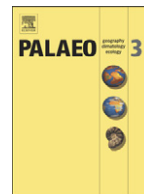




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Biogeographic provincialism in rodent faunas from the Iberocccitanian Region (southwestern Europe) generates severe diachrony within the Mammalian Neogene (MN) biochronologic scale during the Late Miocene

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ABSTRACT

In order to develop paleoecological studies involving many fossil sites, there is a need to establish a consistent time framework, which enables us to arrange the fossil associations according to a sequence of biotic events and subsequently to test a relationship with paleoenvironmental changes. The nature of the continental fossil record has given rise to much controversy with regard to the establishment of general biostratigraphical scales. Additionally, biochronological scales are sometimes all that can be proposed. The primary goal of the present paper is to present a time arrangement for the Iberocccitanian micromammalian fossil sites from the latest Middle Miocene to the Mio–Pliocene boundary, spanning around 7 million years (approximately 12.61–4.95 Ma). Herein we study over one hundred faunal lists of rodents from the Iberocccitanian Region, compiled from the literature. Previous research has described two biogeographical provinces in our study area: a northern one (Vallès–Penedès and southeast France) and a southern one (all the Iberian basins, except the Vallès–Penedès). We therefore conducted Alroy's Maximum Likelihood Appearance Event Ordination (ML AEO) methodology, applying it to the database compiled for each province. Finally, using available numerical dates for a quarter of the sites, we obtained a calibrated ordination for all localities. In each analysis, the results obtained are roughly coherent with the Mammalian Neogene units (MN) and allow estimation of the numerical ages for the entire set of fossil sites included in the study. Nevertheless, our results show severe diachrony between the two biogeographic provinces of the Iberocccitanian Region in relation to the MN boundaries, which might be linked to the existence of a refuge area associated with more humid environments in the northern province.

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1. Introduction

The study of the time framework in which we locate extinct species is very important for developing any paleobiological research, and enables us to identify evolutionary and ecological changes in time and space. In this context, some fossils can provide very important data on the chronology of the deposits in which they were found, if they are correctly interpreted (Eicher, 1973; Murphy, 1994; Aguirre, 1997). Several biostratigraphic and biochronological scales have been developed for European continental sediments and fossils. Undoubtedly, one of the most commonly used is the one based on Mammalian Neogene units (MN), defined by Pierre Mein (1975) for establishing a biochronological framework for Europe; this scale has been reviewed on several occasions (Mein, 1979, 1990, 1999; Fahlbusch, 1991; de Bruijn et al., 1992; Agustí et al., 2001). The MN units were defined according to the first and last appearances of some characteristic taxa,

to characteristic associations between two or more genera, and to evolutionary changes recorded in some lineages. Additionally, one reference locality was defined for each MN unit, and all the Late Miocene reference sites, in particular, are located on the Iberian Peninsula (de Bruijn et al., 1992; Mein, 1999): Can Llobateres (MN 9), Masía del Barbo (MN 10), Crevillente 2 (MN 11), Los Mansuetos (MN12) and Arquillo 1 (MN13)). One problem arising with the MN units, however, is the possibility that some of the genera described in these reference localities might not be present in other localities of the same age. Such a problem is mainly due to biogeographic provinciality (Álvarez-Sierra et al., 1990; Alroy et al., 1998; van Dam et al., 2001; van Dam, 2003; Alba et al., 2006; Kálin and Kempf, 2009; van der Meulen et al., 2011).

The last decade has seen the spread of new studies based on statistical multivariate analysis, which enable time ordination of fossil sites. These statistical tools use all the taxa described in a fossil site, and can be very useful for dating some stratigraphically isolated localities or sites where no characteristic taxa are found (Azanza et al., 1997a; van Dam, 2003; Fortelius et al., 2006). For example, the Maximum Likelihood Appearance Event Ordination (ML AEO; Alroy,

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2000) has been used in biochronological studies of Cenozoic mammals from North America (Alroy, 1992, 1994), South America (Prado et al., 2001), Africa (Alroy, 1994) and Europe (Azanza et al., 1997b; Alroy et al., 1998; Hernández Fernández et al., 2004; Domingo et al., 2007). The ML AEO allows ordination of fossil sites according to values (AEO coefficients) obtained on the basis of their faunal lists. These values can be correlated with the numerical ages of the localities for which geochronological data are available.

The present work relies on the importance of establishing a time context for the rodent fossil sites from the Iberocccitanian Region (Iberian Peninsula and central–southeastern France) between the latest Middle Miocene and the Mio–Pliocene boundary. This time period represents roughly 7 million years, covering six Mammal Neogene units, from MN 7/8 to MN 13. Its interest resides in the important climatic, paleoenvironmental and biotic events that, within a context of global temperature decrease (Agustí et al., 2001; Zachos et al., 2001), have been described for this interval: the Vallesian Crisis (Moyà-Solà and Agustí, 1987; Morales et al., 1999), and later the development of C4 dominated ecosystems (Cerling et al., 1997a, 1997b; Domingo et al., 2009), or the Messinian Salinity Crisis (Hsü et al., 1977; van der Made et al., 2006). The use of ML AEO enabled us to establish numerical ages for all the study sites, and to generate a time framework comparable with previous works, which could be used for future paleoecological or macroevolutionary studies.

2. Materials and method

2.1. Material

The Iberocccitanian Region is interesting due to the considerable present and past environmental differences from the rest of Europe (Wolfe, 1985; Gregor and Velitzelos, 1987; Mai, 1989; Pickford and Morales, 1994; Kovar-Eder et al., 1996; López-Guerrero, 2006; van der Made et al., 2006). These differences are associated with an increase in aridity from northeastern to southwestern Europe (Jiménez-Moreno and Suc, 2007; Furió et al., 2011). At the continental scale, this area could be considered as a uniform biogeographic unit, but when it is examined in detail, two mammalian bioprovinces arise (Álvarez-Sierra et al., 1985; Alberdi and Azanza, 1997; Daams et al., 1998; Morales et al., 1999; Heikinheimo et al., 2007), recognizable since the Eocene (Casanovas-Cladellas and Moyà-Solà, 1992; Peláez-Campomanes, 1993; Badiola et al., 2009). The northern province includes fossil sites from the Rhône, Provence, Cucuron–Basse Durance and Languedoc–Rousillon basins from southeastern France, and the Vallès–Penedès basin from Catalonia. All the other fossil sites from the Iberian Peninsula are included in the southern province.

By reviewing the bibliography available up to June 2010, we compiled more than 200 rodent faunal lists from Iberocccitanian fossil sites dated between the latest Middle Miocene and the Miocene–Pliocene boundary. These fossil sites are from eighteen basins: Alfambra–Teruel, Alicante, Baixo Tejo, Castellón, Calatayud–Daroca, Cucuron–Basse Durance, Duero, Fortuna, Granada, Guadix–Baza, Híjar, Languedoc–Roussillon, Murcia, Provence, Tajo, Rhône, Valencia and Vallès Penedès (Fig. 1). These Cenozoic basins provide the best-known fossil record of rodent faunas on the European continent (Daams et al., 1997; Daams et al., 1998; Agustí et al., 2001; Alba et al., 2001; van Dam, 2003; Sesé, 2006; van der Made et al., 2006; Palombo and Sardella, 2007).

In order to prepare the database on which this research is based, we needed to update the systematics of rodent species to the latest taxonomy. Additionally, some constraints were applied to the fossil sites used in this study. Firstly, the minimum sample required to include a fossil site in our study was 100 molars (including first and second upper and lower molars). This number is considered the minimum necessary to render a representative sample of the original paleocommunity (Daams and van der Weerd, 1978; Daams et al.,

1999b). This restriction was overlooked in the case of those poor localities that were characterized by their interesting geographic location or stratigraphic importance. The second criterion was that the number of taxa defined at the species level cited at any locality should be two or more. Our database considers finally 973 records of 193 rodent species in 130 fossil sites (see Appendix 1).

2.2. Methods

We employed the Maximum Likelihood Appearance Event Ordination (ML AEO), which was developed by Alroy (2000). First, Alroy (1992) developed the Disjunct Distribution Ordination (DDO) methodology, which counts the number of conjunctions (two taxa are found on the same faunal list) and disjunctions (when two taxa are not conjunct on any list) on each faunal list. This method can deduce virtual conjunctions (implied conjunctions) between contemporary taxa that are not really conjunct on any faunal list because the relationships between them can be deduced by comparison with other shared conjunct taxa from different lists. The Conjunction Index (CI = known conjunctions/implied conjunctions) defines the reliability of the analysis (Alroy, 1992, 1994), which augments with an increase in the values of this index. The analysis does not consider species exclusive to one locality, known as singletons. A new version named Appearance Event Ordination (AEO; Alroy, 1994) makes it possible to include available information on stratigraphic superposition between fossil localities (Wing et al., 1995; Hernández Fernández et al., 2004; Hammer and Harper, 2006). This software calculates for each faunal list the First Appearance Event (FAE) of one species with regard to the Last Appearance Event (LAE) of another. In each case, it establishes a relationship between these events, F/L (First/Last), showing which First Appearance Events are known to pre-date which Last Appearance Events. Based on these events for each species, the software documents the concurrent range zone, defined by Alroy (1994) as the interval between the youngest first appearance event and the oldest last appearance event of all the species recorded in each fossil site. Finally, the ML AEO (Alroy, 2000) includes a new statistical framework, based upon the maximum likelihood paradigm (Dempster et al., 1977). This is more suitable for this type of study because the analyses performed in such a new framework usually generate fewer implied conjunctions (Alroy, 2000).

The main difference between ML AEO and other classic methodologies in biochronologic studies is that, whereas the latter are mainly based on characteristic taxa, the former uses all the taxa cited in one fossil locality. The advantage of Alroy's method is that ML AEO can use the temporal information provided by the whole paleocommunity (van Dam, 2003; Fortelius et al., 2006). Furthermore, the data may be independent from the stratigraphic context, which enables us to evaluate the age relationships of stratigraphically isolated sites (Alroy, 1992; Azanza et al., 1997a).

We applied the ML AEO method using the software CONJUNCT (version OS10.4.6), which was developed by Alroy and Kosnik (2006) and which is freely available at <http://www.nceas.ucsb.edu/~alroy/biochronology.html>.

Since the taxonomic information on the rodent fossil record from our study area is highly resolved (López Martínez et al., 1987; Calvo et al., 1993; Sesé, 2006), we performed the analysis at the species level. This provides higher biochronological resolution than if the taxonomic data are used at the genus level (Domingo et al., 2007). The taxa identified as cf., aff. or ? in the bibliography were considered to belong to their nominal species, in consonance with the suggestion by Alroy (1992). We removed taxa that only appeared in one fossil site, known as singletons, because they do not provide temporal information (Alroy, 1996); 30 of these species were from sites in the southern province and 52 were from the northern one.

Several authors have suggested the inclusion of some additional fossil sites in the analysis to avoid mathematical anomalies, which

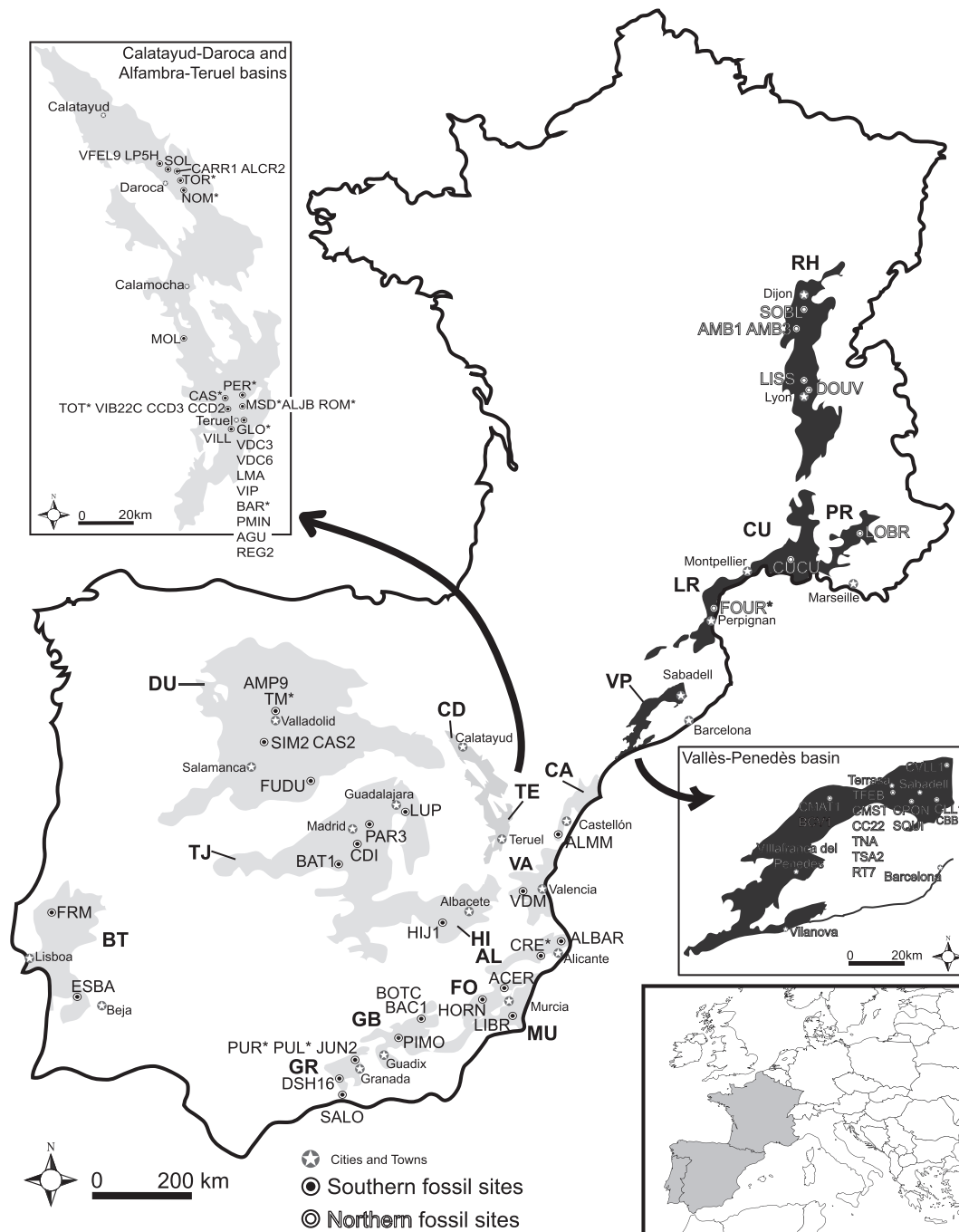


Fig. 1. Miocene fossil sites from the Iberocccitanian Region (Iberian Peninsula and central–southeastern France, Europe) considered in this study. Black basins, northern biogeographic province; Grey basins southern biogeographic province. *, stratigraphic sections with several sites; abbreviations for basins (bold) and fossil sites (regular) as in Tables 3 and 4.

affect the boundaries of the temporal distribution studied (Alroy et al., 1998; Hernández Fernández et al., 2004; Domingo et al., 2007). Therefore, in order to polarize the upper end of the sequence, we included some fossil sites from MN 14 (Caravaca 1, Celadas 9, Gorafe 1, La Gloria 4, Peralejos E and Purcal 4 for the southern province; Celleneuve, Font Estramar, Hautimagne and Vendargues for the northern province), which are younger than the study interval being analyzed. It was not possible to calibrate the lower end of the sequence with fossil sites from the MN 6 unit because of the huge differences between the rodent faunas from MN 6 and MN 7/8. There was a great change in a number of families, with some extinctions and the occurrence of many new species (van der Meulen et al., 2005; Casanovas-Vilar et al., 2010), which could be related to a sudden and

brief environmental change at the MN6–MN7/8 boundary (van der Meulen and Daams, 1992; Daams et al., 1997; Daams et al., 1999b). This generates an excess of singleton species in MN6 sites, which prevents suitable ordination of these associations. In any case, we avail of a broad set of well known fossil sites for the MN7/8 unit, which likely guarantees the correct ordination of this part of the sequence.

