

1 The Aragonian and Vallesian high-resolution micromammal succession from the
2 Calatayud-Montalbán Basin (Aragón, Spain).
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7 Succession haute résolution des micromammifères de l'Aragonien et Vallesien dans le
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9 Bassin de Calatayud-Montalbán (Aragón, Espagne).
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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 to major climate changes based on marine stable oxygen and carbon isotope records. The episodes $\delta^{18}\text{O}$ Mi-2 and Mi-3 are significantly correlated with major micromammal turnover at the boundaries between lower and middle Aragonian and middle and upper Aragonian, respectively. Our results support the existence of a selective turnover during the Aragonian and lower Vallesian.

Keywords: Neogene, Miocene, faunal turnover, Global Climatic Events, biodiversity.

Résumé

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 aux changements climatiques majeurs grâce aux enregistrements isotopiques marins

(oxygène et carbone). Les événements $\delta^{18}\text{O}$ Mi-2 and Mi-3 sont significativement corrélés aux renouvellements fauniques qui touchent les micro-mammifères

respectivement aux limites inférieur/moyen et moyen/terminal de l'Aragonien. La

présente analyse supporte l'existence d'un renouvellement faunique sélectif au cours de l'Aragonien et du Vallésien inférieur.

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3 **Mots-clés:** Néogène, Miocène, renouvellements fauniques, Événements Climatiques
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5 Globales, biodiversité.
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10 **1.Introduction**

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12 The Calatayud-Montalbán Basin (North Central Spain; Fig. 1) has yielded a rich and
13 comprehensive lowerto upperMiocene mammal record whichforms the basis of the
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15 Ramblian (Daams et al., 1987) and Aragonian (Daams et al., 1977) continental
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17 stages,and the widely used local zonation that has been defined in this basin(Daams et
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19 al., 1999a; Van der Meulen et al., 2012). The area owes its importance to a number of
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21 factors. First, there is the sheer multitude of small mammal localities.In the northern
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23 part of the basin, in the vicinity of the villages ofVillafeliche,Daroca, and Nombrevilla,
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25 over 150 small mammal assemblages have been collected from alluvial fan and shallow-
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27 lake deposits. These localities have been found in superposition in a series of sections,
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29 allowing good stratigraphic control. The stratigraphic span of these localities ranges
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31 from the uppermost Ramblian (~17 Ma) till the uppermost lower Vallesian (~10 Ma)
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33 (Daams et al., 1999a; Van Dam et al., 2014)., The second important characteristic of the
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35 area is its suitability for magnetostratigraphy, sincemost of the sections preserved good
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37 palaeomagnetic signal (Garcés et al., 2003; Krijgsman et al., 1994; Krijgsman et al.,
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39 1996; Van Dam et al., 2014). In combination with the superposition of localities and the
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41 biostratigraphy, the magnetostratigraphy provides excellent time control for the major
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43 part of the sequence. This allows straightforward correlations and the building of
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45 palaeobiogeographical hypotheses at European scale (Álvarez-Sierra et al., 2013; Oliver
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47 and Peláez-Campomanes, 2013; Oliver and Peláez-Campomanes, 2014a; Van den Hoek
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49 Ostende et al., 2015; Van der Meulen et al., 2011).
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1 The study of the basin also included analyses involving the long-term evolution of
2 micromammal communities alongwide temporal periods (e.g., Daams et al., 1999c; Van
3 der Meulen and Daams, 1992), which have started to increase especially over the last
4 decade (e.g., Hordijk, 2010; Peláez-Campomanes et al., 2015; Van Dam et al., 2006;
5 Van der Meulen et al., 2005).

