa (Van der Meulen et al., 2005), which help us to interpret the patterns of change.

The first of these smaller faunal turnovers that could be correlated with climatic changes is at the base of Zone

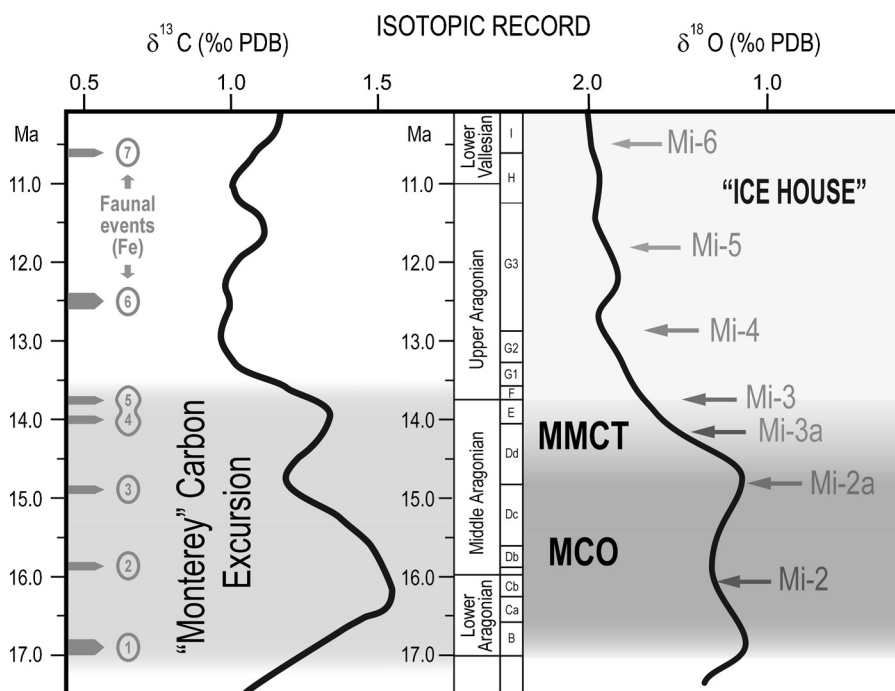


Fig. 3. Simplified scheme of global climatic conditions based on stable isotopes for the period equivalents to Aragonian and Early Vallesian ages. Circles with numbers indicate main faunal events (Fe) discussed in the text.

Fig. 3. Schéma simplifié, et basé sur les isotopes stables, des conditions climatiques aux périodes équivalentes à l'Aragonien et au Vallésien basal. Les cercles numérotés indiquent les principaux événements fauniques (Fe) discutés dans le texte.

Modified after Cramer et al. (2009) and Mourik (2010).

Dd (Fig. 2, Fe 3), and approximately corresponds to the Mi-2a at the beginning of the MMCT and the carbon isotope decrease (Cramer et al., 2009) shown on Fig. 3. This was the onset of a presumably dryer period in the basin, leading the extinction of common taxa that were generally frequent in environments considered as more humid, such as *Spermophilinus* and *Eumyarion* (Casanovas-Vilar and Agustí, 2007).

Another important faunal turnover, but more gradual than the one discussed above, is that occurring across the end of Zone Dd and the beginning of Zone E (Fig. 2, Fe 4). The general climatic trend is towards colder temperatures and this could promote the migration of northern representatives that enter the central Spanish basins for the first time. The transition between Dd and E faunas can be related to the oxygen isotopic zone Mi-3a (Fig. 3) correlated to the base of the chron C5.Acr (Abels et al., 2005). This event could not be differentiated by Van Dam et al. (2006) from the turnover detected at the end of the Middle Aragonian due to the coarser taxonomical resolution of the data.

As discussed above, Zone G3 shows important community changes although there is not a high turnover rate restricted to a shorter period (Fig. 2, Fe 6). There are two important events within this zone such as the re-entry of the castorids into the basin after more than 7 Ma of absence (Álvarez-Sierra et al., 2003; López-Guerrero et al., 2007) and the entrance of northern species of *Hispanomys* and carnivores into the basin (Abella et al., 2012; Álvarez-Sierra et al., 2003; López-Guerrero, 2014). The latter turnover event could be related to Mi-5 at the base of chron C5r.2r.