As an additional course of action to polarize the upper boundary, we followed Alroy (1996) and Alroy et al. (1998), adding to the software CONJUNCT a list with the rodent species exceeding the MN 14 unit (surviving taxa *sensu* Wing et al., 1995). This second polarization helps to correctly arrange even the most modern part of the sequence, and it could be seen as a supplementary security

protocol to obtain the most accurate ordination of fossil sites for the time interval of interest.

CONJUNCT supplies an algorithm named 'square graph' that can infer F/L statements among taxa that appear to be geographically disjunct making use of widespread species. Therefore, it theoretically can provide a non-problematic temporal ordination of fossil sites located in different biogeographic provinces (see Alroy, 1996; Domingo et al., 2007). For that reason, we performed a ML AEO analysis considering together the fossil sites from the two provinces. Nevertheless, following considerations of the presence of two very differentiated biogeographical provinces in our study area (Álvarez-Sierra et al., 1990; Alberdi and Azanza, 1997; Daams et al., 1998; Morales et al., 1999), we also developed an independent ML AEO analysis for each province, which allow us to avoid biogeographic effects on our analysis. In order to establish whether this approach provides a better arrangement of the fossil sites than the one based on the whole Iberocccitanian region we finally took into account the ML AEO analyses with the highest CI values.

Finally, we made a time calibration of the best ordinations obtained by the ML AEO analyses using magnetostratigraphic data on 30 fossil sites included in the study (Table 1). We developed a linear regression for each province, which relates the coefficient AEO and the numerical age obtained by geochronologic dating (mean of the chron or subchron associated to each fossil site), following the Geomagnetic Polarity Time Scale (GPTS) developed by Gee and Kent (2007). Thus, we obtained a mathematical function for each

biogeographic province that enabled us to establish the numerical age for each fossil site included in the study (Alroy, 1992; Prado et al., 2001; Hernández Fernández et al., 2004; Domingo et al., 2007).

3. Results

The ML AEO analysis of the Iberocccitanian Region obtained a CI value substantially lower than the ones in the independent analyses for the northern and southern biogeographic provinces (Table 2), which reinforces the interpretations on the existence of different contemporaneous rodent assemblages in the two areas. Therefore, although the ordination results for the analysis of the whole Iberocccitanian region are available as supplementary material (Appendix 2), we consider that the results provided by the independent analyses of the bioprovinces are more accurate. Consequently, henceforth we only comment on the results of the approach that considers separately these provinces.

Following deletion of the species recorded at only one locality, the analyses were undertaken with 99 fossil sites for the southern province and 31 for the northern province. In the case of the southern province, the analysis was developed with 116 species demonstrating 785 conjunctions (Table 2). All the faunal lists of the southern province showed 1570 F/L relationships. The relationships among the faunal lists of fossil sites in stratigraphic sections involved 328 additional F/L relationships, achieving a total of 1898 F/L relationships. In the case of the northern province, the 120 species included

Table 1
Numerical dates derived from previous magnetostratigraphic studies, associated with faunal lists, used for the calibration of the sequence of appearance events for the northern (A) and southern (B) provinces.

| Fossil site | Chron | Age (Ma) ^a | | References |
|---------------------------------|-----------------|-----------------------|--------|---|
| | | Upper | Lower | |
| A. | | | | |
| Can Vilella 1 | C3An.2n-C3An.1n | 5.894 | 6.567 | Agustí et al., 2006 |
| Torrent de Febulines 3 | C4An | 8.699 | 9.025 | Garcés et al., 1996; Agustí et al., 1997; Casanovas-Vilar, 2007 |
| Torrent de Febulines | C4An | 8.699 | 9.025 | Casanovas-Vilar, 2007 |
| Trinxera Nord Autopista | C4Ar.1r | 9.117 | 9.230 | Agustí et al., 1997; Garcés et al., 1996 |
| Trinxera Sud Autopista II | C4Ar.1r | 9.117 | 9.230 | Agustí et al., 1997; Garcés et al., 1996 |
| Can Llobateres 1 | C4Ar.3r | 9.642 | 9.740 | Agustí et al., 1997; Casanovas-Vilar, 2007 |
| Autopista Rubí-Terrasa 7 | C4Ar.3r | 9.642 | 9.740 | Agustí et al., 1997; Garcés et al., 1996 |
| Creu Conill 22 | C5r.1r | 10.949 | 11.052 | Agustí et al., 1997; Garcés et al., 1996 |
| Can Mata I (Bretxa de Can Mata) | C5r.2r | 11.099 | 11.476 | Alba et al., 2009 |
| Barranc de Can Vila 1 | C5r.3r | 11.531 | 11.935 | Alba et al., 2009 |
| B. | | | | |
| Purcal 3 | C3r | 5.230 | 5.894 | García-Alix et al., 2008 |
| Venta del Moro | C3r | 5.230 | 5.894 | Garcés et al., 1998 |
| Crevillente 6 | C3An.1n | 5.894 | 6.137 | Garcés et al., 1998 |
| Librilla | C3An.1n | 5.894 | 6.137 | Garcés et al., 1998 |
| Masia del Barbo 2A | C4Ar.1n | 9.233 | 9.308 | van Dam et al., 2006 |
| Masia del Barbo 2B | C4Ar.2r | 9.308 | 9.580 | van Dam et al., 2006 |
| Nombrevilla (classical) | C5n.2n | 9.920 | 10.949 | Garcés et al., 2003; van Dam et al., 2006 |
| Torremormojón 3 | C5n.2n | 9.920 | 10.949 | Krijgsman et al., 1996 |
| Torremormojón 4 | C5n.2n | 9.920 | 10.949 | Krijgsman et al., 1996 |
| Torremormojón 5 | C5n.2n | 9.920 | 10.949 | Krijgsman et al., 1996 |
| Nombrevilla 10 | C5r.1n | 11.052 | 11.099 | Garcés et al., 2003; van Dam et al., 2006 |
| Nombrevilla 9 | C5r.1n | 11.052 | 11.099 | Garcés et al., 2003 |
| Nombrevilla 4 | C5r.3r | 11.531 | 11.935 | Garcés et al., 2003 |
| Nombrevilla 3 | C5r.3r | 11.531 | 11.935 | Garcés et al., 2003 |
| Nombrevilla 2 | C5r.3r | 11.531 | 11.935 | Garcés et al., 2003 |
| Las Planas 5H | C5Ar.1r | 12.401 | 12.678 | Garcés et al., 2003; van Dam et al., 2006 |
| Toril 3B | C5Ar.1r | 12.401 | 12.678 | Daams et al., 1999b; Álvarez-Sierra et al., 2003; Garcés et al., 2003; van Dam et al., 2006 |
| Toril 3A | C5Ar.1r | 12.401 | 12.678 | Daams et al., 1999b; Álvarez-Sierra et al., 2003; Garcés et al., 2003; van Dam et al., 2006 |
| Toril 2 | C5Ar.1r | 12.401 | 12.678 | Daams et al., 1999b; Álvarez-Sierra et al., 2003; Garcés et al., 2003; van Dam et al., 2006 |
| Toril 1 | C5Ar.1r | 12.401 | 12.678 | Daams et al., 1999b; Álvarez-Sierra et al., 2003; Garcés et al., 2003; van Dam et al., 2006 |

^a The ages follow Gee and Kent (2007): Upper, youngest age assigned to each chron; Lower, oldest age assigned to each chron.

Table 2
Results for the biochronological analysis of the rodent faunas from southern and northern provinces.

| | Iberocccitanian Region | | Southern province | | Northern province | |
|-----------------------------|------------------------|------------------------------|-------------------|------------------------------|-------------------|------------------------------|
| | Conjunctions | Cumulative F/L relationships | Conjunctions | Cumulative F/L relationships | Conjunctions | Cumulative F/L relationships |
| Faunal lists | 1517 | 3034 | 785 | 1570 | 697 | 1394 |
| Stratigraphic relationships | 156 | 3346 | 164 | 1898 | 0 ^a | 1394 |
| Event sequence | 2973 | 10956 | 1250 | 4782 | 856 | 3110 |
| Conjunction Index | 0.51 | | 0.63 | | 0.81 | |

^a New conjunctions and F/L relationships due to stratigraphic relationships among levels were not found in the northern province.

described 697 conjunctions. The faunal lists of this province showed 1394 F/L relationships. In this case, we did not find new F/L relationships due to stratigraphic relationships among fossiliferous levels placed within stratigraphic sections (Table 2).

Data on the temporal concurrent zone (*sensu* Alroy, 1994) of the species in each fossil site are shown in Tables 3 and 4 for each analysis developed for the southern and northern provinces respectively.

Both linear regressions between the mean numerical age obtained from geochronological dating of some fossil sites and the value of the AEO coefficients obtained for these localities explained over 90% of the variance (Fig. 2). Application of these regressions to all the fossil sites allowed estimation of numerical ages for all the fossil sites studied (Tables 3 and 4).

The inferred numerical ages for the fossil sites from each biogeographical province were compared to previous biochronologic age assignments, and enabled us to calibrate the MN boundaries (Table 5, Fig. 3). In the case of the southern province, the seriation of three fossil sites was not in agreement with the MN scale (Crevillente 17, Los Valles de Fuentidueña, Freiria do Rio maior) and their data were therefore not included for the estimate of the ages of MN boundaries. Comparison of the results obtained for the two provinces shows severe diachrony of the boundaries between MN units in both provinces. The MN boundaries in the southern province were older than in the northern province, and the magnitude of such diachrony ranges, on average, from 0.5 to 1.7 million years.

4. Discussion

Our results indicate a high degree of consistency of the MN scale within both biogeographical provinces. The MN units are clearly differentiated in time and only three problematic fossil sites have been detected in the southern province.

One of these localities is the fossil site of Crevillente 17 from the Alicante Basin (SE of the Iberian Peninsula). While the results of 75% fossil sites evaluated present minimal concurrent range zones (1 unit), which indicates a high level of confidence for the values of the AEO coefficients obtained, the result for Crevillente 17 was a concurrent range zone of 5 units. This is due to the presence in this fossil level of several species with temporal distributions associated with both the MN12 and MN13 units (*Hispanomys adroveri*, *Neocricetodon lucentensis*, *Occitanomys adroveri* and *Castromys littoralis*), or even longer-lived ones (*Eliomys truci*). Paying attention to the variation of the entire concurrent range zone we could resolve the problem of this fossil site, which might be situated in an ordination consistent with the MN scale, if placed in the lower part of its range.

Although Los Valles de Fuentidueña and Freiria do Rio Maior show small ranges of the AEO value, their placements are not in agreement with the MN system. In this case, their faunal lists have low numbers of species, all with relatively long temporal ranges and, consequently, offering poor temporal resolution for these fossil sites. For example, data exist on the presence of *Megacricetodon* sp. (lineage *minor-debruijini*) in Los Valles de Fuentidueña (Alberdi et al., 1981; Sesé and López Martínez, 1981); this fact constitutes an important datum in itself because it would allow us to set the locality in the MN 9 unit and not in the MN 10 (Sesé and López Martínez, 1981; van Dam et al., 1997, 2001; Sesé, 2006).

However this taxon has not been identified at the species level and, therefore, the present analysis cannot take this information into account. Additionally, none of the taxa described at the species level in this fossil site (*Heteroxerus huerzeleri*, *Atlantoxerus adroveri*, *Chalicomys jaegeri* and *Myomimus dehmi*) is diagnostic of the MN 9 unit (Daams et al., 1998; Sesé, 2006). Similarly, the problematic placement of Freiria do Rio Maior (Antunes and Mein, 1979; Antunes et al., 1992) is derived from the absence of species truly characteristic of any particular MN unit (*Rotundomys freirensis*, *Spermophilinus bredai*, *Trogontherium minutum*, *Hispanomys peralensis* and *Progonomys hispanicus*). The species used by Antunes and Mein (1979) for the inclusion of this fossil site at the base of MN 10, *R. freirensis*, is considered a singleton in our analysis and therefore does not provide temporal information.

These kinds of problems associated with faunal composition have already been pointed out by Domingo et al. (2007). Nevertheless, as can be seen here, they constitute a marginal difficulty in time spans and areas where a great amount of fieldwork and research time have been invested, as is the case of the Iberian Peninsula for the last few decades (Daams, 1989; Daams et al., 1999a; van Dam et al., 2001; Sesé, 2006).

In reference to the ordination of localities from the Vallès–Penedès and the French basins, our results reveal a highly consistent pattern, which does not present any fossil site with conflicting positions according to the MN scale. Such congruence within this area supports the existence of environmental homogeneity and high faunal similarities among the fossil sites within the northern province (Casanovas-Vilar, 2007). Additionally, it is interesting to note that our analysis was able to separate the localities of the MN7 and MN8 units within the northern province, which supports the observations of previous authors on this issue (Agustí et al., 2001; Alba et al., 2006; Casanovas-Vilar et al., 2008; Moyà-Solà et al., 2009a; 2009b).

4.1. Diachrony of MN boundaries between southern and northern provinces

The severe diachrony found in the boundaries between MN units in both provinces is surely related to the many questions associated with the meaning of MN units, which have already been pointed out by Daams and Freudenthal (1981), Fahlbusch (1991), de Bruijn et al. (1992), Kälin and Kempf (2009) and van der Meulen et al. (2011).

Diachronic disparity in the ages of the MN units in different areas may be due to the long duration of the dispersal events of some taxa, which might result in their occurrence at different times in each bioprovince (Daams and Freudenthal, 1981; Álvarez-Sierra et al., 1985, 1990; Sen, 1997; Alroy, 1998; Steininger, 1999; van Dam et al., 2001; van Dam, 2003; Kälin and Kempf, 2009). Some authors have suggested that the time that one species takes to colonize distant areas or regions with different environments could be longer than 1 million years, which is a time lapse on the order of one MN unit (Alroy, 1998; van Dam et al., 2001; van Dam, 2003). This might be related with restrictions on dispersal, particularly in small mammals, which are characterized by slower dispersal rates, involving less distance, and less successful colonization events (Gaston and Blackburn, 1996; Moreno Bofarull et al., 2008; Maridet and Costeur, 2010).