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11 This brings us to the third important characteristic of the sequence, which is the
12 homogeneity of depositional environments. Because all localities are from alluvial fan
13 and shallow-lake deposits with similar sedimentation rates (see Daams et al., 1999a for
14 details on the sedimentology of the studied area), the taphonomic bias is reduced to a
15 minimum, allowing for direct comparison of assemblages. Although a certain degree of
16 bias cannot be excluded (e.g., accumulation by different types of raptors), we can safely
17 assume that these will not influence the major patterns in community changes observed
18 in the sequence (Van der Meulen et al., 2005). Additionally, the sampling coverage of
19 thesequence was calculated by Van der Meulen et al. (2005) using the number of upper
20 and lower first and second molars of rodents from 96 localities of the studied area. The
21 cumulative curve of sample sizes of the temporally ordered localities yields a good fit
22 with the linear regression line ($R^2 = 0.98$), indicating that the sections have been
23 sampled quite evenly (Van der Meulen et al., 2005:fig. A1).

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29 Recent studies, dealing with different aspects of the Calatayud-Montalbán Basin, have
30 resulted in the proposition of more refined biostratigraphic scale and new numerical ages
31 for the fossil localities succession (Van der Meulen et al., 2012; Fig. 2). All these new
32 interpretations are based on an increased number of localities studied (Álvarez Sierra et
33 al., 2003; López-Guerrero et al., 2011), new magnetostratigraphic information (Garcés
34 et al., 2003; Van Dam et al., 2014), and recent important revisions on micromammal
35 groups recorded in the basin (García-Paredes, 2006; García-Paredes et al., 2009; García-

1 Paredes et al., 2010; Hordijk, 2010; López-Guerrero, 2014; López-Guerrero et al., 2008;
2 López-Guerrero et al., 2013; López-Guerrero et al., 2014a; López-Guerrero et al., 2014b;
3 Oliver, 2015; Oliver and Peláez-Campomanes, 2013; Oliver and Peláez-Campomanes,
4 2014b; Van den Hoek Ostende and Furió, 2005; Van den Hoek Ostende et al., 2009;
5 Van den Hoek Ostende et al., 2012; Van der Meulen et al., 2003).

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7 Here, we use all new information to present an updated framework for the evolution of
8 the Aragonian and lower Vallesian faunas in the Calatayud-Montalbán Basin and to
9 identify possible global environmental factors that may have triggered faunal changes.
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11 **2. The small mammal fossil record from the Aragonian and Vallesian of the** 12 **Calatayud-Montalbán Basin**

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

18 Since the last synthesis by Daams et al. (1999a), which involved the rodents
19 exclusively, the published information on the small mammals from the Aragonian and
20 lower Vallesian of the Calatayud-Montalbán Basin has increased considerably. In this
21 way, Van der Meulen et al. (2012) provided an important update in the taxonomical
22 information for the lower and middle Aragonian. Figure 2 summarizes the most recent
23 taxonomical and biostratigraphical information published on the Aragonian and lower
24 Vallesian from the Calatayud-Montalbán micromammal fossil record (Álvarez Sierra et
25 al., 2003; García-Paredes, 2006; García-Paredes et al., 2009; García-Paredes et al.,
26 2010; Hordijk, 2010; López-Guerrero, 2014; López-Guerrero et al., 2011; López-
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1 Guerrero et al., 2013; López-Guerrero et al., 2014a; López-Guerrero et al., 2014b; Oliver
2 et al., 2009a; Oliver, 2015; Oliver et al., 2009b; Oliver Pérez et al., 2008; Van Dam et
3 al., 2006; Van Dam et al., 2014; Van den Hoek Ostende and Furió, 2005; Van den Hoek
4 Ostende et al., 2009; Van den Hoek Ostende et al., 2012; Van der Meulen et al., 2003).
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9 The increase on the palaeontological information was accompanied by new
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2.1. The lower Aragonian