Finally, there is an important turnover between Zones H and I, as pointed out by Álvarez-Sierra et al. (2003) and Van Dam et al. (2014), characterized mainly by the replacement of the large representatives of *Democricetodon* and *Megacricetodon* by the new immigrant *Cricetulodon*. This replacement may be correlated to Mi-6 (Fig. 3), situated at the lower part of chron C5N (Miller et al., 1998) with an approximate age of 10.45–10.35 Ma (Van Dam et al., 2006).

4. Final remarks

The seven intervals of faunal turnover detected in the small mammal succession in the Calatayud-Montalban Basin, based on quantitative calculations of origination and extinction of taxa (Van Dam et al., 2006) and the qualitative ecological preferences assigned to the different taxa recorded (Van der Meulen and Daams, 1992; Van der Meulen et al., 2005), are confidentially correlated to main features in the stable marine oxygen and carbon isotope records. This correlation indicates that, even though interactions between community members are theoretically very important for the establishment of the community structure and turnover, the strongest changes in the micro-mammal turnover pattern are explained by the local effects of global changes in climate.

The analyses carried out on the assemblages from the Calatayud-Montalbán Basin have shown the existence of a selective turnover during the Aragonian and Lower Vallesian, as pointed out already by Van der Meulen and Daams (1992) and Van der Meulen et al. (2005). As discussed

throughout this work, there is a correspondence between the direction of the climatic changes and the associated taxa that originate or went extinct in the basin.

In addition to the major changes in community composition, the revised taxonomy of many micromammal groups has shown a progressive morphometric change in many lineages; such as, the lineages *Democricetodon hispanicus*-*D. lacombai* and *D. franconicus*-*D. crusafonti*, which show size increase and parallel evolution during their stratigraphical range (Van der Meulen et al., 2003), the glirid genus *Simplomys* across the Lower and Middle Aragonian (García-Paredes et al., 2009), also with changes in size and morphology, or the lagomorph *Lagopsis* (Hordijk, 2010).

Apart from the turnover of species, most of these global climatic changes also induced important morphological and metrical changes of micromammal taxa (Peláez-Campomanes et al., 2015; Van der Meulen et al., 2003).

Acknowledgements

First and foremost, we thank all the colleagues and students who participated in the fieldwork and helped us to prepare the material for many years. We specially acknowledge Remmert Daams and Albert Van der Meulen, the driving forces behind the “Daroca projects” during many years, for the tremendously important work they have done as groundbreakers in using long sections for palaeoenvironmental studies; without them this paper would not be possible. We also want to express our recognition to Hans de Bruijn and Matthijs Freudenthal, pioneers in the study of micromammal palaeontology from the Calatayud-Montalbán Basin. We acknowledge Jerome Prieto for helping us with the French translation of parts of the text and for his constructive comments as reviewer. We also want to express our gratitude to an anonymous reviewer and to the guest editor, Isaac Casanovas-Vilar, for their helpful remarks. The Spanish MICINN/MINECO projects CGL2004-02094/BTE, CGL2007-65208, CGL2008-04200/BTE; CGL2011-28877 support this study. IG-P acknowledges a JAE-Doc contract (CSIC program “Junta para la Ampliación de Estudios”) co-funded by the European Social Fund. VH-B was supported by a FPI predoctoral contract. PL-G acknowledges a UCM Predoctoral contract and a “Martin-Fellowship” at the NBC. AO was supported by a FPU Predoctoral Fellowship and a SYNTHESYS grant at NL-TAF. This work is a contribution by the Research group UCM-910607 “Evolution of Cenozoic Mammals and Continental Palaeoenvironments”.

References

Abella, J., Alba, D.M., Robles, J.M., Valenciano, A., Rotgers, C., Carmona, R., Montoya, P., Morales, J., 2012. *Kretzoiarctos* gen. nov., the oldest member of the Giant Panda Clade. *PLoS One* 7 (11), e48985.