Table 3
Appearance Event Ordination (AEO) mean value and concurrent range zones, defined by the youngest first appearance event (FAE) and oldest last appearance event (LAE), for the 93 fossil sites maintained in the analysis for the southern province. Their calculated numerical ages are also shown.

| Basin ^a | Fossil site | Fossil site abbreviation | S ^b | MN unit | AEO coefficient | Youngest FAE | Oldest LAE | Age (Ma) |
|--------------------|---------------------------|--------------------------|----------------|---------|-----------------|--------------|------------|----------|
| GR | Purcal 24A | PUR24A | 8 | 13 | 150.5 | 150 | 151 | 4.953 |
| GR | Purcal 25 | PUR25 | 7 | 13 | 150.5 | 150 | 151 | 4.953 |
| AL | Alcoy Barranco | ALBAR | 6 | 13 | 147.0 | 143 | 151 | 5.148 |
| AL | Crevillente 6 | CRE6 | 5 | 13 | 146.5 | 146 | 147 | 5.176 |
| TJ | Canteras de Iberia | CDI | 3 | 13 | 145.0 | 139 | 151 | 5.260 |
| GB | Botardo C | BOTC | 8 | 13 | 143.5 | 143 | 144 | 5.343 |
| BT | Esbarrondoiro | ESBA | 10 | 13 | 141.5 | 139 | 144 | 5.455 |
| VA | Los Mingos 1C | MIN1C | 2 | 13 | 141.0 | 131 | 151 | 5.482 |
| GB | Bacochas 1 | BAC1 | 7 | 13 | 139.5 | 139 | 140 | 5.566 |
| GR | Purcal 3 | PUR3 | 5 | 13 | 139.0 | 127 | 151 | 5.594 |
| TE | Las Casiones superior | KSSS | 7 | 13 | 137.5 | 131 | 144 | 5.677 |
| MU | Librilla | LIBR | 7 | 13 | 134.0 | 121 | 147 | 5.872 |
| GR | Dehesa 16 | DHS16 | 9 | 13 | 131.5 | 131 | 132 | 6.011 |
| TE | Las Casiones | KSS | 9 | 13 | 131.5 | 131 | 132 | 6.011 |
| GR | Purcal 23 | PUR23 | 7 | 13 | 131.5 | 131 | 132 | 6.011 |
| TE | Villastar | VILL | 9 | 13 | 131.5 | 131 | 132 | 6.011 |
| CA | Almenara M | ALMM | 9 | 13 | 127.5 | 127 | 128 | 6.234 |
| GB | Pino Mojón | PIMO | 6 | 13 | 126.5 | 125 | 128 | 6.290 |
| GB | Negratín 1 | NGR1 | 7 | 13 | 125.5 | 125 | 126 | 6.346 |
| GR | Salobreña | SALO | 12 | 13 | 125.5 | 125 | 126 | 6.346 |
| TE | Masada Del Valle 7 | MDV7 | 7 | 13 | 124.0 | 116 | 132 | 6.429 |
| VA | Venta del Moro | VDM | 10 | 13 | 121.5 | 121 | 122 | 6.568 |
| TE | Gloria 5 | GLO5 | 9 | 13 | 116.5 | 116 | 117 | 6.847 |
| TE | Valdecebro 3 | VDC3 | 9 | 13 | 116.5 | 116 | 117 | 6.847 |
| TE | Valdecebro 6 | VDC6 | 9 | 13 | 116.5 | 116 | 117 | 6.847 |
| AL | Crevillente 14 | CRE14 | 8 | 13 | 111.5 | 111 | 112 | 7.125 |
| AL | Crevillente 22 | CRE22 | 6 | 13 | 111.5 | 111 | 112 | 7.125 |
| AL | Crevillente 17 | CRE17 | 5 | 12 | 109.5 | 107 | 112 | 7.237 |
| FO | Hornera | HOR | 4 | 13 | 107.5 | 107 | 108 | 7.348 |
| TE | Concud 2 | CCD2 | 7 | 12 | 107.5 | 98 | 117 | 7.348 |
| GR | Jun 2 | JUN2 | 5 | 12 | 107.5 | 107 | 108 | 7.348 |
| TE | Tortajada | TOT | 5 | 12 | 107.5 | 98 | 117 | 7.348 |
| TE | Tortajada D | TOTD | 5 | 12 | 107.5 | 98 | 117 | 7.348 |
| TE | Villalba baja 22C | VIB22C | 5 | 12 | 107.5 | 98 | 117 | 7.348 |
| FO | Casa del Acero | ACER | 4 | 12 | 106.5 | 101 | 112 | 7.404 |
| AL | Crevillente 8 | CRE8 | 6 | 12 | 106.5 | 101 | 112 | 7.404 |
| AL | Crevillente 15 | CRE15 | 9 | 12 | 101.5 | 101 | 102 | 7.682 |
| AL | Crevillente 5A | CRE5A | 5 | 12 | 100.0 | 98 | 102 | 7.766 |
| TE | Los Mansuetos | LMA | 9 | 12 | 100.0 | 98 | 102 | 7.766 |
| TE | Masada del Valle 5 | MDV5 | 8 | 12 | 100.0 | 98 | 102 | 7.766 |
| TE | Concud 3 | CCD3 | 7 | 12 | 98.5 | 98 | 99 | 7.849 |
| TE | Masada del Valle 2 | MDV2 | 9 | 12 | 98.5 | 98 | 99 | 7.849 |
| TE | Aljezar B | ALJB | 7 | 12 | 94.5 | 94 | 95 | 8.072 |
| TE | Aguanaces | AGU | 7 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | Aguanaces 1 | AGU1 | 3 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | Aguanaces 3 | AGU3 | 7 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | La Gloria 10 | GLO10 | 7 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | Tortajada A | TOTA | 8 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | Vivero de Pinos | VIP | 8 | 11 | 87.5 | 87 | 88 | 8.462 |
| TE | Regajo 2 | REG2 | 4 | 11 | 85.0 | 82 | 88 | 8.601 |
| AL | Crevillente 2 | CRE2 | 7 | 11 | 82.5 | 82 | 83 | 8.740 |
| AL | Crevillente 4B | CRE4B | 7 | 11 | 82.5 | 82 | 83 | 8.740 |
| TE | Pino Mojón | PMIN | 9 | 11 | 82.5 | 82 | 83 | 8.740 |
| AL | Crevillente 3 | CRE3 | 4 | 11 | 78.5 | 78 | 79 | 8.963 |
| TE | Peralejos D | PERD | 6 | 11 | 75.5 | 75 | 76 | 9.130 |
| TE | Peralejos C | PERC | 6 | 10 | 75.5 | 75 | 76 | 9.130 |
| TE | Masia del Barbo 2A | MB2A | 5 | 10 | 69.5 | 69 | 70 | 9.464 |
| TE | Masia del Barbo 2B | MB2B | 8 | 10 | 69.5 | 69 | 70 | 9.464 |
| TE | Masia la Roma 11 | ROM11 | 7 | 10 | 67.5 | 67 | 68 | 9.576 |
| DU | Los Valles de Fuentidueña | FUDU | 4 | 9 | 64.5 | 64 | 65 | 9.743 |
| TJ | Batallones 1 | BAT1 | 3 | 10 | 63.5 | 51 | 76 | 9.798 |
| TE | Masia la Roma 7 | ROM7 | 6 | 10 | 59.0 | 53 | 65 | 10.049 |
| HI | Hijar 1 | HIJ1 | 4 | 10 | 58.0 | 51 | 65 | 10.105 |
| DU | Ampudia 1 | AMP1 | 2 | 10 | 57.5 | 57 | 58 | 10.133 |
| DU | Torremormojón 1 | TM1 | 6 | 10 | 57.5 | 57 | 58 | 10.133 |
| CD | Pedregueras 2A D | PED2A | 6 | 9 | 57.5 | 57 | 58 | 10.133 |
| CD | Pedregueras 2C | PED2C | 6 | 9 | 57.5 | 57 | 58 | 10.133 |
| TE | Peralejos 5 | PER5 | 7 | 9 | 55.5 | 53 | 58 | 10.244 |
| DU | Ampudia 9 | AMP9 | 7 | 9 | 53.5 | 53 | 54 | 10.355 |
| DU | Torremormojón 3 | TM3 | 5 | 9 | 53.5 | 53 | 54 | 10.355 |
| DU | Torremormojón 4 | TM4 | 4 | 9 | 53.5 | 53 | 54 | 10.355 |
| BT | Freiria do Rio Maior | FRM | 5 | 10 | 51.5 | 51 | 52 | 10.467 |
| CD | Carrilanga 1 | CARR1 | 7 | 9 | 47.5 | 47 | 48 | 10.689 |
| DU | Torremormojón 5 | TM5 | 4 | 9 | 46.5 | 45 | 48 | 10.745 |

Table 3 (continued)

| Basin ^a | Fossil site | Fossil site abbreviation | S ^b | MN unit | AEO coefficient | Youngest FAE | Oldest LAE | Age (Ma) |
|--------------------|-------------------------|--------------------------|----------------|---------|-----------------|--------------|------------|----------|
| DU | Casasola 2 | CAS2 | 4 | 9 | 45.5 | 45 | 46 | 10.801 |
| TE | Molina de Aragón | MOL | 9 | 9 | 43.5 | 43 | 44 | 10.912 |
| CD | Nombrevilla (classical) | NOM | 8 | 9 | 40.5 | 40 | 41 | 11.079 |
| CD | Nombrevilla 10 | NOM10 | 4 | 7/8 | 40.5 | 40 | 41 | 11.079 |
| CD | Nombrevilla 9 | NOM9 | 4 | 7/8 | 37.5 | 34 | 41 | 11.246 |
| CD | Solera | SOL | 10 | 7/8 | 37.5 | 37 | 38 | 11.246 |
| CD | Nombrevilla 4 | NOM4 | 3 | 7/8 | 34.5 | 34 | 35 | 11.413 |
| CD | Nombrevilla 3 | NOM3 | 8 | 7/8 | 34.5 | 34 | 35 | 11.413 |
| CD | Nombrevilla 2 | NOM2 | 8 | 7/8 | 34.5 | 34 | 35 | 11.413 |
| TJ | Lupiana | LUP | 7 | 7/8 | 29.5 | 29 | 30 | 11.692 |
| DU | Simancas 2 | SIM2 | 8 | 7/8 | 26.5 | 26 | 27 | 11.859 |
| CD | Alcozer 2 | ALCR2 | 6 | 7/8 | 23.5 | 23 | 24 | 12.026 |
| TJ | Paracuellos 3 | PAR3 | 6 | 7/8 | 23.5 | 23 | 24 | 12.026 |
| CD | Villafeliche 9 | VFEL9 | 5 | 7/8 | 19.0 | 14 | 24 | 12.277 |
| CD | Las Planas 5H | LP5H | 6 | 7/8 | 18.5 | 18 | 19 | 12.305 |
| CD | Toril 3B | TOR3B | 13 | 7/8 | 14.5 | 14 | 15 | 12.527 |
| CD | Toril 3A | TOR3B | 12 | 7/8 | 14.5 | 14 | 15 | 12.527 |
| CD | Toril 2 | TOR2 | 7 | 7/8 | 14.5 | 14 | 15 | 12.527 |
| CD | Toril 1 | TOR1 | 10 | 7/8 | 14.5 | 14 | 15 | 12.527 |

^a Basin abbreviations: TE, Alfambra–Teruel; AL, Alicante; BT, Baixo Tejo; CA, Castellón; CD, Calatayud–Daroca; DU, Duero; FO, Fortuna; GR, Granada; GB, Guadix–Baza; HI, Híjar; MU, Murcia; TJ, Tajo; VA, Valencia.

^b S, number of species (without singletons).

Faunal changes associated with the distinction of each MN unit occurred later in the northern province, which was characterized by a more humid environment (Fauquette et al., 2006, 2007; van Dam, 2006; van Dam et al., 2006; Jiménez-Moreno and Suc, 2007; Casanovas-Vilar et al., 2008). These environmental conditions tally with the portrayal of the northern province as a refuge area where the rodent communities “typical” of one MN unit remained to later periods of time, in the same way suggested by Vrba (1988) and Hernández Fernández and Vrba (2006) after studying the mammalian fossil record of some areas in Africa. Within the general context of global cooling and aridification of the climate during the time interval studied here (Zachos et al., 2001), the relatively more humid area that

represents the northern province of the Iberocccitanian Region could constitute a place in which some species from the southern province could temporarily survive following the progressive aridity increase in the Iberian Peninsula. This differential species survival in both provinces, which would have been a recurrent phenomenon through the Miocene, may be responsible for the diachrony observed in our results for the boundaries of the MN units.

Interestingly, this diachrony is maintained throughout the whole time span studied in this research. This would suggest that subsequent aridification would cause successive repetition of the dispersal process of “southern species” to the northern province, as well as the final disappearance of such species also from the northern province.

Table 4

Appearance event ordination (AEO) mean value and concurrent range zone, defined by the youngest first appearance event (FAE) and oldest last appearance event (LAE), for the 27 fossil sites maintained in the analysis for the northern province. Their calculated numerical ages are also shown.

| Basin ^a | Fossil site | Fossil site abbreviation | S ^b | MN units | AEO coefficient | Oldest LAE | Youngest FAE | Age (Ma) |
|--------------------|---------------------------------|--------------------------|----------------|----------|-----------------|------------|--------------|----------|
| VP | Can Vilella 1 | CVLL1 | 6 | 13 | 114.5 | 114 | 115 | 6.054 |
| RH | Lissieu | LISS | 12 | 13 | 114.5 | 114 | 115 | 6.054 |
| CU | Cucuron | CUCU | 6 | 12 | 109.5 | 109 | 110 | 6.358 |
| RH | Amberieu 3 | AMB3 | 15 | 11 | 99.5 | 99 | 100 | 6.965 |
| RH | Amberieu 1 | AMB1 | 20 | 11 | 89.5 | 89 | 90 | 7.572 |
| PR | Lobieu | LOBR | 11 | 11 | 89.5 | 89 | 90 | 7.572 |
| LR | Lo Fournas 6C | FOUR6C | 6 | 11 | 81.5 | 81 | 82 | 8.058 |
| LR | Lo Fournas 7 | FOUR7 | 7 | 10 | 79.5 | 79 | 80 | 8.179 |
| RH | Douvre | DOUV | 15 | 10 | 74.5 | 74 | 75 | 8.482 |
| RH | Soblay | SOBL | 19 | 10 | 70.5 | 70 | 71 | 8.725 |
| VP | Autopista Rubí-Terrasa 7 | RT7 | 5 | 10 | 60.5 | 60 | 61 | 9.332 |
| VP | Torrent de Febulines | TFEB | 6 | 10 | 60.5 | 60 | 61 | 9.332 |
| VP | Torrent de Febulines 3 | TFEB3 | 2 | 10 | 60.5 | 60 | 61 | 9.332 |
| VP | Trinxera Nord Autopista | TNA | 4 | 10 | 60.5 | 60 | 61 | 9.332 |
| VP | Trinxera Sud Autopista II | TSA2 | 6 | 10 | 60.5 | 60 | 61 | 9.332 |
| VP | Can Llobateres 1 | CLL1 | 19 | 9 | 51.5 | 51 | 52 | 9.879 |
| VP | Can Ponsic | CPON | 10 | 9 | 46.5 | 46 | 47 | 10.182 |
| VP | Creu Conill 22 | CC22 | 5 | 9 | 42.5 | 42 | 43 | 10.425 |
| VP | Can Mata I (Bretxa de Can Mata) | CMAT1 | 8 | 8 | 39.5 | 39 | 40 | 10.607 |
| VP | Sant Quirze | SQUI | 18 | 8 | 35.5 | 35 | 36 | 10.850 |
| VP | Castell de Barberà | CMST | 15 | 8 | 30.5 | 30 | 31 | 11.153 |
| VP | Can Misert | CBB | 9 | 8 | 30.5 | 30 | 31 | 11.153 |
| VP | Sant Quirze A | SQUIA | 6 | 8 | 21.5 | 21 | 22 | 11.700 |
| VP | Barranc de Can Vila 1 | BCV1 | 8 | 7 | 16.5 | 16 | 17 | 12.003 |
| LR | Lo Fournas 2 | FOUR2 | 8 | 7 | 10.5 | 10 | 11 | 12.367 |
| LR | Lo Fournas 3 | FOUR10 | 8 | 7 | 6.5 | 6 | 7 | 12.610 |
| LR | Lo Fournas 10 | FOUR3 | 8 | 7 | 6.5 | 6 | 7 | 12.610 |

^a Basin abbreviations: CU, Cucuron–Basse Durance; LR, Languedoc–Roussillon; PR, Provence; RH, Rhône; VP, Vallès–Penedès.

^b S, number of species (without singletons).