22 Since its redefinition by Daams et al. (1987), the lower Aragonian includes the
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44 Within the lower Aragonian, three different migration events involving cricetids are
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1 Most of these taxa had survived the Ramblian-Aragonian boundary, and their
2 association is typical for Iberian Early Miocene faunas. Across Zone Cb, the decrease in
3 glirid species continues. The cricetids increase in species richness with the entrance in
4 the basin of a second lineage of *Democricetodon* of small size (*D. franconicus*) and the
5 genus *Eumyarion*. The arrival of these cricetids, which present affinities with the central
6 European representatives, co-occur with the first occurrence of a second *Prolagus*
7 lineage (*P. vargasensis*). Across the zones Ca and Cb there is a momentary occurrence of
8 the heterosoricid shrew *Heterosorex*. For the first time during the early Aragonian, the
9 assemblages are dominated by eomyids (*Ligerimys ellipticus*) and cricetids instead of
10 eomyids and glirids.
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27 **2.2. The middle Aragonian**

28 The middle Aragonian includes the Zones Da to E, from ~15.93 Ma to
29 ~13.78 Ma, (Daams et al., 1999a; Van der Meulen et al., 2012). In central Spain, it
30 represents a period of low richness in rodent species, with cricetids as the most abundant
31 group, while the genus *Ligerimys*, dominant during the Ramblian and lower Aragonian,
32 went extinct. At the same time, the Talpidae, represented since the Ramblian by the
33 genus *Desmanodon*, disappear from the area, as does the small
34 gymnure *Galerix symeonidisi*. The glirids show low relative abundances; *Microdyromys*
35 increases in relative abundances compared to the glirids of simpler dental pattern, which
36 were dominant through the Early Miocene in the Iberian Peninsula. The beginning of
37 the middle Aragonian includes a period of high turnover with quick replacement of
38 species, some of them with very short distributions. This rapid substitution of species is
39 reflected in the short duration of the two first biozones, Da and Db, from ~15.93 Ma to
40 ~15.60 Ma (Van der Meulen et al., 2012). Both, and especially Zone Db (~15.85 Ma,
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~15.60Ma), includes rodent species with affinities with central European taxa, such as *Megacricetodon vandermeulenii* and *Prodryomys* (Oliver and Peláez-Campomanes, 2013 and García-Paredes, 2006, respectively). Zone Dc (~15.60 Ma, ~14.82Ma) includes the last occurrence of *Atlantoxerus blacki* and *Spermophilinus besanus*. *Microdyromys* for the first time represented by three species in the area (García-Paredes et al., 2010). Zone Dd (~14.81Ma, ~14.75Ma) contains impoverished faunas with a strong dominance of cricetids. Across all Zone Dd, there are three species of *Microdyromys*, 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 *Pseudodryomys rex*, *Tempestia ovilis* and *Muscardinus thaleri*. For a short period of time, *Keramidomys* 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, ~13.78Ma), *Pseudodryomys sibericus*, *Simplomyssimplificidens*, *Microdyromys 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.

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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 *Megacricetodonibericus* lineage combined with the presence of representatives of small-sized *Megacricetodon*. In addition to the *Megacricetodon* evolution, López-Guerrero et al. (2013, 2014a,b) 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, ~13.62Ma) can be recognized by the presence of *Megacricetodonrafaeli* and *Cricetodonsansaniensis*. 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, ~13.27Ma) can be easily recognized by the presence of *Megacricetodon minor* and *Cricetodonjotae*, a smaller and more advanced Cricetodontini (López-Guerrero et al., 2014b). The next local biozone, Zone G2 (~13.27 Ma, ~13.00Ma), 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 *Turiasorexpierremani* within this zone. The cricetids are very abundant, with *Megacricetodoncrusafonti* as the most characteristic and abundant taxon.