Abels, H.A., Hilgen, F.J., Krijgsman, W., Kruk, R.W., Raffi, I., Turco, E., Zachariasse, W.J., 2005. Long-period orbital control on Middle Miocene global cooling: integrated stratigraphy and astronomical tuning of the Blue Clay Formation on Malta. *Paleoceanography* 20, PA4012, <http://dx.doi.org/10.1029/2004PA001129>.

Álvarez-Sierra, M.Á., Calvo, J.P., Morales, J., Alonso-Zarza, M.A., Azanza, B., García-Paredes, I., Hernández Fernández, M., Van der Meulen, A.J.,

Peláez-Campomanes, P., Quiralte, V., Salesa, M.J., Sánchez, I.M., Soria, D., 2003. El tránsito Aragoniense Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). *Coloq. Paleontol. Vol. Extr.* 1, 25–33.

Álvarez-Sierra, M.Á., García-Paredes, I., Hernández-Ballarín, V., Van den Hoek Ostende, L.W., Hordijk, K., López-Guerrero, P., Van der Meulen, A.J., Oliver, A., Peláez-Campomanes, P., 2013. Models of historical biogeography and continental biochronology. *Span. J. Palaeontol.* 28, 131–140.

Casanovas-Vilar, I., Agustí, J., 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 248, 169–189.

Cramer, B.S., Toggweiler, J.R., Wright, J.D., Katz, M.E., Miller, K.G., 2009. Ocean overturning since the Late Cretaceous: inferences from a new benthic foraminiferal isotope compilation. *Paleoceanography* 24, PA4216, <http://dx.doi.org/10.1029/2008PA001683>.

Daams, R., Freudenthal, M., 1988. Synopsis of the Dutch-Spanish collaboration program in the Neogene of the Calatayud-Teruel basin. In: Freudenthal, M. (Ed.), *Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin (Spain)*. *Scripta Geol. Spec. Issue* 1, 3–18.

Daams, R., Alcalá, L., Álvarez-Sierra, M.A., Azanza, B., Van Dam, J.A., Van der Meulen, A.J., Morales, J., Nieto, M., Peláez-Campomanes, P., Soria, D., 1998. A stratigraphical framework for Miocene (MN4-MN13) continental sediments of Central Spain. *C. R. Acad. Sci. Paris, Ser. Ila* 327, 625–631.

Daams, R., Freudenthal, M., Álvarez-Sierra, M.A., 1987. Ramblian: a new stage for continental deposits of Early Miocene age. *Geol. Mijnb.* 65, 297–308.

Daams, R., Freudenthal, M., Van de Weerd, A., 1977. Aragonian, a new stage for continental deposits of Miocene age. *Newsl. Stratigr.* 6, 42–55.

Daams, R., Van der Meulen, A.J., Álvarez-Sierra, M.A., Peláez-Campomanes, P., Calvo, J.P., Alonso-Zarza, M.A., Krijgsman, W., 1999a. Stratigraphy and sedimentology of the Aragonian (Early to Middle Miocene) in its type area (North central Spain). *Newsl. Stratigr.* 37, 103–139.

Daams, R., Van der Meulen, A.J., Álvarez-Sierra, M.A., Peláez-Campomanes, P., Krijgsman, W., 1999b. Aragonian stratigraphy reconsidered, and a re-evaluation of the Middle Miocene mammal biochronology in Europe. *Earth Planet. Sci. Lett.* 165, 287–294.

Daams, R., Van der Meulen, A.J., Peláez-Campomanes, P., Álvarez-Sierra, M.A., 1999c. Trends in rodent assemblages from the Aragonian (Early-Middle Miocene) of the Calatayud-Daroca Basin, Aragón, Spain. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge, pp. 127–139.

De Bruijn, H., 1967. Gliridae, Sciuridae y Eomyidae (Rodentia, Mammalia) miocenos de Calatayud (provincia de Zaragoza, España) y su relación con la bioestratigrafía del área. *Bol. Inst. Geol. Min. España* 78, 189–373.

Garcés, M., Krijgsman, W., Peláez-Campomanes, P., Álvarez-Sierra, M.A., Daams, R., 2003. *Hipparion* dispersal in Europe: magnetostratigraphic constraints from the Daroca area (Spain). *Coloq. Paleontol. Vol. Extr.* 1, 171–178.