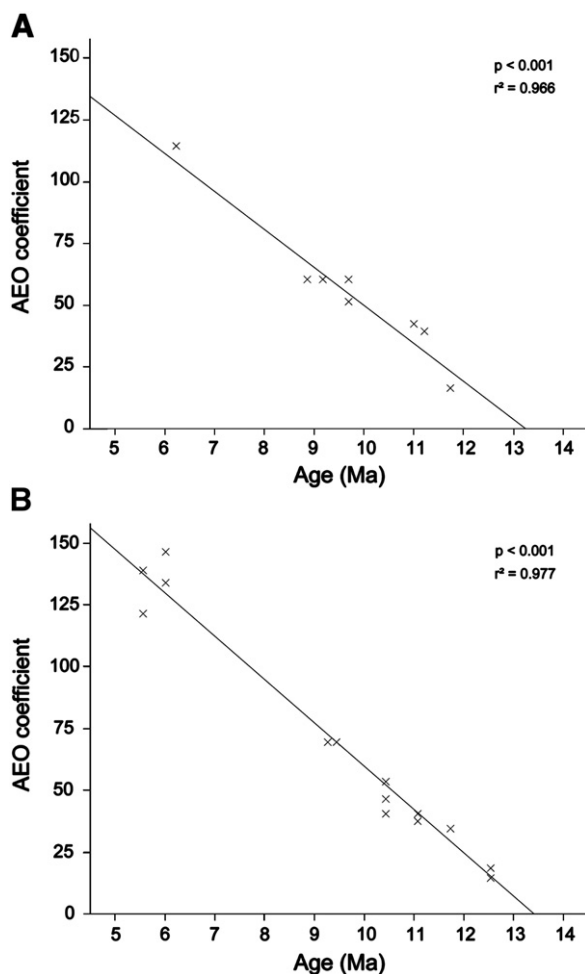


Fig. 2. Calibrations of the Iberocctanian mammal fossil site sequences for the northern (A) and southern (B) provinces, showing the linear regressions of the concurrent range zone mean value for each fossil site obtained in the appearance event ordination of mammal faunas (AEO coefficient) against the numerical dates for them.

This question raises the possibility that the MN units, which have always been considered as a biochronological system for the whole of Europe and Western Asia, and sometimes even for Central and Eastern Asia (Flynn, 1997; Sotnikova et al., 1997), could in fact constitute ecological/evolutionary units (Raia et al., 2009) at the continental scale, while maintaining their biochronological character only within the limits of a biogeographical province.

4.2. Comparison with previous works

Comparison with ages for the MN boundaries derived from other studies (Agustí et al., 2001; van Dam et al., 2006; Domingo et al.,

2007) indicates some differences that might be related to different factors.

In the first place, it is important to take into account that our study has separated two different biogeographic provinces, each with a different age calibration, while Agustí et al. (2001) and Domingo et al. (2007) studied both bioprovinces conjunctly. It is therefore not surprising that most of the ages defined by these authors for the different MN boundaries are intermediate between those defined in the present research for the southern and northern provinces (Table 5).

Secondly, the study by Domingo et al. (2007) is exclusively based on large mammal sites, which in a sense might also have some influence, due to the lower number of sites included in their study. Furthermore, there are certain differences between small and large mammals, based upon their life history and ecological characteristics, which may cause the discrepancies observed between Domingo et al.'s (2007) study and ours. Large mammals usually need broad distribution ranges to maintain evolutionarily viable populations (Sauer and Slade, 1987; Hernández Fernández and Vrba, 2005a,b; Moreno Bofarull et al., 2008). This could dilute to some extent the faunal differences found between the biogeographical provinces, which probably attenuates diachrony of biotic events in large mammal faunas when compared with the ones observed in our rodent-based study. In addition, due to their larger body size, large mammals have greater dispersal capabilities than small ones (Gaston and Blackburn, 1996; Hernández Fernández and Vrba, 2005c). This might have a big influence on the fact that the diachrony observed between southern and northern provinces for rodent faunas is not apparent in the study of large mammals. This is to say that large and small mammals may show different biogeographic patterns due to the influence of their biological characteristics at different spatial and temporal scales (Maridet and Costeur, 2010). Thus, all these differences indicate that rodent assemblages may exhibit higher time and biogeographical resolution at smaller scales.

Thirdly, in the case of the ages defined by van Dam et al. (2006), which are based on sites from the Calatayud–Daroca and Alfambra–Teruel basins, our results on the southern province indicate slightly older ages (Table 5). This is probably related to the use of faunal lists of sites from a much larger area in the present study, which might provide a better cover of the time lapse studied herein.

Finally, an additional difference is based on the different Geomagnetic Polarity Time Scale used in each study to calibrate the ordination; we employed the scale proposed by Gee and Kent (2007), whereas preceding studies used earlier versions (Cande and Kent, 1995; Lourens et al., 2004). Nevertheless, the differences associated with this change in the Geomagnetic Polarity Time Scale are not significant.

5. Conclusions

The results yielded by the ML AEO analyses allowed us to estimate the numerical ages of 130 rodent fossil sites from the Iberocctanian

Table 5
Ages for the boundaries of the Mammal Neogene units (MN) from the latest Middle Miocene to the Upper Miocene in the Iberocctanian region as derived from the study of rodent fossil sites, and comparison with previous works.

| MN boundaries | This work | | Domingo et al. (2007) | Van Dam et al. (2006) | Agustí et al. (2001) |
|---------------|-------------------|-------------------|-----------------------|-----------------------|----------------------|
| | Southern province | Northern province | | | |
| MN12–MN13 | 7.348 | 6.358–6.054 | 7.011–6.319 | 7.10–7.00 | 7.2–6.8 |
| MN11–MN12 | 8.462–8.072 | 6.965–6.358 | 7.834–7.494 | 7.91–7.60 | 7.5 |
| MN10–MN11 | 9.130 | 8.179–8.058 | 8.520–8.163 | 8.80–8.75 | 8.7 |
| MN9–MN10 | 10.133 | 9.879–9.332 | 9.547–9.195 | 9.94–9.87 | 9.7 |
| MN7/8–MN9 | 11.079 | – | 11.008–10.873 | >10.76 | 11.5–11.1 |
| MN8–MN9 | – | 10.607–10.425 | – | – | – |
| MN7–MN8 | – | 12.003–11.700 | – | – | – |

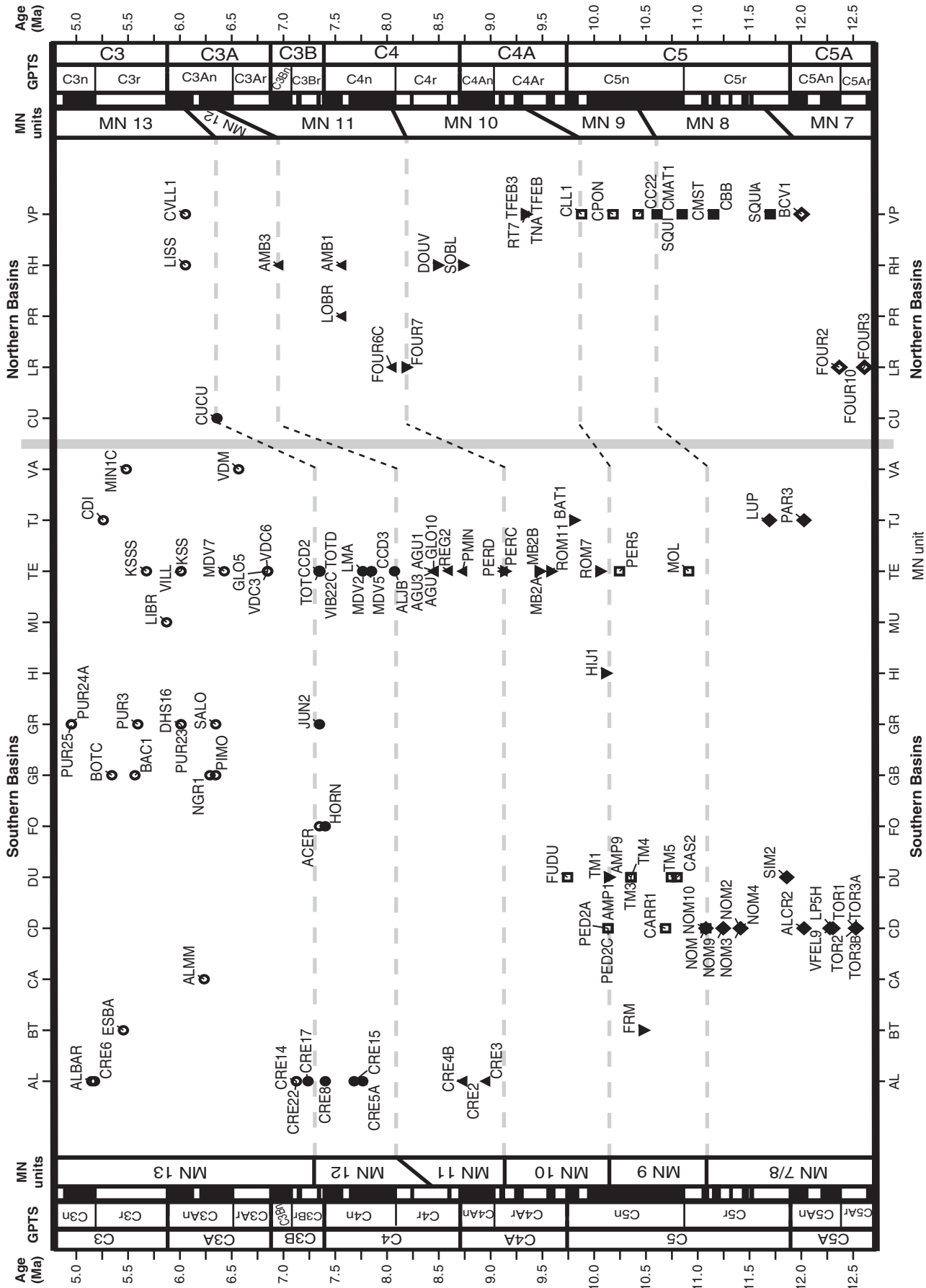


Fig. 3. Temporal distribution of the Iberocretan rodent fossil sites obtained following calibration of the ordination with the AEO coefficient. Geomagnetic polarity time-scale after Gee and Kent (2007). The Mammalian Neogene units (MN) are shown. Dashed lines represent the diachrony between the northern and southern provinces. Abbreviations for basins and fossil sites as used in Tables 3 and 4.

Region. This kind of study could be developed due to the rich Miocene rodent faunas and the high number of studies describing them.

Although our results agree with the MN system in both the northern and southern biogeographic provinces and allowed for the dating of the boundaries of MN units, they evidenced the existence of a severe diachrony in the MN boundaries between the two provinces. These differences could be related to the presence of distinctive environments in these bioprovinces and the existence of a “refugium effect” associated to the more humid habitats in the northern province.

Finally, the time framework established in this work will be indispensable for the future development of paleoecological and paleoclimatic studies, which could help to further explain the differences between these two biogeographical provinces.

Supplementary materials related to this article can be found online at doi:10.1016/j.palaeo.2011.05.014.

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References

- Aguirre, E., 1997. Contenidos informativos de los fósiles y desarrollos actuales de su estudio. In: Aguirre, E., Morales, J., Soria, D. (Eds.), *Registros fósiles e Historia de la Tierra*. Editorial Complutense, Madrid, pp. 11–25.
- Agustí, J., Cabrera, L., Garcés, M., Pares, J.M., 1997. The Vallesian mammal succession in the Valles-Penedes basin (northeast Spain): paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 149–180.
- Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. *State of the art. Earth-Science Reviews* 52, 247–260.
- Agustí, J., Oms, O., Furió, M., Perez-Vila, M.-J., Roca, E., 2006. The Messinian terrestrial record in the Pyrenees: the case of Can Vilella (Cerdanya Basin). *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 179–189.
- Alba, D.M., Agustí, J., Moyà-Solà, S., 2001. Completeness of the mammalian fossil record in the Iberian Neogene. *Paleobiology* 27, 79–83.
- Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7 + 8) de la cuenca del Vallès-Penedès. *Campañas 2002–2003, 2004 y 2005. Estudios Geológicos* 62, 295–312.
- Alba, D.M., Robles, J.M., Rotgers, C., Casanovas-Vilar, I., Galindo, J., Moyà-Solà, S., Garcés, M., Cabrera, L., Furió, M., Carmona, R., Bertó Mengual, J.V., 2009. Middle Miocene vertebrate localities from Abocador de Can Mata (Els Hostalets de Pierola, Vallès-Penedès Basin, Catalonia, Spain): an update after the 2006–2008 field campaigns. *PaleoIusitana* 1, 59–74.
- Alberdi, M.T., Azanza, B., 1997. Comentarios al artículo Magnetostratigrafía preliminar de los materiales pliocenos de la cubeta de Villarroya (Sierra de Cameros, La Rioja), de E. Pueyo Morer, A. Muñoz Jiménez y J.M. Parés (1996). *Geogaceta* 22, 7–10.
- Alberdi, M., López Martínez, N., Morales, J., Sesé, C., Soria, D., 1981. Biostratigrafía y biogeografía de la fauna de mamíferos de Los Valles de Fuentidueña (Segovia). En: *Geología y Paleontología del yacimiento neógeno continental de Los Valles de Fuentidueña, Segovia (España)*. Estudios Geológicos 37, 503–511.
- Alroy, J., 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. *Paleobiology* 18, 326–343.
- Alroy, J., 1994. Appearance Event Ordination: a new biochronologic method. *Paleobiology* 20 (2), 191–207.
- Alroy, J., 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology* 127, 285–311.
- Alroy, J., 1998. Diachrony of mammalian appearance events: implications for biochronology. *Geology* 26, 23–26.
- Alroy, J., 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* 26, 707–733.
- Alroy, J., Kosnik, M.A., 2006. Conjunction Version OS 10.4.6 available online <http://www.nceas.ucsb.edu/~alroy/biochronology.html> 2006.
- Alroy, J., Bernor, R.L., Fortelius, M., Werdelin, L., 1998. The MN system: regional or continental? *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 38, 243–258.
- Álvarez-Sierra, M.A., García Moreno, E., López Martínez, N., 1985. Biostratigraphy and paleoecological interpretation of Middle–Upper Miocene successions in continental sediments of the Duero basin, Northern Spain, VIII congrès Regional du Comité Méditerranéen de Stratigraphie du Néogène, Budapest, pp. 66–68.
- Álvarez-Sierra, M.A., Civis, J., Corrochano, A., Daams, R., Dabrio, C.J., García, E., González, A., López Martínez, N., Mediavilla, R., Rivas Carballo, R., Valle, M.F., 1990. Un estratotipo del límite Aragoniense–Vallesiense (Mioceno medio–Mioceno superior) en la sección de Torremormojón (Cuenca del Duero, Provincia de Palencia). *Studia Geologica Salmanticensis, Actas de Paleontología*, pp. 57–64.
- Álvarez-Sierra, M.A., Calvo, J.P., Morales, J., Alonso-Zarza, A., Azanza, B., García Paredes, I., Hernández Fernández, M., van der Meulen, A., Peláez-Campomanes, P., Quirarte, V., Salesa, M.J., Sánchez, I.M., Soria, D., 2003. El tránsito Aragoniense–Vallesiense en el área de Daroca-Nombrevilla (Zaragoza, España). *Coloquios de Paleontología, Volumen Extraordinario* 1, 25–33.
- Antunes, M.T., Mein, P., 1979. Le gisement de Freiria de Rio Maior, Portugal, et sa faune de mammifères; nouvelle espèce de *Rotundomys*, conséquences stratigraphiques. *Geobios* 12, 913–919.
- Antunes, M.T., Soulie-Marsche, L., Mein, P., Pais, J., 1992. Le gisement de Asseiceira, Portugal (Miocène supérieur) Données complémentaires sur Freiria de Rio Maior. *Universidade Nova de Lisboa Ciências da Terra* 11, 219–253.
- Azanza, B., Alberdi, M.T., Cerdeño, E., Prado, J.L., 1997a. Contribución de los análisis multivariantes a la biochronología continental. In: Calvo, J.P., Morales, J. (Eds.), *Avances en el conocimiento del Terciario Ibérico*. Universidad Complutense de Madrid, Museo Nacional de Ciencias Naturales, Museo de Cuenca, Cuenca, pp. 37–40.
- Azanza, B., Alberdi, M., Cerdeño, E., Prado, J., 1997b. Biochronology from latest Miocene to Middle Pleistocene in the western mediterranean area. *Montpellier In: Aguilar, J., Legendre, S., Michaux, J. (Eds.), A Multivariate Approach: Biochron*, 97, pp. 567–574.
- Badiola, A., Checa, L., Cuesta, M.A., Quer, R., Hooker, J.L., Astibia, H., 2009. The role of new Iberian finds in understanding European Eocene mammalian palaeobiogeography. *Geologica Acta* 7, 243–258.
- Calvo, J.P., Daams, R., Morales, J., López Martínez, N., Agustí, J., Anadón, P., Armenteros, I., Cabrera, L., Civis, J., Corrochano, A., Díaz-Molina, M., Elizaga, E., Hoyos, M., Martín-Suarez, E., Martínez, J., Moissenet, E., Muñoz, A., Pérez-García, A., Pérez-González, A., Portero, J.M., Robles, F., Santisteban, C., Torres, T., Meulen, A.J.V.d., Vera, J.A., Mein, P., 1993. Up-to-date Spanish continental Neogene synthesis and paleoclimatic interpretation. *Revista de la Sociedad Geológica de España* 6, 29–40.
- Cande, S.C., Kent, D.V., 1995. Revised calibration of the geomagnetic polarity timescale for the Late Cretaceous and Cenozoic. *Journal of Geophysical Research* 100 (B4), 6093–6095.
- Casanovas-Cladellas, M.L., Moyà-Solà, S., 1992. La sucesión de faunas de mamíferos durante el Paleógeno Europeo. In: Astibia, H. (Ed.), *Paleontología de Vertebrados: Faunas y Filogenia, Aplicación y Sociedad*. Servicio Editorial de la Universidad del País Vasco, pp. 187–231.
- Casanovas-Vilar, I., 2007. The rodent assemblages from the Late Aragonian and the Vallesian of the Vallès-Penedès Basin (Catalonia, Spain). PhD. Thesis, Universitat Autònoma de Barcelona, Barcelona, p. 286.
- Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J.M., Köhler, M., Angelone, C., 2008. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Homiidae). *Journal of Human Evolution* 55, 589–603.
- Casanovas-Vilar, I., García-Paredes, I., Alba, D.M., van den Hoek Ostende, L.W., Moyà-Solà, S., 2010. The European Far West: Miocene mammal isolation, diversity and turnover in the Iberian Peninsula. *Journal of Biogeography* 37, 1079–1093.
- Cerling, T.E., Harris, J.M., Ambrose, S.H., Leakey, M.G., Solouian, N., 1997a. Dietary and environmental reconstruction with stable isotope analysis of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. *Journal of Human Evolution* 33, 635–650.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997b. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153–158.
- Daams, R., 1989. Miscellaneous Gliiridae from the Miocene of the Calatayud–Teruel Basin, Aragón, Spain. *Scripta Geologica* 89, 13–26.