Approximately the second half of the upper Aragonian corresponds to the Zone G3 (~13.00 Ma, ~11.26Ma). This long zone represents a transition towards the Vallesian faunas. In the basin, common taxa such as *Armantomys*, *Paragilirulus*, *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

1 different species. Also notable is the achievement of the ‘*Hispanomys* evolutionary
2 degree’ in the representatives of the tribe Cricetodontini. Although this tribe is not very
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4 abundant across this biozone, its representatives had an important turnover involving
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6 four species (López-Guerrero, 2014; López-Guerrero et al., 2014a; López-Guerrero et
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8 al., 2014b). Zone G3 also includes the re-entry of the castorids in the Calatayud-
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10 Montalbán Basin, after a time interval of absence spanning ~7 Ma (Álvarez Sierra et al.,
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12 2003; López-Guerrero et al., 2007), and the first appearance of the gymnure *Parasorex*.
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14 Álvarez-Sierra et al. (2003) pointed out that representatives from other northern Spanish
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16 basins enter in the upper half of the Zone G3. These results, indicating a decrease in
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18 isolation among different basins, have been further supported by López-Guerrero et al.
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20 (2008) studying the Cricetodontini and, also, by Abella et al. (2012) with carnivores.
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29 **2.4. The lower Vallesian**

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31 Zone H was defined by Daams and Freudenthal (1988) based on the presence of
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33 *Megacricetodon ibericus*. Álvarez Sierra et al. (2003) informally used the co-occurrence
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35 of latter species and *Hispanomys* to define Zone H. Nevertheless, López-Guerrero et al.
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37 (2008, 2014b), demonstrated the presence of *Hispanomys* representatives already in G3
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39 localities. Therefore, Van Dam et al. (2014) implicitly modified that informal definition of
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41 the Zone H using, as lower boundary, the first occurrence
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43 of *Hispanomys nombrevillae*. According to Van Dam et al. (2014), the age of the lower
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45 boundary of Zone H could be older than 11.2 Ma, implying that it was about 500 ky
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47 before the first *Hippotherium* record in the basin at the Nombrevilla classic locality.
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51 This new way to define the Zone H therefore implies, as previously pointed out by
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53 Álvarez Sierra et al. (2003), that the change towards ‘Vallesian’ micromammal faunas
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55 was already achieved in the upper part of the Aragonian.
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1 The upper parts of the sections in the Daroca-Nombrevilla area correspond to the Zone
2 I. The faunas of this period show strong differences with previous ones by the absence
3 of members of the *Megacricetodonibericus* lineage (the most abundant and
4 characteristic lineage of the upper Aragonian) and the presence of *Cricetulodon*. The
5 glirid *Ramys* has also been considered as a typical genus for Zone I in the Calatayud-
6 Montalbán Basin. However, after the study of the material available from the Cañada
7 localities, a recently published stratigraphic section near the Carrilanga one, this taxon
8 has been recorded associated with *H. nombrevillae*, indicating that its first occurrence in
9 the basin predates the replacement of the *Hispanomys* forms (López-Guerrero et al.,
10 2011). Around the same time, moles, now represented by *Desmanella*, also return to the
11 basin (Van den Hoek Ostende et al., 2012). The uppermost part of this biozone contains
12 the first occurrence of the murid *Progonomys*, the regular presence of which defines the
13 lower boundary of the upper Vallesian (10 Ma, Van Dam et al., 2014).

34 **3. Micromammal turnover in Miocene of the Calatayud-Montalbán Basin and** 35 **their correlation to global climatic changes**

41 **3.1. Tripartite division of the Aragonian.**

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

1 early Aragonian, characterized by a high diversity and relative abundance of endemic
2 Spanish glirids, combined with the progressive presence of modern cricetids coming
3 from the East; b) the middle Aragonian, characterized by the decline of glirids and the
4 rise of cricetids, with communities that are relatively poor in micromammal species; c)
5 the late Aragonian, characterized by an increase in species richness but still with a clear
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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 in Figure 2), and the second one to the community reorganization (Fe 5 in Figure 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 equivalent to Aragonian and early Vallesian ages (Cramer et al., 2009; Miller et al., 1991; Miller et al., 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), which 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 “Ice-House”, 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