García-Paredes, I., (Doctoral Thesis) 2006. *Patrones evolutivos de los Gliridae (Rodentia, Mammalia) del Mioceno inferior y medio del área tipo de Aragoniense (Cuenca de Calatayud-Montalbán)*. Universidad Complutense de Madrid, Madrid (676 p.).

García-Paredes, I., Peláez-Campomanes, P., Álvarez-Sierra, M.A., 2009. Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene. *Zool. J. Linn. Soc.* 157, 622–652.

García-Paredes, I., Peláez-Campomanes, P., Álvarez-Sierra, M.A., 2010. *Microdyromys remmertii*, sp. nov., a new Gliridae (Rodentia, Mammalia) from the Aragonian type area (Miocene, Calatayud-Montalbán basin, Spain). *J. Vertebr. Paleontol.* 30, 1594–1609.

Holbourn, A., Kuhnt, W., Schulz, M., Flores, J.A., Andersen, N., 2007. Orbitally-paced climate evolution during the Middle Miocene “Monterey” carbon isotope excursion. *Earth Planet. Sci. Lett.* 261, 534–550.

Hordijk, K., 2010. Perseverance of pikas in the Miocene. Interplay of climate and competition in the evolution of Spanish Ochotonidae (Lagomorpha, Mammalia). *Geol. Ultraiectina* 333, 1–232.

Kälin, D., Kempf, O., 2009. High-resolution stratigraphy from the continental record of the Middle Miocene northern Alpine foreland Basin of Switzerland. *Neues Jahrb. Geol. Paläontol. Abh.* 254, 177–235.

Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., Van Dam, J.A., Van der Meulen, A.J., Agustí, J., Cabrera, L., 1996. A new chronology for the Middle to Late Miocene continental record in Spain. *Earth Planet. Sci. Lett.* 142, 367–380.

Krijgsman, W., Langereis, C.G., Daams, R., Van der Meulen, A.J., 1994. Magnetostratigraphic dating of the Middle Miocene climate change in the