- Daams, R., Freudenthal, M., 1981. Aragonian: the Stage concept versus Neogene Mammal Zones. *Scripta Geologica* 62, 1–17.
- Daams, R., van de Weerd, A., 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications. I & II. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, sér B 81, 448–473.
- Daams, R., Álvarez Sierra, M.A., van der Meulen, A.J., Peláez-Campomanes, P., 1997. Los micromamíferos como indicadores de paleoclimas y evolución de las cuencas continentales. In: Aguirre, E., Morales, J., Soria, D. (Eds.), *Registros fósiles e Historia de la Tierra*. Editorial Complutense, Madrid, pp. 281–296.
- 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. *Comptes Rendus de l'Académie des sciences de Paris* 327, 625–631.
- Daams, R., van der Meulen, A.J., Álvarez Sierra, M.A., Peláez-Campomanes, P., Krijgsman, W., 1999a. Aragonian stratigraphy reconsidered, and a re-evaluation of the middle Miocene mammal biochronology in Europe. *Earth and Planetary Science Letters* 165, 287–294.
- Daams, R., van der Meulen, A.J., Peláez-Campomanes, P., Álvarez-Sierra, M.A., 1999b. Trends in rodent assemblages from the Aragonian (Early–Middle Miocene) of the Calatayud–Daroca Basin, Aragon, Spain. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *Hominoid Evolution and Climatic Change in Europe*. Vol. 1. The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, pp. 127–139.
- de Bruijn, H., Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J., 1992. Report of the RCMNS working group on fossil mammals, Reimsburg 1990. *Newsletters on Stratigraphy* 26, 65–118.
- Dempster, A.P., Laird, N.M., Rubin, D.B., 1977. Maximum likelihood from incomplete data via the EM algorithm. *Journal of the Royal Statistical Society Series: B* 39, 1–38.
- Domingo, M.S., Alberdi, M.T., Azanza, B., 2007. A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255, 361–376.
- Domingo, L., Grimes, S.T., Domingo, M.S., Alberdi, M.T., 2009. Paleoenvironmental conditions in the Spanish Miocene–Pliocene boundary: isotopic analyses of *Hipparion* dental enamel. *Naturwissenschaften* 96, 503–511.
- Eicher, D.L., 1973. El tiempo geológico. Omega, Barcelona, p. 150.
- Fahlbusch, V., 1991. The meaning of MN-zonation: considerations for a subdivision of the European continental tertiary using mammals. *Newsletters on Stratigraphy* 24, 159–173.
- Fauquette, S., Suc, J.-P., Bertini, A., Ppocess, S.M., Wary, S., Taoufiq, N.B., Perez Villa, M.J., Chikhi, H., Feddi, Najat, Subally, D., Clauzon, G., Ferrier, J., 2006. How much did climate force the Messinian salinity crisis? Quantified climatic conditions from pollen records in the Mediterranean region. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 281–301.
- Fauquette, S., Suc, J.-P., Jiménez-Moreno, G., Favre, E., Jost, A., Micheels, A., Bachiri-Taoufiq, N., Bertini, A., Clet-Pellerin, M., Diniz, F., Farjanel, G., Feddi, N., Zheng, Z., 2007. Latitudinal climatic gradients in Western European and Mediterranean regions from the Mid-Miocene (~15 Ma) to the Mid-Pliocene (~3.6 Ma) as quantified from pollen data. In: Williams, M., Haywood, A.M., Gregory, F.J., Schmidt, D.N. (Eds.), *Deep-time Perspectives on Climate Change: Marrying the Signal from Computer Models and Biological Proxies*. The Micropalaeontological Society, Special Publications. The Geological Society, London, pp. 481–502.
- Flynn, L.J., 1997. Late Neogene mammalian events in North China. In: Aguilar, J.-P., Legendre, S., Michaux, J. (Eds.), *Actes du Congrès Biochron'97*. École Pratique des Hautes Études Institut de Montpellier, Montpellier, pp. 183–192.
- Fortelius, M., Gionis, A., Jernvall, J., Mannila, H., 2006. Spectral ordering and biochronology of European fossil mammals. *Paleobiology* 32, 206–214.
- Furió, M., Casanovas-Vilar, I., van den Hoek Ostende, L.W., 2011. Predictable structure of Miocene insectivore (Lipotyphla) faunas in Western Europe along a latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304, 219–229.
- Garcés, M., Agustí, J., Cabrera, L., Pares, J.M., 1996. Magnetostratigraphy of the Vallesian (Late Miocene) in the Valles–Penedes Basin (northeast Spain). *Earth and Planetary Science Letters* 142, 381–396.
- Garcés, M., Krijgsman, W., Agustí, J., 1998. Chronology of the late Turolian deposits of the Fortuna basin (SE Spain): implications for the Messinian evolution of the eastern Betics. *Earth and Planetary Science Letters* 163, 69–81.
- 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). *Coloquios de Paleontología Volumen Extraordinario* 1, 171–178.
- García-Alix, A., Minwer-Barakat, R., Martín Suárez, E., Freudenthal, M., 2008. Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain). *Lethaia* 41, 431–446.
- Gaston, K.J., Blackburn, T.M., 1996. Conservation implications of geographic range size body size relationships. *Conservation Biology* 10, 638–646.
- Gee, J.S., Kent, D.V., 2007. Source of oceanic magnetic anomalies and the geomagnetic polarity timescale. In: Kono, M., Schubert, G. (Eds.), *Treatise on Geophysics*. Elsevier, pp. 455–507.
- Gregor, H.-J., Velitzelos, E., 1987. Evolution of Neogene Mediterranean vegetation and the question of a dry Upper Miocene period (Salinity Crisis). *Annales Instituti Geologici Publici Hungarici* 70, 489–496.
- Hammer, O., Harper, D.A.T., 2006. Chapter 8. Quantitative biostratigraphy. In: Hammer, O., Harper, D.A.T. (Eds.), *Paleontological Data Analysis*. Blackwell Publishing, Malden, Oxford & Carlton, pp. 279–316.
- Heikinheimo, H., Fortelius, M., Eronen, J., Mannila, H., 2007. Biogeography of European land mammals shows environmentally distinct and spatially coherent clusters. *Journal of Biogeography* 34, 1053–1064.
- Hernández Fernández, M., Vrba, E.S., 2005a. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis. *Journal of Biogeography* 32, 903–918.
- Hernández Fernández, M., Vrba, E.S., 2005b. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. *Evolutionary Ecology* 19, 199–219.
- Hernández Fernández, M., Vrba, E.S., 2005c. Body size, biomic specialization and range size of African large mammals. *Journal of Biogeography* 32, 1243–1256.
- Hernández Fernández, M., Vrba, E.S., 2006. Plio-Pleistocene climatic change in the Turkana Basin (East Africa): evidence from large mammal faunas. *Journal of Human Evolution* 50, 595–626.
- Hernández Fernández, M., Azanza, B., Álvarez-Sierra, M.A., 2004. Iberian Plio-Pleistocene biochronology: micromammalian evidence for MNs and ELMA's calibration in southwestern Europe. *Journal of Quaternary Science* 19, 605–616.
- Hsü, K.J., Montadert, L., Bernoulli, D., Cita, M.B., Erickson, A., Garrison, R.E., Kidd, R.B., Mèlierès, F., Müller, C., Wright, R., 1977. History of the Mediterranean salinity crisis. *Nature* 267, 399–410.
- Jiménez-Moreno, G., Suc, J.-P., 2007. Middle Miocene latitudinal climatic gradient in Western Europe: evidence from pollen records. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 208–225.
- Kälin, D., Kempf, O., 2009. High-resolution stratigraphy from the continental record of the Middle Miocene northern Alpine foreland basin of Switzerland. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 254, 177–235.
- Kovar-Eder, J., Kvacek, Z., Zasadniak, E., Givulescu, R., Hably, L., Mihajlovic, D.M., Teslenko, J., Walther, H., 1996. Floristic trends in the vegetation of the Paratethys surrounding areas during Neogene time. In: Bernor, R.L., Fahlbusch, V., Mittmann, H.W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 395–413.
- Krijgsman, W., Garcés, M., Langereis, C.G., Daams, R., Dam, J.v., van der Meulen, A.J., Agustí, J., Cabrera, L., 1996. A new chronology for the Middle to Late Miocene continental record in Spain. *Earth and Planetary Science Letters* 142, 367–380.
- López Martínez, N., Agustí, J., Cabrera, L., Calvo, J.P., Civis, J., Corrochano, A., Daams, R., Díaz, M., Elizaga, E., Hoyos, M., Martínez, J., Morales, J., Portero, J.M., Robles, F., Santisteban, C., Torres, T., 1987. Approach to the Spanish continental Neogene synthesis and paleoclimatic interpretation, VIIIth congress of RCMNS (Regional Committee on Mediterranean Neogene Stratigraphy). *Annales Instituti Geologici Publici Hungarici*, Budapest 1985, 383–391.
- López-Guerrero, P., 2006. Paleoclimatología de Europa occidental en el Aragoniense. XXII Jornadas de la Sociedad Española de Paleontología, León, pp. 56–57.
- Lourens, L.J., Hilgen, F.J., Laskar, J., Shackleton, N.J., Wilson, D., 2004. The Neogene Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), *Geologic Time Scale 2004*. Cambridge University Press, Cambridge, pp. 409–440.
- Mai, D.H., 1989. Development and regional differentiation of the European vegetation during the Tertiary. *Plant Systematics and Evolution* 162, 79–91.
- Maridet, O., Costeur, L., 2010. Diversity trends in Neogene European ungulates and rodents: large scale comparisons and perspectives. *Naturwissenschaften* 97 (2), 161–172.
- Mein, P., 1975. Biozonation du Néogène Méditerranéen à partir des Mammifères. Report on Activity of the RCMNS working groups, Bratislava, 78–81. *Geologicae Helveticae* 37, 453–457.
- Mein, P., 1979. Rapport d'activité du groupe de travail vertébrés mise à jour de la biostratigraphie du Néogène basée sur les mammifères. *Annales Géologiques des Pays Héliéniques* 3, 1367–1372.
- Mein, P., 1990. Updating MN zones. In: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), *European Neogene Mammal Chronology*. Plenum, New York, pp. 73–90.
- Mein, P., 1999. European Miocene mammal biochronology. In: Heisig, G.R.K. (Ed.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 25–38.
- Morales, J., Nieto, M., Peláez-Campomanes, P., Soria, D., Álvarez Sierra, M.A., Alcalá, L., Amezuza, L., Azanza, B., Cerdeño, E., Daams, R., Fraile, S., Guillem, J., Hoyos, M., Merino, L., de Miguel, I., Monparler, R., Montoya, P., Pérez, B., Salesa, M.J., Sánchez, I.M., 1999. Vertebrados continentales del Terciario de la cuenca de Loranca (Provincia de Cuenca). In: Aguirre, E., Rábano, I. (Eds.), *La huella del pasado: Fósiles de Castilla-La Mancha*. Junta de Comunidades de Castilla-La Mancha, Toledo, pp. 237–260.
- Moreno Bofarull, A., Arias Royo, A., Hernández Fernández, M., Ortiz-Jaureguizar, E., Morales, J., 2008. Influence of continental history on the ecological specialization and macroevolutionary processes in the mammalian assemblage of South America: differences between small and large mammals. *BMC Evolutionary Biology* 8, 97.
- Moyà-Solà, S., Agustí, J., 1987. The Vallesian in the type area (Vallès–Penedès, Barcelona, Spain). *Annals of the Hungarian Geological Institute* 70, 93–99.
- Moyà-Solà, S., Alba, D.M., Almécija, S., Casanovas-Vilar, I., Köhler, M., De Esteban-Trivigno, S., Robles, J.M., Galindo, J., Fortuny, J., 2009a. A unique Middle Miocene European hominoid and the origins of the great ape and human clade. *Proceedings of the National Academy of Sciences* 106, 9601–9606.
- Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Cabrera, L., Garcés, M., Almécija, S., Beamad, E., 2009b. First partial face and upper dentition of the Middle Miocene hominoid *Dryopithecus fontani* from Abocador de Can Mata (Vallès–Penedès Basin, Catalonia, NE Spain): taxonomic and phylogenetic implications. *American Journal of Physical Anthropology* 139, 126–145.
- Murphy, M.A., 1994. Fossils as a basis for chronostratigraphic interpretation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 192, 255–271.
- Palombo, M.R., Sardella, R., 2007. Biochronology and biochron boundaries: a real dilemma or a false problem? An example based on the Pleistocene large mammalian faunas from Italy. *Quaternary International* 160, 30–42.
- Peláez-Campomanes, P., 1993. *Micromamíferos del Paleogeno Continental Español: Sistemática, Biocronología y Paleocología*. PhD. Thesis, Universidad Complutense de Madrid, Madrid, p. 388.
- Pickford, M., Morales, J., 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology* 112, 297–322.