1 appear to be predominantly open country dwellers (Daams et al., 1999c; Van der
2 Meulen et al., 2005). Hordijk (2010) pointed out that, in the Calatayud-Montalbán
3 Basin, Zone B is dominated by herbivores, especially *Lagopsis penai*. Their dominance
4 could indicate the presence of open landscapes at that time, as was also noted by Van der
5 Meulen and Daams (1992).
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12 The faunal change that occurred between the lower and middle Aragonian (Fig. 2, Fe 2),
13 involving the beginning of the dominion of cricetids over the eomyids and glirids, is
14 included within the MCO and the Monterrey Carbon Excursion (Fig. 3). It corresponds
15 approximately with the Mi2 Oxygen isotope zone of Miller et al. (1991) that represents
16 a relative cooling period within the warm conditions of the MCO (Fig. 3).
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25 The strongest taxonomical turnover is marked by the collapse of the early and middle
26 Aragonian community (Fig. 2, Fe 5) and their replacement by a new community
27 (Daams et al., 1999a; Daams et al., 1999c; Hordijk, 2010; Van der Meulen and Daams,
28 1992; Van der Meulen et al., 2005). In the general context, this corresponds
29 approximately with the end of the MMCT (Fig. 3), marked by the Mi-3 of Miller et al.
30 (1991), which is a major step in the Middle Miocene climatic cooling (Mi-3b in Abels
31 et al., 2005). The new upper Aragonian community is defined by the presence of a new
32 set of sciurids and cricetids together with glirids associated to woodlands replacing the
33 old resident open-land dwellers (Van der Meulen et al., 2005).
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50 **3.2. Correlation between climatic changes and local biozonation**

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52
53 Van Dam et al. (2006) studied this relationship between climate and rodent turnover
54 detecting turnover cycles of 2.4-2.5 and 1.0 over a long record of more than 20 Myr
55 based on the rodent record from the Spanish central basins. They calculated the
56 statistically significant rodent turnover peaks and related them with the major marine
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1 benthic stable oxygen isotope events and with the predicted time of rodent turnover
2 based obliquity and eccentricity cycles. Hordijk (2010), at a lower scale and including
3 lagomorphs in the analyses, explained changes in the structure of the small mammal
4 community based on their relationship with the local effects of global changes in
5 climate.
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10 The refined taxonomic and stratigraphic information available allows us to propose the
11 correlation of smaller faunal turnover corresponding to biostratigraphical zonal
12 boundaries with several global climatic changes. The discussion is not only based on the
13 quantitative aspects, number of originations and extinctions, of the micromammal
14 turnover (Van Dam et al., 2006), but also in qualitative ecological preferences of the
15 taxa (Van der Meulen et al., 2005), which help us to interpret the patterns of change.
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27 The first of these smaller faunal turnovers that could be correlated with climatic changes
28 is at the base of Zone Dd (Fig. 2, Fe 3), and approximately corresponds to the Mi-2a at
29 the beginning of the MMCT and the carbon isotope decrease (Cramer et al., 2009)
30 shown in Figure 3. This was the onset of a presumably dryer period in the basin, leading
31 the extinction of common taxa that were generally frequent in environments considered
32 as more humid, such as *Spermophilinus* and *Eumyarion* (Casanovas-Villar and Agustí,
33 2007).
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45 Another important faunal turnover, but more gradual than the one discussed above, is
46 that occurring across the end of Zone Dd and the beginning of Zone E (Fig. 2, Fe 4). The
47 general climatic trend is towards colder temperatures and this could promote the
48 migration of northern representatives that enter the central Spanish basins for the first
49 time. The transition between Dd and E faunas can be related to the oxygen isotopic zone
50 Mi-3a (Fig. 3) correlated to the base of the chron C5.Acr (Abels et al., 2005). This event
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1 could not be differentiated by Van Dam et al. (2006) from the turnover detected at the
2 end of the middle Aragonian due to the coarser taxonomical resolution of the data.
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5 As discussed above, Zone G3 shows important community changes although there is
6
7 not a high turnover rate restricted to a shorter period (Fig. 2, Fe 6). There are two
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9 important events within this zone such as the re-entry of the castorids into the basin
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11 after more than 7 Ma of absence (ÁlvarezSierra et al., 2003; López-Guerrero et al.,
12
13 2007) and the entrance of northern species of *Hispanomys* and carnivores into the basin
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15 (Abella et al., 2012; ÁlvarezSierra et al., 2003; Lopez-Guerrero, 2014). The latter
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17 turnover event could be related to Mi-5 at the base of chron C5r.2r.
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23 Finally, there is an important turnover between Zone H and I, as pointed out by
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25 ÁlvarezSierra et al. (2003) and Van Dam et al. (2014), characterized mainly by the
26
27 replacement of the large representatives of *Democricetodon* and *Megacricetodon* by the
28
29 new immigrant *Cricetulodon*. This replacement may be correlated to Mi-6 (Fig. 3),
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31 situated at the lower part of chron C5N (Miller et al., 1998) with an approximate age of
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33 10.45-10.35 Ma (Van Dam et al., 2006).
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41 **4. Final remarks**