- continental deposits of the Aragonian type area in the Calatayud-Teruel basin (Central Spain). *Earth Planet. Sci. Lett.* 128, 513–526.
- López-Guerrero, P., (Doctoral Thesis) 2014. *Cricetodontini (Rodentia, Mammalia) del Mioceno Medio y Superior del área de Daroca (Aragón, España): Sistemática y Filogenia*. Universidad Complutense de Madrid, Madrid (391 p.).
- López-Guerrero, P., Álvarez-Sierra, M.A., García-Paredes, I., Peláez-Campomanes, P., 2014a. *New Cricetodontini from the Middle Miocene of Europe: an example of mosaic evolution*. *Bull. Geosci.* 89, 573–592.
- López-Guerrero, P., Álvarez-Sierra, M.A., López-Antoñanzas, R., Oliver Pérez, A., Peláez-Campomanes, P., 2008. *Cricetodontini (Cricetidae, Rodentia) del Aragoniense superior (Mioceno medio) de Nombrevilla 2, (Zaragoza, España)*. In: Esteve, J., Meléndez, G. (Eds.). In: *Palaeontologica Nova, SEPAZ 8*, pp. 259–271.
- López-Guerrero, P., García-Paredes, I., Álvarez-Sierra, M.A., 2013. *Revision of *Cricetodon soriae* (Rodentia, Mammalia), new data from the Middle Aragonian (Middle Miocene) of the Calatayud–Daroca basin (Zaragoza, Spain)*. *J. Vertebr. Paleontol.* 33, 169–184.
- López-Guerrero, P., García-Paredes, I., Álvarez-Sierra, M.A., Peláez-Campomanes, P., 2014b. *Cricetodontini from the Calatayud-Daroca Basin (Spain): a taxonomical description and up-to-date of their stratigraphical distributions*. *C. R. Palevol* 13, 647–664.
- López-Guerrero, P., García-Paredes, I., Van den Hoek Ostende, L.W., Van Dam, J.A., Álvarez-Sierra, M.A., Hernández-Ballarín, V., Van der Meulen, A.J., Oliver, A., Peláez-Campomanes, P., 2011. *Cañada: a new micromammal succession from the Lower Vallesian and Turolian of the Daroca area (Calatayud-Montalbán basin, Spain)*. *Estud. Geol.* 67, 443–453.
- López-Guerrero, P., Oliver Pérez, A., Álvarez-Sierra, M.A., García-Paredes, I., Peláez-Campomanes, P., 2007. *El registro de los Castoridae (Rodentia, Mammalia) del Aragoniense y Vallesiense (Mioceno Medio y Superior) de las cuencas centrales Españolas*. In: Braga, J.C., Checa, A., Company, M. (Eds.), *Libro de resúmenes de las XXIII Jornadas de Paleontología de la Sociedad Española de paleontología*. Instituto Geológico y Minero de España, Universidad de Granada, Granada, pp. 118–119.
- Miller, K.G., Mountain, G.S., Browning, J.V., Kominz, M., Sugarman, P.J., Christie-Blick, N., Katz, M.E., Wright, J.D., 1998. *Cenozoic global sea level, sequences, and the New Jersey transect: results from coastal plain and continental slope drilling*. *Rev. Geophys.* 36, 569–601.
- Miller, K.G., Wright, J.D., Fairbanks, R.G., 1991. *Unlocking the icehouse: Oligocene-Miocene oxygen isotopes, eustasy, and margin erosion*. *J. Geophys. Res.* 96, 6829–6848.
- Mourik, A.A., 2010. *The Middle Miocene climate transition in the Central Mediterranean*. *Geol. Ultraiectina* 326, 1–132.
- Mourik, A.A., Abels, H.A., Hilgen, F.J., Di Stefano, A., Zachariasse, W.J., 2011. *Improved astronomical age constraints for the Middle Miocene climate transition based on high-resolution stable isotope records from the central Mediterranean Maltese Islands*. *Paleoceanography* 26, PA1210, <http://dx.doi.org/10.1029/2010PA001981>.
- Mudelsee, M., Bickert, T., Lear, C.H., Lohmann, G., 2014. *Cenozoic climate changes: a review based on time series analysis of marine benthic delta O-18 records*. *Rev. Geophys.* 52, 333–374.
- Oliver, A., (Doctoral Thesis) 2015. *Evolución del género *Megacricetodon* del Aragoniense y Vallesiense (Mioceno) de la Península Ibérica*. Universidad Complutense de Madrid, Madrid (321 p.).
- Oliver, A., Peláez-Campomanes, P., 2013. **Megacricetodon vandermeuleni*, sp. nov. (Rodentia, Mammalia), from the Spanish Miocene: a new evolutionary framework for *Megacricetodon**. *J. Vertebr. Paleontol.* 33, 943–955.
- Oliver, A., Peláez-Campomanes, P., 2014a. *Early Miocene evolution of the genus *Megacricetodon* in Europe and its palaeobiogeographical implications*. *Acta Palaeontol. Pol.*, <http://dx.doi.org/10.4202/app.00099.2014>.