- Prado, J.L., Alberdi, M.T., Azanza, B., Sánchez, B., 2001. Climate and changes in mammal diversity during the Late Pleistocene–Holocene in the Pampean Region (Argentina). *Acta Palaeontologica Polonica* 46, 261–276.
- Raia, P., Carotenuto, F., Meloro, C., Piras, P., Barbera, C., Kotsakis, T., 2009. More than three million years of community evolution. The temporal and geographical resolution of the Plio–Pleistocene Western Eurasia mammal faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology* 276, 15–23.
- Sauer, J.R., Slade, N.A., 1987. Size-based demography of vertebrates. *Annual Review of Ecology and Systematics* 18, 71–90.
- Sen, S., 1997. Magnetostratigraphic calibration of the European Neogene mammal chronology. In: Lindsay, E.H. (Ed.), *Correlation of Eurasian late Cenozoic Mammal Chronology with the Magnetic Polarity Time Scale*. Elsevier, pp. 181–204.
- Sesé, C., 2006. Los roedores y lagomorfos del Neógeno de España. *Estudios Geológicos* 62, 429–480.
- Sesé, C., López Martínez, N., 1981. Los micromamíferos (Insectivora, Rodentia y Lagomorpha) del Vallesense inferior de los Valles de Fuentidueña. *Estudios Geológicos* 37, 369–481.
- Sotnikova, M.V., Dodonov, A.E., Pen'Kov, A.V., 1997. Upper Cenozoic bio-magnetic stratigraphy of Central Asian mammalian localities. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 243–258.
- Steininger, F.F., 1999. Chronostratigraphy, geochronology and biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)". In: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 9–24.
- van Dam, J.A., 2003. European Neogene mammal chronology: past, present and future. *Deinsea* 10, 85–95.
- van Dam, J., 2006. Geographic and temporal patterns in the Late Neogene (12–3 Ma) aridification of Europe: the use of small mammals as paleoprecipitation proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 190–218.
- van Dam, J., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 1997. The small mammals from the Upper Miocene of the Teruel–Alfambra region (Spain): paleobiology and paleoclimatologic reconstructions. *Geologica Ultraiectina* 156, 1–204.
- van Dam, J., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The Upper Miocene mammal record from the Teruel–Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *Journal Vertebrate Paleontology* 21, 367–385.
- van Dam, J.A., Aziz, H.A., 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 der Made, J., Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 228–246.
- van der Meulen, A.J., Daams, R., 1992. Evolution of early–middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 93, 227–253.
- van der Meulen, A.J., Peláez-Campomanes, P., Levin, S.A., 2005. Age structure, residents, and transients of Miocene rodent communities. *American Naturalist* 165, E108–E125.
- 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. *Géobios* 44 (2–3), 309–321.
- Vrba, E.S., 1988. Late Pliocene climatic events and hominid evolution. In: Grine, F.E. (Ed.), *The Evolutionary History of Robust Australopithecines*. Aldine Publishing Company, New York, pp. 405–426.
- Wing, S.L., Alroy, J., Hickey, L.J., 1995. Plant and mammal diversity in the Paleocene to Early Eocene of the Bighorn Basin. *Palaeogeography, Palaeoclimatology, Palaeoecology* 115, 117–155.
- Wolfe, J.A., 1985. Distribution of major vegetational types during the Tertiary. *Am Geophys Un Monogr* 32, 357–375.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693.

Appendix 1

Fossil sites analysed in this work and references for faunal lists. Basin abbreviations: AL, Alicante; BT, Baixo Tejo; CA, Castellón; CD, Calatayud-Daroca; CU, Cucuron-Basse Durance; DU, Duero; FO, Fortuna; GR, Granada; GB, Guadix-Baza; HI, Hajar; MU, Murcia; LR, Languedoc-Roussillon; PR, Provence; RH, Rhône; TE, Alfambra-Teruel; TJ, Tajo; VA, Valencia; VP, Vallès Penedès. N, northern province and S, southern province. Gray background indicates the MN14 fossil sites used to calibrate each analysis.

| Province | Basin | Fossil site | References |
|----------|-------|---------------------------|--|
| N | CU | Cucuron | Mein and Michaux, 1979; Agustí, 1986a; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Freudenthal and Martín-Suárez, 1999; Hugueney, 1999; Minwer-Barakat, 2005; García-Alix, 2006; García-Alix et al., 2008a |
| N | FR | Celleneuve | Michaux, 1966; Mein and Michaux, 1970; Chaline and Michaux, 1974; Bachelet, 1990; Ambert et al., 1998; Martín-Suárez and Mein, 1998; de Bruijn, 1999 |
| N | FR | Font Estramar | Bachelet, 1990; Aguilar et al., 1991; Ambert et al., 1998; Geraads, 1998; Martín-Suárez and Mein, 1998; Minwer-Barakat, 2005 |
| N | FR | Hautimagne | Agustí, 1982; Bachelet, 1990; Aguilar et al., 1995; Daams and de Bruijn, 1995; Michaux et al., 1997; Martín-Suárez and Mein, 1998; Minwer-Barakat, 2005; García-Alix, 2006; Montuire et al., 2006; García-Alix et al., 2007, 2008a |
| N | FR | Vendargues | Mein and Michaux, 1970; Chaline and Michaux, 1974; Bachelet, 1990; Fejfar et al., 1997; Michaux et al., 1997; Minwer-Barakat, 2005; García-Alix, 2006; Montuire et al., 2006 |
| N | LR | Lo Fournas 10 | Aguilar et al., 1999; Lazzari and Aguilar, 2007 |
| N | LR | Lo Fournas 2 | Aguilar et al., 1999; Lazzari and Aguilar, 2007 |
| N | LR | Lo Fournas 3 | Aguilar et al., 1999; Kálin, 1999; Lazzari and Aguilar, 2007 |
| N | LR | Lo Fournas 6c | Martín-Suárez and Mein, 1998; Aguilar et al., 1999; Freudenthal and Martín-Suárez, 1999 |
| N | LR | Lo Fournas 7 | Michaux et al., 1997; Aguilar et al., 1999; Renaud et al., 1999; Montuire et al., 2006; Casanovas-Vilar, 2007 |
| N | PR | Lobrieu | van Dam, 1997; Martín-Suárez and Mein, 1998; Mein, 1999; Montuire et al., 2006 |
| N | RH | Ambérieu 1 | Farjanel and Mein, 1984; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; Mein, 1999; Renaud et al., 1999; Montuire et al., 2006; Casanovas-Vilar, 2007 |
| N | RH | Ambérieu 3 | Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Hugueney, 1999; Mein, 1999; García-Alix, 2006; Montuire et al., 2006; García-Alix et al., 2008a |
| N | RH | Douvre | Mein, 1999; van Dam and Weltje, 1999; Casanovas-Vilar, 2007 |
| N | RH | Lissieu | Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daams, 1999; Freudenthal and Martín-Suárez, 1999; Kálin, 1999; Mein, 1999; Montuire et al., 2006; García-Alix et al., 2008a |
| N | RH | Soblay | Martín-Suárez and Mein, 1998; Bolliger, 1999; Fejfar, 1999; Hugueney, 1999; Kálin, 1999; Mein, 1999 |
| N | VP | Autopista Rubí-Terrassa 7 | Garcés et al., 1996; Agustí et al., 1997; Casanovas-Vilar and Agustí, 2007 |
| N | VP | Barranc de Can Vila 1 | Alba et al., 2006; Casanovas-Vilar, 2007; Casanovas-Vilar et al., 2008 |

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| N | VP | Can Llobateres 1 | Agustí, 1978; Aguilar et al., 1979; Agustí, 1981, 1982; Aguilar et al., 1991; Aldana, 1992a, b; Daams and de Bruijn, 1995; Aguilar et al., 1997; Michaux et al., 1997; Bolliger, 1999; Daams, 1999; de Bruijn, 1999; Hugueney, 1999; Kälín, 1999; Rummel, 1999; van Dam et al., 2001; Aguilar and al., 2004; Aguilar et al., 2004; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007; García-Alix et al., 2008a |
| N | VP | Can Mata I (Bretxa de Can Mata) | Agustí et al., 1985; van der Meulen et al., 2003; Alba et al., 2006 |
| N | VP | Can Missert | Agustí et al., 1985; Aldana, 1992a; Daams and de Bruijn, 1995; Agustí et al., 1997; van der Meulen et al., 2003; Agustí et al., 2005; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007 |
| N | VP | Can Ponsic | Agustí, 1978; Aguilar et al., 1979; Agustí, 1981, 1982; Aldana, 1992a, b; Daams and de Bruijn, 1995; Agustí et al., 1997; de Bruijn, 1999; Hugueney, 1999; Aguilar et al., 2004; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007 |
| N | VP | Can Vilella 1 | Agustí, 1989; Freudenthal et al., 1998; Geraads, 1998; Agustí et al., 2006 |
| N | VP | Castell de Barberà | Agustí, 1978; Aguilar et al., 1979; Agustí, 1981, 1982; Agustí et al., 1985; Aguilar et al., 1991; Aldana, 1992a, b; Daams and de Bruijn, 1995; Bolliger, 1999; de Bruijn, 1999; Hugueney, 1999; Kälín, 1999; Agustí and al., 2005; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007; Casanovas-Vilar et al., 2008; García-Alix et al., 2008c |
| N | VP | Creu Conill 22 | Agustí et al., 1997; Alba et al., 2006; Aarssen, 2007; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007 |
| N | VP | Sant Quirze | Agustí, 1981; Agustí and Gibert, 1982; Agustí et al., 1985; Aldana, 1992a, b; Agustí et al., 1997; Bolliger, 1999; de Bruijn, 1999; Hugueney, 1999; Kälín, 1999; Agustí et al., 2001; López-Guerrero et al., 2007; Casanovas-Vilar et al., 2008 |
| N | VP | Sant Quirze A | Alba et al., 2006; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007 |
| N | VP | Torrent de Febulines | Golpe Posse et al., 1979; Agustí, 1981; Agustí and Gibert, 1982; Agustí et al., 1997 |
| N | VP | Torrent de Febulines 3 | Casanovas-Vilar and Agustí, 2007 |
| N | VP | Trinxera Nord Autopista | Agustí, 1981, 1982; Agustí and Gibert, 1982; Aldana, 1992a; Casanovas-Vilar and Agustí, 2007 |
| N | VP | Trinxera Sud Autopista II | Agustí, 1981; Agustí and Gibert, 1982; Aldana, 1992a; Agustí et al., 1997; Bolliger, 1999; Casanovas-Vilar, 2007; Casanovas-Vilar and Agustí, 2007 |
| S | AL | Alcoy-Barranco | Adrover, 1969; Brandy, 1979; Agustí et al., 1989; Freudenthal et al., 1998; Minwer-Barakat, 2005; García-Alix, 2006; Montoya et al., 2006; Montuire et al., 2006 |
| S | AL | Crevillente 14 | Martín-Suárez and Freudenthal, 1998; Martín-Suárez et al., 2001 |
| S | AL | Crevillente 15 | Martín-Suárez and Freudenthal, 1993; Mein et al., 1993; Martín-Suárez and Freudenthal, 1994; Montoya and Alberdi, 1995; Martín-Suárez and Freudenthal, 1998; Kälín, 1999; Martín-Suarez et al., 2001 |
| S | AL | Crevillente 17 | Martín-Suárez and Freudenthal, 1994; Freudenthal et al., 1998; Martín-Suárez and Freudenthal, 1998; Freudenthal and Martín-Suárez, 1999; Martín-Suárez et al., 2001 |

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| S | AL | Crevillente 2 | de Bruijn et al., 1975; Mein et al., 1993; Martín-Suárez and Freudenthal, 1994; Martín-Suárez and Mein, 1998; Kálin, 1999; Sen, 1999; Martín-Suárez et al., 2001; Montuire et al., 2006 |
| S | AL | Crevillente 22 | Martín-Suárez and Freudenthal, 1998 |
| S | AL | Crevillente 3 | de Bruijn et al., 1975; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Freudenthal and Martín-Suárez, 1999; Martín-Suárez et al., 2001; Sesé, 2006 |
| S | AL | Crevillente 4B | Mein et al., 1993; Martín-Suárez and Freudenthal, 1994, 1998; Martín-Suárez et al., 2001 |
| S | AL | Crevillente 5A | Mein et al., 1993; Martín-Suárez and Freudenthal, 1998; Martín-Suárez et al., 2001 |
| S | AL | Crevillente 6 | de Bruijn et al., 1975; Freudenthal et al., 1998; Geraads, 1998; Martín-Suárez and Freudenthal, 1998; Kálin, 1999; Martín-Suárez et al., 2001 |
| S | AL | Crevillente 8 | Martín-Suárez and Freudenthal, 1998; Martín-Suárez and Mein, 1998; Martín-Suárez et al., 2001 |
| S | BT | Esbarrondadoiro | Antunes and Mein, 1995; Geraads, 1998; Minwer-Barakat, 2005; García-Alix, 2006; García-Alix et al., 2008a |
| S | BT | Freiria de Rio Maior | Antunes and Mein, 1979; Antunes et al., 1992; Freudenthal et al., 1998 |
| S | CA | Almenara M (=Casablanca M) | Agustí and Galobart, 1986; Agustí et al., 1989; Freudenthal et al., 1998; Wessels, 1998, 1999; Agustí et al., 2006; Montuire et al., 2006 |
| S | CD | Alcocer 2 | Cuenca-Bescós, 1988; Daams and Freudenthal, 1988; Daams et al., 1988; Daams, 1989, 1990; van der Meulen et al., 2003; Casanovas-Vilar and Agustí, 2007 |
| S | CD | Carrilanga 1 | Daams and Freudenthal, 1981; Daams and van der Meulen, 1984; Daams, 1985; Daams and Freudenthal, 1988; Daams et al., 1988; Daams, 1989; van der Meulen et al., 2003; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007 |
| S | CD | Las Planas 5H | van de Weerd and Daams, 1978; Daams and Freudenthal, 1981; Daams and van der Meulen, 1984; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; van der Meulen et al., 2003; Freudenthal and Martín-Suárez, 2007 |
| S | CD | Nombrevilla (classical) | van de Weerd and Daams, 1978; Daams and Freudenthal, 1981; Daams and van der Meulen, 1984; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; Lacomba, 1988; van Dam et al., 2001; Hugueney, 1999; Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Montuire et al., 2006; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007; López-Guerrero et al., 2009 |
| S | CD | Nombrevilla 10 | Álvarez-Sierra et al., 2003; López-Guerrero et al., 2009 |
| S | CD | Nombrevilla 2 | Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Casanovas-Vilar, 2007; López-Guerrero et al., 2007; López-Guerrero et al., 2009 |
| S | CD | Nombrevilla 3 | Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; López-Guerrero et al., 2009 |
| S | CD | Nombrevilla 4 | Álvarez-Sierra et al., 2003 |
| S | CD | Nombrevilla 9 | Daams and Freudenthal, 1988; Álvarez-Sierra et al., 2003; López-Guerrero et al., 2007 |
| S | CD | Pedregueras 2A | Daams and Freudenthal, 1981; Daams and van der Meulen, 1984; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; Daams, 1999; Hugueney, 1999; Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007; López-Guerrero et al., 2009 |