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43 Theseven intervals of faunal turnover detected in the small-mammal succession in the
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45 Calatayud-Montalban Basin, based on quantitative calculations of origination and
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47 extinction of taxa (Van Dam et al., 2006) and the qualitative ecological preferences
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49 assigned to the different taxa recorded (Van der Meulen and Daams, 1992; Van der
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51 Meulen et al., 2005), are confidentially correlated to main features in the stable marine
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53 oxygen and carbon isotope records. This correlation indicates that,even though
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55 interactions between community members are theoretically very important for the
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57 establishment of the community structure and turnover, the strongest changes in the
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1 micromammal turnover pattern are explained by the local effects of global changes in
2 climate.
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5 The analyses carried out on the assemblages from the Calatayud-Montalbán Basin have
6 shown the existence of a selective turnover during the Aragonian and lower Vallesian,
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8 as pointed out already by Van der Meulen and Daams (1992) and Van der Meulen et al.
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10 (2005). As discussed throughout this work, there are a correspondence between the
11
12 direction of the climatic changes and the associated taxa that originate or went extinct in
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14 the basin.
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20 In addition to the major changes in community composition, the revised taxonomy of
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22 many micromammal groups has shown a progressive morphometric change in many
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24 lineages; such as, the lineages *Democricetodon hispanicus*-*D. lacombai* and
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26 *Democricetodon franconicus*-*D. crusafonti*, which show size increase and parallel
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28 evolution during their stratigraphical range (Van der Meulen et al., 2003), the glirid
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30 genus *Simplomys* across the lower and middle Aragonian (García-Paredes et al., 2009),
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32 also with changes in size and morphology, or the lagomorph *Lagopsis* (Hordijk, 2010).
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38 Apart from the turnover of species, most of these global climatic changes also induced
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40 important morphological and metrical changes of micromammal taxa (Peláez-
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42 Campomanes et al., 2015; Van der Meulen et al., 2003).
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Figures and table captions:

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Figure 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).

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

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

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

Figure 3. Simplified scheme of global climatic conditions based on stable isotopes for the period equivalent to Aragonian and early Vallesian ages. Circles with numbers

1 indicate main faunal events (Fe) discussed in the text. Modified after Cramer et al.

2 (2009) and Mourik et al. (2010).

3
4 Figure 3. Schéma simplifié, et basé sur les isotopes stables, des conditions climatiques

5 aux périodes équivalentes à l'Aragnien et au Vallésien basal. Les cercles chiffrés

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7 indiquent les principaux événements fauniques (Fe) discutés dans le

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9 texte. Modifié après Cramer et al. (2009) et Mourik et al. (2010).