- Oliver, A., Peláez-Campomanes, P., 2014b. *Evolutionary patterns of Early and Middle Aragonian (Miocene) of *Megacricetodon* (Rodentia, Mammalia) from Spain*. *Palaeontogr. Abt. A* 303, 85–135.
- Oliver, A., García-Paredes, I., Peláez-Campomanes, P., 2009a. *A geometric morphometric analysis of *Megacricetodon* (Cricetodontinae, Rodentia, Mammalia) from the Db biozone, Middle Aragonian*. *Paleontol. Evol. Mem. Especial* 6, 101–102.
- Oliver, A., López-Guerrero, P., García-Paredes, I., Álvarez-Sierra, M.A., Peláez-Campomanes, P., 2009b. *Evolution of *Megacricetodon* tooth pattern through geometric morphometric analysis*. *J. Vertebr. Paleontol.* 29 (Suppl. 3), 158A.
- Oliver Pérez, A., López-Guerrero, P., Peláez-Campomanes, P., 2008. *Primer representante del género *Megacricetodon* de la Cuenca de Calatayud-Daroca (Zaragoza, España)*. In: Esteve, J., Meléndez, G. (Eds.). In: *Palaeontologica Nova, SEPAZ 8*, pp. 317–329.
- Peláez-Campomanes, P., Hernández-Ballarín, V., Oliver, A., 2015. *New approaches to examining and interpreting patterns of dental morphological variability in Miocene cricetidids*. *Palaeobiol. Palaeoenvir.* 95, 405–414.
- Van Dam, J.A., Abdul Aziz, H., Álvarez-Sierra, M.A., Hilgen, F.J., Van den Hoek Ostende, L.W., Lourens, L.J., Mein, P., Van der Meulen, A.J., Peláez-Campomanes, P., 2006. *Long-period astronomical forcing of mammal turnover*. *Nature* 443, 687–691.
- Van Dam, J.A., Krijgsman, W., Abels, H., Álvarez-Sierra, M.A., García-Paredes, I., López-Guerrero, P., Peláez-Campomanes, P., Venstra, D., 2014. *Updated chronology for the Middle to Late Miocene mammal sites of the Daroca Area (Calatayud-Montalbán Basin, Spain)*. *Geobios* 47, 325–334.
- Van den Hoek Ostende, L.W., Furió, M., 2005. *Spain*. In: Van den Hoek Ostende, L.W., Doukas, C.S., Reumer, J.W.F. (Eds.), *The fossil record of the Eurasian Neogene insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I. Scripta Geol. Spec. Issue* 5, 149–284.
- Van den Hoek Ostende, L.W., Furió, M., García-Paredes, I., 2009. *New data on *Paenelimmocetus* from the Middle Miocene of Spain in support of the subfamily Allosoricinae (Soricidae, Mammalia)*. *Acta Palaeontol. Pol.* 54, 159–164.
- Van den Hoek Ostende, L.W., López-Guerrero, P., Peláez-Campomanes, P., Álvarez-Sierra, M.A., García-Paredes, I., 2012. *Early Late Miocene insectivores (Eulipotyphla, Mammalia) from the Cañada section (Province of Zaragoza, east Central Spain)*. *C. R. Palevol* 11, 495–506.
- Van den Hoek Ostende, L.W., Mayda, S., Oliver, A., Madern, A., Hernández-Ballarín, V., Peláez-Campomanes, P., 2015. *Aliveri revisited, a biogeographical appraisal of the Early Miocene mammals from the eastern Mediterranean*. *Palaeobiol. Palaeoenvir.* 95, 271–284.
- Van der Meulen, A.J., Daams, R., 1992. *Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 93, 227–253.
- Van der Meulen, A.J., Peláez-Campomanes, P., Daams, R., 2003. *Revision of medium-sized Cricetidae from the Miocene of the Daroca-Villafeliche area in the Calatayud-Teruel basin (Zaragoza, Spain)*. In: López-Martínez, N., Peláez-Campomanes, P., Hernández-Fernández, M. (Eds.), *En torno a Fósiles de Mamíferos: Datación, Evolución y Paleoambiente*. *Coloq. Paleontol. Vol. Extr.* 1, 385–441.
- Van der Meulen, A.J., García-Paredes, I., Álvarez-Sierra, M.A., Van den Hoek Ostende, L.W., Hordijk, K., Oliver, A., López-Guerrero, P., Hernández-Ballarín, V., Peláez-Campomanes, P., 2011. *Biostratigraphy or biochronology? Lessons from the Early and Middle Miocene small Mammal Events in Europe*. *Geobios* 44, 309–321.
- Van der Meulen, A.J., García-Paredes, I., Álvarez-Sierra, M.A., Van den Hoek Ostende, L.W., Hordijk, K., Oliver, A., Peláez-Campomanes, P., 2012. *Updated Aragonian biostratigraphy: small mammal distribution and its implications for the Miocene European Chronology*. *Geol. Acta* 10, 159–179.
- Van der Meulen, A.J., Peláez-Campomanes, P., Levin, S.A., 2005. *Age structure, residents, and transients of Miocene rodent communities*. *Am. Nat.* 165, E108–E125.
- Zachos, J.C., Pagani, M., Sloan, L., Billups, K., Thomas, E., 2001. *Trends, rhythms, and aberrations in global climate 65 Ma to present*. *Science* 292, 686–693.