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| S | CD | Pedregueras 2C | Agustí, 1978; van de Weerd and Daams, 1978; Daams and Freudenthal, 1981; Daams and van der Meulen, 1984; Daams, 1985; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; Lacomba, 1988; Aguilar et al., 1991; Daams, 1999; Kálin, 1999; Rummel, 1999; Álvarez-Sierra et al., 2003; Casanovas-Vilar and Agustí, 2007; García-Alix et al., 2008c |
| S | CD | Solera | van de Weerd and Daams, 1978; Daams and Freudenthal, 1981; Daams, 1985; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; Daams, 1989; Aguilar et al., 1991; Hugueneý, 1999; López-Guerrero et al., 2007 |
| S | CD | Toril 1 | van de Weerd and Daams, 1978; Daams and van der Meulen, 1984; Daams, 1985; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2009 |
| S | CD | Toril 2 | Daams and Freudenthal, 1988; Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; López-Guerrero et al., 2009 |
| S | CD | Toril 3A | Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Azanza et al., 2004; López-Guerrero et al., 2007; López-Guerrero et al., 2009 |
| S | CD | Toril 3B | Álvarez-Sierra et al., 2003; van der Meulen et al., 2003; Azanza et al., 2004; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2009 |
| S | CD | Villafeliche 9 | Daams and van der Meulen, 1984; Daams et al., 1987; Daams and Freudenthal, 1988; Daams et al., 1988; van der Meulen et al., 2003; Casanovas-Vilar and Agustí, 2007 |
| S | DU | Ampudia 1 | Álvarez-Sierra and García-Moreno, 1986; García-Moreno, 1987; Daams and de Bruijn, 1995; Daams, 1999 |
| S | DU | Ampudia 9 | López Martínez et al., 1986; García-Moreno, 1987; Daams and Freudenthal, 1988; Álvarez-Sierra et al., 1990; Daams, 1999; Kálin, 1999 |
| S | DU | Casasola 2 | García-Moreno, 1987; Daams and Freudenthal, 1988; Álvarez-Sierra et al., 1990; Daams and de Bruijn, 1995; Hugueneý, 1999 |
| S | DU | Los Valles de Fuentidueña | Agustí, 1978; Sesé and López Martínez, 1981; Sesé, 2006 |
| S | DU | Simancas 2 | López Martínez et al., 1986; García-Moreno, 1987; Daams and Freudenthal, 1988; Álvarez-Sierra et al., 1990; Daams, 1999; Kálin, 1999 |
| S | DU | Torremormojón 1 | Álvarez-Sierra and García-Moreno, 1986; López Martínez et al., 1986; García-Moreno, 1987; Álvarez-Sierra et al., 1990; Daams and de Bruijn, 1995; Daams, 1999; Hugueneý, 1999 |
| S | DU | Torremormojón 3 | López Martínez et al., 1986; Daams and Freudenthal, 1988; Álvarez-Sierra et al., 1990 |
| S | DU | Torremormojón 4 | López Martínez et al., 1986; García-Moreno, 1987; Daams and Freudenthal, 1988; Álvarez-Sierra et al., 1990; Hugueneý, 1999; Casanovas-Vilar and Agustí, 2007 |
| S | DU | Torremormojón 5 | García-Moreno, 1987; Álvarez-Sierra et al., 1990; Hugueneý, 1999; Casanovas-Vilar and Agustí, 2007 |
| S | FO | Casa del Acero | Agustí et al., 1985; Agustí, 1986b; Freudenthal et al., 1991; Freudenthal et al., 1998; Geraads, 1998; Martín-Suárez and Mein, 1998; Kálin, 1999; Sesé, 2006; García-Alix et al., 2008b; López Guerrero et al., 2008 |
| S | FO | La Hornera | Agustí et al., 1985; Garcés et al., 1998; Minwer-Barakat, 2005 |
| S | GB | Bacochas 1 | Freudenthal et al., 1998; Geraads, 1998; Wessels, 1998, 1999; Minwer-Barakat, 2005; García-Alix, 2006 |
| S | GB | Botardo C | Martín-Suárez, 1988; Agustí, 1989; Wessels, 1998, 1999; Minwer-Barakat, 2005; García-Alix et al., 2008e |

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| S | GB | Embalse de Negratin 1 | Minwer-Barakat, 2005 |
| S | GB | Gorafe 1 | de Bruijn, 1974; Aguirre et al., 1995; Martín-Suárez and Mein, 1998; Wessels, 1998; Mein, 1999; Wessels, 1999; Martín-Suárez et al., 2000; Hernández Fernández, 2005; Minwer-Barakat, 2005; Montuire et al., 2006; García-Alix et al., 2007 |
| S | GB | Pino Mojon | Geraads, 1998; Wessels, 1998, 1999; Minwer-Barakat, 2005 |
| S | GR | juni-02 | García-Alix et al., 2008a |
| S | GR | Dehesa 16 | Hugueneu, 1999; García-Alix, 2006; García-Alix et al., 2008a; García-Alix et al., 2008e |
| S | GR | Purcal 23 | Freudenthal et al., 1998; García-Alix et al., 2008c; García-Alix et al., 2008e |
| S | GR | Purcal 24 A | Freudenthal et al., 1998; García-Alix et al., 2007, 2008b, a; García-Alix et al., 2008e |
| S | GR | Purcal 25 (=25 + 25A) | Freudenthal et al., 1998; García-Alix, 2006; García-Alix et al., 2007, 2008a; García-Alix et al., 2008e |
| S | GR | Purcal 3 | Freudenthal et al., 1998; García-Alix, 2006; García-Alix et al., 2008c; García-Alix et al., 2008e |
| S | GR | Purcal 4 | Geraads, 1998; Hernández Fernández, 2005; Minwer-Barakat, 2005; García-Alix, 2006; García-Alix et al., 2007 |
| S | GR | Salobreña | Aguilar et al., 1984; Sanz et al., 1992; Wessels, 1998, 1999; Aguirre, 2003; Hernández Fernández, 2005; Minwer-Barakat, 2005; Montuire et al., 2006; Sesé, 2006 |
| S | HI | Hijar 1 | Calvo et al., 1978 |
| S | MU | Caravaca 1 | de Bruijn et al., 1975; Aguirre et al., 1995; Martín-Suárez and Mein, 1998; Hernández Fernández and Peláez-Campomanes, 2003; Hernández Fernández, 2005 |
| S | MU | Librilla | de Bruijn et al., 1975; Morales, 1984; Lacomba et al., 1986; Agustí, 1989; Freudenthal et al., 1998; Garcés et al., 1998; Hernández Fernández, 2005; Minwer-Barakat, 2005; García-Alix, 2006; García-Alix et al., 2008b |
| S | TE | Aljezar B (=Los Aljezares) | Adrover, 1986; Mein et al., 1993; Adrover and Mein, 1996; van Dam, 1997; Martín-Suárez and Freudenthal, 1998; Minwer-Barakat, 2005; García-Alix, 2006; Montuire et al., 2006; Sesé, 2006; Minwer-Barakat et al., 2008 |
| S | TE | Celadas 9 | Adrover et al., 1993; Fejfar et al., 1997; Minwer-Barakat, 2005; García-Alix, 2006 |
| S | TE | Concud 2 | van Dam, 1997; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Concud 3 | van de Weerd, 1976; van de Weerd and Daams, 1978; Daams and Freudenthal, 1988; van Dam, 1997; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | La Gloria 10 | van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; van Dam et al., 2001 |
| S | TE | La Gloria 4 | Adrover et al., 1993; Albesa et al., 1997; Fejfar et al., 1997; Geraads, 1998; Martín-Suárez and Mein, 1998; Wessels, 1998; de Bruijn, 1999; Wessels, 1999; van Dam et al., 2001; Hernández Fernández and Peláez-Campomanes, 2003; Aaris-Sorensen and Liljegren, 2004; Hernández Fernández, 2005; Minwer-Barakat, 2005; García-Alix, 2006 |
| S | TE | La Gloria 5 | Adrover et al., 1993; van Dam, 1997; Freudenthal et al., 1998; de Bruijn, 1999; van Dam et al., 2001 |
| S | TE | Las Casiones | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Freudenthal et al., 1998; van Dam et al., 2001; van der Meulen et al., 2003 |

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| S | TE | Las Casiones superior | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Freudenthal et al., 1998; van Dam et al., 2001 |
| S | TE | Los Aguanaces | Adrover, 1986; van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; van Dam et al., 2001 |
| S | TE | Los Aguanaces 1 | van Dam, 1997; van Dam et al., 2001 |
| S | TE | Los Aguanaces 3 | van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; van Dam et al., 2001 |
| S | TE | Los Mansuetos | van de Weerd, 1976; van de Weerd and Daams, 1978; Mein et al., 1993; Michaux et al., 1997; van Dam, 1997; Freudenthal et al., 1998; de Bruijn, 1999; Freudenthal and Martín-Suárez, 1999; Hugueney, 1999; Rummel, 1999; López Guerrero, 2007 |
| S | TE | Masada del Valle 2 | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; de Bruijn, 1999; Hugueney, 1999; van Dam et al., 2001 |
| S | TE | Masada del Valle 5 | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Masada del Valle 7 | van de Weerd, 1976; van de Weerd and Daams, 1978; Daams and Freudenthal, 1988; Adrover et al., 1993; van Dam, 1997; Freudenthal et al., 1998; Hugueney, 1999; van Dam et al., 2001 |
| S | TE | Masía de la Roma 11 | van Dam, 1997; van Dam et al., 2001; Casanovas-Vilar and Agustí, 2007 |
| S | TE | Masía de la Roma 7 | van Dam, 1997; van Dam et al., 2001; Casanovas-Vilar and Agustí, 2007 |
| S | TE | Masía del Barbó 2A (=Masía del Barbó A) | van de Weerd, 1976; van de Weerd and Daams, 1978; Lacomba, 1988; van Dam, 1997; Freudenthal et al., 1998; Daams, 1999; Rummel, 1999; van Dam et al., 2001; Hernández Fernández, 2005; Casanovas-Vilar and Agustí, 2007 |
| S | TE | Masía del Barbó 2B (=Masía del Barbo B) | van de Weerd, 1976; van de Weerd and Daams, 1978; Lacomba, 1988; van Dam, 1997; Daams, 1999; Hugueney, 1999; van Dam et al., 2001; Hernández Fernández, 2005; Casanovas-Vilar and Agustí, 2007; López-Guerrero et al., 2007 |
| S | TE | Molina de Aragón | Lacomba, 1988; de Bruijn, 1999; Kálin, 1999; van der Meulen et al., 2003; Casanovas-Vilar, 2007 |
| S | TE | Peralejos 5 | van de Weerd and Daams, 1978; van Dam, 1997; van Dam et al., 2001 |
| S | TE | Peralejos C | van de Weerd, 1976; van de Weerd and Daams, 1978; Lacomba, 1988; van Dam, 1997; Guerra-Merchan et al., 2001; van Dam et al., 2001 |
| S | TE | Peralejos D | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; van Dam et al., 2001 |
| S | TE | Peralejos E | Aguilar et al., 1995; Fejfar, 1999; van Dam, 2004; Hernández Fernández, 2005; Minwer-Barakat, 2005; García-Alix, 2006; García-Alix et al., 2008d, a; Minwer-Barakat et al., 2008 |
| S | TE | Puente Minero | Alcalá et al., 1991; van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; van Dam et al., 2001 |
| S | TE | Regajo 2 | van Dam et al., 2001; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Tortajada | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Tortajada A | van de Weerd, 1976; van de Weerd and Daams, 1978; van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; Freudenthal and Martín-Suárez, 1999; van Dam et al., 2001 |

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| S | TE | Tortajada D | van Dam, 1997; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Valdecebro 3 | van de Weerd, 1976; van de Weerd and Daams, 1978; Adrover et al., 1993; van Dam, 1997; Freudenthal et al., 1998; Freudenthal and Martín-Suárez, 1999; Hugueneu, 1999; van Dam et al., 2001 |
| S | TE | Valdecebro 6 | Adrover et al., 1993; van Dam, 1997; Freudenthal et al., 1998; Hugueneu, 1999; van Dam et al., 2001 |
| S | TE | Villalba Baja 2/2C | van Dam, 1997; Martín-Suárez and Mein, 1998; van Dam et al., 2001 |
| S | TE | Villastar | Adrover et al., 1993; Freudenthal et al., 1998; Geraads, 1998; Hugueneu, 1999 |
| S | TE | Vivero de Pinos | van Dam, 1997; Freudenthal et al., 1998; Martín-Suárez and Mein, 1998; Daxner-Höck, 1999; Hugueneu, 1999; van Dam et al., 2001 |
| S | TJ | Canteras de Iberia | Sanz et al., 1992; Freudenthal and Martín-Suárez, 1999 |
| S | TJ | Cerro de los Batallones 1 | Morales et al., 1992; Morales et al., 2004; López Guerrero, 2007; López Guerrero et al., 2008; López-Antoñanzas et al., 2008; Morales et al., 2008 |
| S | TJ | Lupiana | Sesé et al., 1990; van der Meulen et al., 2003 |
| S | TJ | Paracuellos 3 | Morales et al., 2000; van der Meulen et al., 2003; Montes et al., 2006 |
| S | VA | Los Mingos 1 C | Freudenthal et al., 1998; Benavent et al., 2008 |
| S | VA | Venta del Moro | Freudenthal et al., 1998; Hugueneu, 1999; Montoya et al., 2006; van der Made et al., 2006 |

References:

- Aaris-Sorensen, K., Liljegren, R., 2004. Late Pleistocene remains of giant deer (*Megaloceros giganteus* Blumenbach) in Scandinavia: chronology and environment. *Boreas* 33, 61-73.
- Aarssen, L.W., 2007. Some bold evolutionary predictions for the future of mating in humans. *Oikos* 116, 1768-1778.
- Adrover, R., 1969. Los micromamíferos del Plioceno inferior de los lignitos de Alcoy. *Boletín de la Real Sociedad española de Historia Natural* 67, 245-272.
- Adrover, R., 1986. Nuevas faunas de roedores en el Mio-Plioceno continental de la region de Teruel (España). Interés bioestratigráfico y paleoecológico. PhD. Thesis, Instituto de Estudios Turolenses. Diputación Provincial de Teruel, Teruel, p.423.
- Adrover, R., Mein, P., Moissenet, E., 1993. Roedores de la transición Mio-Plioceno de la región de Teruel. *Paleontologia i Evolució* 26-27, 47-84.
- Adrover, R., Mein, P., 1996. Nuevo *Ruscinomys* (Rodentia, Mammalia) en el Mioceno Superior de la región de Teruel (España). *Estudios Geológicos* 52, 361-365.
- Aguilar, J.-P., Agustí, J., Gibert, J., 1979. Rongeurs Miocènes dans le Vallès Penedès 2. Les rongeurs de Castell de Barbera. *Paleovertebrata* 9, 17-31.
- Aguilar, J.-P., Brandy, L.D., Thaler, L., 1984. Les rongeurs de Salobreña (Sud de l'Espagne) et le probleme de la migration messinienne. *Paleobiologie Continentale* 14, 3-17.
- Aguilar, J.-P., Michaux, J., Bachelet, B., Calvet, M., Faillat, J.-P., 1991. Les nouvelles faunes de rongeurs proches de la limite Mio-Pliocene en Rousillon. Implications biostratigraphiques et biogeographiques. *Palaeovertebrata* 20, 147-174.
- Aguilar, J.-P., Escarguel, G., Michaux, J., 1997. Biochronologie du Miocène Inférieur et Moyen du Sud de la France à partir des faunes karstiques. Le problème du genre *Neocometes*, in: Aguilar, J.-P., Legendre, S., Michaux, J. (Eds.), *Actes du Congrès BiochroM'97*. École Pratique des Hautes Études Institut de Montpellier, Montpellier, pp. 575-579.
- Aguilar, J.-P., Calvet, M., Michaux, J., 1995. Les rongeurs du gisement karstique Miocène Supérieur de Caltelnuou 1 (Pyrénées-Orientales, France). *Geobios* 28, 501-510.