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Figure 1

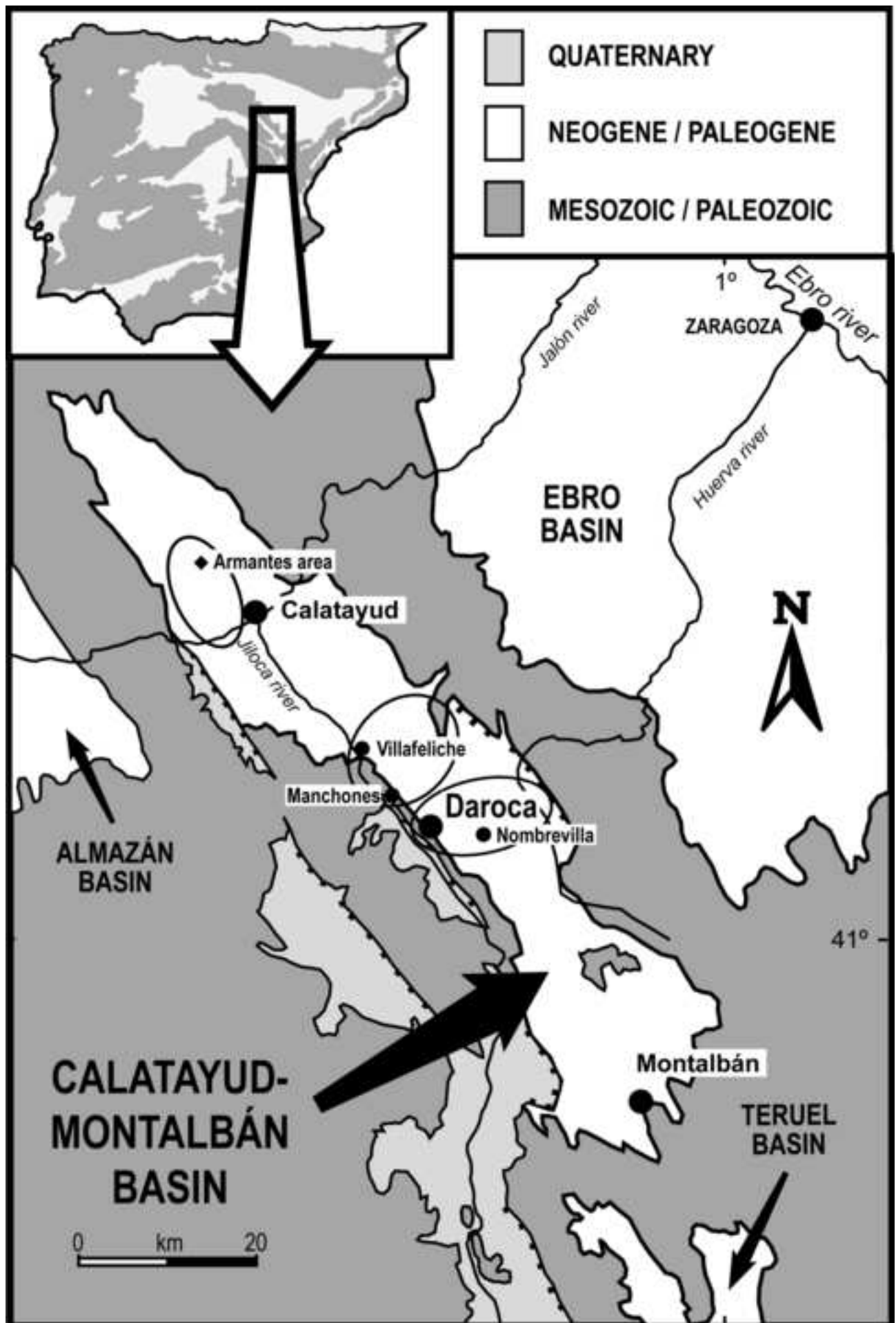


Figure 2