- Aguilar, J.-P., Escarguel, G., Michaux, J., 1999. A succession of Miocene rodent assemblages from fissure fillings in southern France: palaeoenvironmental interpretation and comparison with Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 145, 215-230.
- Aguilar, J.-P., al, e., 2004. Mid-Neogene Mediterranean marine-continental correlations: an alternative interpretation. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 204, 165-186.
- Aguilar, J.P., Berggren, W.A., Aubry, M.P., Kent, D.V., Clauzon, G., Benammi, M., Michaux, J., 2004. Mid-Neogene Mediterranean marine-continental correlations: an alternative interpretation. *Palaeogeography Palaeoclimatology Palaeoecology* 204, 165-186.
- Aguirre, E., 2003. Messiniense: Compleja y grave crisis ecológica. *Estudios Geológicos* 59, 205-212.
- Aguirre, J., Castillo, C., Ferriz, F.J., Agustí, J., Oms, O., 1995. Marine-Continental Magnetobiostratigraphic Correlation of the *Dolomys* Subzone (Middle of Late Ruscinian) - Implications for the Late Ruscinian Age. *Palaeogeography Palaeoclimatology Palaeoecology* 117, 139-152.
- Agustí, J., 1978. El Vallesiense inferior de la península Iberica y su fauna de Ruedores (Mam.). *Acta Geologica Hispanica* (Instituto Nacional de Geología, Barcelona) 13, 137-141.
- Agustí, J., 1981. Roedores miomorphos del Neogeno de Cataluña. PhD. Thesis, Universidad de Barcelona, Barcelona, p. 293.
- Agustí, J., 1982. Biozonación del Neógeno continental de Cataluña mediante roedores (Mammalia). *Acta Geologica Hispanica* 17, 21-26.
- Agustí, J., 1986a. Nouvelles espèces de Cricétidés vicariantes dans le Turolien moyen de Fortuna (Province de Murcia, Espagne). *Geobios* 19, 5-11.
- Agustí, J., 1986b. Biostratigraphic Synthesis of the Pliopleistocene from Guadix-Baza (Granada Province, Southeast of Spain). *Geobios* 19, 505-510.
- Agustí, J., 1989. On the peculiar distribution of some muroid taxa in the Western Mediterranean region, in: Torre, D. (Ed.), *Bollettino della Societa Paleontologica Italiana*. *Bollettino della Societa Paleontologica Italiana*, pp. 147-154.
- Agustí, J., Gibert, J., 1982. Roedores e insectívoros del Mioceno superior de Hostalets de Pierola (Vallès-Penedès, Cataluña). *Institut de Paleontologia de Sabadell. Butlletí Informatiu* 14, 19-38.
- Agustí, J., Cabrera, L., Moyà-Solà, S., 1985. Sinopsis estratigràfica del Neógeno de la fosa del Vallès-Penedès. *Paleontologia i Evolució* 18, 57-81.
- Agustí, J., Galobart, A., 1986. La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. *Paleontologia i Evolució* 20, 57-62.
- Agustí, J., Moyà-Solà, S., Martín-Suárez, L., 1989. Review of the late Miocene-early Pliocene mammalian faunas from eastern Spain. *Bollettino della Societa Paleontologica Italiana* 28, 155-160.
- Agustí, J., Cabrera, L., Garcés, M., Parés, J.M., 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): Paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 149-180.
- Agustí, J., Cabrera, L., Garcés, M., Krijgsman, W., Oms, O., Parés, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews* 52, 247-260.
- Agustí, J., Casanovas-Vilar, I., Furió, M., 2005. Rodents, insectívoros and chiropterans (Mammalia) from the Late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès Basin, Spain). *Geobios* 38, 575-583.
- Agustí, J., Garcés, M., Krijgsman, W., 2006. Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 5-14.
- Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una

- sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003, 2004 y 2005. *Estudios Geológicos* 62, 295-312.
- Albesa, J., Calvo, J.P., Alcalá, L., Alonso, A.M., 1997. Interpretación paleoambiental del yacimiento de La Gloria 4 (Plioceno, Fosa de Teruel) a partir del análisis de facies y de asociaciones de gasterópodos y de mamíferos. *Cuadernos de Geología Ibérica* 22, 239-264.
- Alcalá, L., Sesé, C., Herraiz, E., Adrover, R., 1991. Mamíferos del Turolense inferior de Puente Minero (Teruel, España). *Bol. R. Soc. Esp. Hist. Nat. (Sec. Geol.)* 86, 205-251.
- Aldana, E.J., 1992a. Los Sciurinae (Rodentia, Mammalia) del Mioceno de la Cuenca del Vallès-Penedes (Cataluña-España). *Treballs del Museu de Geologia de Barcelona* 2, 69-97.
- Aldana, E.J., 1992b. Los Castoridae (Rodentia, Mammalia) del Neógeno de Cataluña (España). *Treballs del Museu de Geologia de Barcelona* 2, 99-141.
- Álvarez-Sierra, M.A., García-Moreno, E., 1986. New Gliridae and Cricetidae from the Middle and Upper Miocene of the Duero Basin, Spain. *Studia Geologica Salmanticensia* 22, 145-189.
- Álvarez-Sierra, M.A., Civis, J., Corrochano, A., Daams, R., Dabrio, C.J., García, E., González, A., López Martínez, N., Mediavilla, R., Rivas Carballo, R., Valle, M.F., 1990. Un estratotipo del límite Aragoniense-Vallesiense (Mioceno medio-Mioceno superior) en la sección de Torremormojón (Cuenca del Duero, Provincia de Palencia). *Studia Geologica Salmanticensia, Actas de Paleontología* 68, 57-64.
- Álvarez-Sierra, M.A., 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). *Coloquios de Paleontología Volumen Extraordinario* 1, 25-33.
- Ambert, P., Aguilar, J.P., Michaux, J., 1998. Messino-Pliocene geodynamic evolution in the Languedoc central: the Orb and Herault hydrographic paleo-network (southern France). *Geodinamica Acta* 11, 139-146.
- Antunes, M.T., Mein, P., 1979. Le gisement de Freiria de Rio Maior, Portugal, et sa faune de mammifères; nouvelle espèce de *Rotundomys*, conséquences stratigraphiques. *Geobios* 12, 913-919.
- Antunes, M.T., Soulie-Marsche, I., Mein, P., Pais, J., 1992. Le gisement de Asseiceira, Portugal (Miocène supérieur) Données complémentaires sur Freiria de Rio Maior. *Universidade Nova de Lisboa Ciências da Terra* 11, 219-253.
- Antunes, M.T., Mein, P., 1995. New data on the small mammals of the Upper Miocene of Alvalade Basin, Portugal. *Comunicacoes do Instituto Geologico e Mineiro* 81, 85-96.
- Azanza, B., Alonso-Zarza, A., Álvarez-Sierra, M.A., Calvo, J.P., Fraile, S., García Paredes, I., Gómez, E., Hernández Fernández, M., van der Meulen, A., Miguel, D.d., Montoya, P., Morales, J., Murelaga, X., Peláez-Campomanes, P., Pérez, B., Quiralte, V., Salesa, M.J., Sánchez, I.M., Sánchez Marco, A., Soria, D., 2004. Los yacimientos de vertebrados continentales del Aragoniense superior (Mioceno medio) de Toril, Cuenca de Calatayud-Daroca. *Geo-Temas* 6, 271-274.
- Bachelet, B., 1990. Muridae et Arvicolidae (Rodentia, Mammalia) du Pliocène du Sud de la France: Systématique, Évolution, Biochronologie. *PhD. Thesis*, Université de Montpellier, Montpellier, p. 180.
- Benavent, J.V., Gascó, F., Ruiz Sanchez, F.J., Montoya, P., 2008. Un nuevo yacimiento con micromamíferos en el Mioceno Superior del área de Venta del Moro (Cuenca del Cabrien, Valencia). *Studia Geologica Salmanticensia* 8, 95-105.
- Bolliger, T., 1999. Family Anomalomyidae., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 411-420.
- Brandy, L.D., 1979. Etude de rongeurs muroides du Neogene supérieur et du Quaternaire d'Europe, d'Afrique du Nord et d'Afghanistan. *Evolution. Biogeographie. Correlations. PhD. Thesis*, Academie de Montpellier. Université des Sciences et Techniques du Languedoc, p. 210.

- Calvo, J.P., Elizaga, E., López Martínez, N., Robles, F., 1978. El Mioceno superior continental del Prebetico externo: evolucion del Estrecho Nordbetico. Boletín del Instituto Geológico y Minero de España 89, 407-426.
- Casanovas-Vilar, I., 2007. The rodent assemblages from the Late Aragonian and the Vallesian of the Vallès-Penedès Basin (Catalonia, Spain). *PhD. Thesis*, Universitat Autònoma de Barcelona, Barcelona, p. 286.
- Casanovas-Vilar, I., Agustí, J., 2007. Ecogeographical stability and climate forcing in the Late Miocene (Vallesian) rodent record of Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 248, 169-189.
- Casanovas-Vilar, I., Alba, D.M., Moyà-Solà, S., Galindo, J., Cabrera, L., Garcés, M., Furió, M., Robles, J.M., Köhler, M., Angelone, C., 2008. Biochronological, taphonomical and paleoenvironmental background of the fossil great ape *Pierolapithecus catalaunicus* (Primates, Hominidae). *Journal of Human Evolution* 55, 589-603.
- Chaline, J., Michaux, J., 1974. Les rongeurs du Pléistocène inférieur de France. *Mémoires du Bureau de Recherches Géologiques et Minières* 78, 89-96.
- Cuenca-Bescós, G., 1988. Revision de los Sciuridae del Aragoniense y del Rambliense en la Fosa de Calatayud-Montalban. *Scripta Geologica* 87, 1-116.
- Daams, R., 1985. Glirinae (Glir. Rod.) from the type area of the Aragonian and adjacent areas (province of Teruel and Zaragoza, Spain). *Scripta Geologica* 77, 1-20.
- Daams, R., 1989. Miscellaneous Gliridae from the Miocene of the Calatayud-Teruel Basin, Aragón, Spain. *Scripta Geologica* 89, 13-26.
- Daams, R., 1990. Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and the Oligocene-Miocene boundary interval of Spain. *Scripta Geologica* 95, 62 p.
- Daams, R., 1999. Family Gliridae, in: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 301-318.
- Daams, R., Freudenthal, M., 1981. Aragonian: the Stage concept versus Neogene Mammal Zones. *Scripta Geologica* 62, 1-17.
- Daams, R., van der Meulen, A.J., 1984. Paleoenvironmental and paleoclimatic interpretation of micromammal faunal successions in the upper Oligocene and Miocene of north central Spain, in: Meulenkamp, J. (Ed.), *Paleoenvironnements continentaux en Méditerranée au Néogène et évolution paléoclimatique*. *Paleobiologie Continentale*, pp. 241-257.
- Daams, R., Freudenthal, M., Álvarez-Sierra, M., 1987. Ramblian: a new stage for continental deposits of early Miocene age. *Geologie en Mijnbouw* 65, 297-308.
- Daams, R., Freudenthal, M., 1988. Synopsis of the Dutch-Spanish collaboration program in the Aragonian type area, 1975-1986, in: Freudenthal, M. (Ed.), *Biostratigraphy and paleoecology of the Neogene micromammalian faunas from the Calatayud-Teruel Basin*. *Scripta Geologica*, pp. 3-19.
- Daams, R., Freudenthal, M., van der Meulen, A.J., 1988. Ecostratigraphy of micromammal faunas from the Neogene of Spain. *Scripta Geologica Special Issue* 1, 287-302.
- Daams, R., de Bruijn, H., 1995. A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix* (n. s.) 6, 3-50.
- Daxner-Höck, G., 1999. Family Zapodidae., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 337-342.
- de Bruijn, H., 1974. The Ruscinian rodent succession in southern Spain and its implications for the biostratigraphic correlation of Europe and north America. *Senckenbergiana Lethaea* 55, 435-443.
- de Bruijn, H.d., 1999. Superfamily Sciuroidea., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 271-280.
- de Bruijn, H., Mein, P., Montenat, C., van de Weerd, A., 1975. Corrélations entre les gisements de rongeurs et les formations marines du Miocène terminal de l'Espagne méridionale I (province

- d'Alicante et de Murcia). Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B 78, 1-31.
- Farjanel, G., Mein, P., 1984. Une association de mammifères et de pollens dans la formation continentale des 'Marnes de Bresse' d'âge Miocène supérieur, à Amberieu (Ain). *Geologie de la France* 1-2, 131-148.
- Fejfar, O., 1999. Microtoid Cricetids., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 365-372.
- Fejfar, O., Heinrich, W.-D., Pevzner, M.A., Vangengeim, E.A., 1997. Late Cenozoic sequences of mammalian sites in Eurasia: an updated correlation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133, 259-288.
- Freudenthal, M., Lacomba, J.I., Suárez, E.M., 1991. The Cricetidae (Mammalia, Rodentia) from the Late Miocene of Crevillente (prov. Alicante, Spain). *Scripta Geologica* 96, 9-46.
- Freudenthal, M., Mein, P., Martín-Suárez, E., 1998. Revision of the late miocene and pliocene cricetinae (rodentia, mammalia) from Spain and France. *Treballs del Museu de Geologia de Barcelona* 7, 11-93.
- Freudenthal, M., Martín-Suárez, E., 1999. Family Muridae, in: Rössner, G., Heissig, K. (Eds.), *The Miocene land mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 401-409.
- Freudenthal, M., Martín-Suárez, E., 2007. An index for concavity of the occlusal surface of the cheek teeth and an assessment of concavity in Gliridae (Mammalia, Rodentia). *Palaeontologia Electronica* 10, 9A:24.
- Garcés, M., Agustí, J., Cabrera, L., Pares, J.M., 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Valles-Penedes Basin (northeast Spain). *Earth and Planetary Science Letters* 142, 381-396.
- Garcés, M., Krijgsman, W., Agustí, J., 1998. Chronology of the late Turolian deposits of the Fortuna basin (SE Spain): implications for the Messinian evolution of the eastern Betics. *Earth and Planetary Science Letters* 163, 69-81.
- García-Alix, A., 2006. Bioestratigrafía de los depósitos continentales de la transición Mio-Plioceno de la cuenca de Granada. *PhD. Thesis*, Universidad de Granada, Granada p. 386.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2007. New data on Mio-Pliocene Sciuridae (Rodentia, Mammalia) from southern Spain. *Comptes Rendus Palevol* 6, 269-279.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008a. Muridae from the Mio-Pliocene boundary in the Granada Basin (southern Spain). *Biostratigraphic and phylogenetic implications*. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 248, 183-215.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008b. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136, 1-37.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008c. *Muscardinus meridionalis* sp. nov., a new species of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of *Muscardinus*. *Journal of Vertebrate Paleontology* 28, 568-573.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008d. Biostratigraphy and sedimentary evolution of Late Miocene and Pliocene continental deposits of the Granada Basin (southern Spain) *Lethaia* 41, 431-446.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., Martín, J.M., 2008e. Late Miocene-Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265, 214-225.
- García-Moreno, E., 1987. *Roedores y Lagomorphos del Mioceno de la Zona central de la Cuenca del Duero*. *Sistemática, Bioestratigrafía y Paleoecología*. PhD Thesis. Universidad Complutense, Madrid, p. 258.

- Geraads, D., 1998. Biogeography of circum-Mediterranean Miocene-Pliocene rodents; a revision using factor analysis and parsimony analysis of endemism. *Palaogeography, Palaeoclimatology, Palaeoecology* 137, 273-288.
- Golpe Posse, J.M., Santafe, L., Lopis, J.V., Casanovas, C., 1979. Datos sobre el Vallesiense medio-superior de los alrededores de Terrassa, in: Orloi, R.i.A. (Ed.), *Homenatge a Lluís Solé i Sabarís*, Instituto Nacional de Geología, Barcelona ed. *Acta Geologica Hispanica*, pp. 356-361.
- Guerra-Merchan, A., Ramallo, D., Bustos, A.R., 2001. New data on the Upper Miocene micromammals of the betic cordillera and their interest for marine-continental correlations. *Geobios* 34, 85-90.
- Hernández Fernández, M., Peláez-Campomanes, P., 2003. Ecomorphological characterization of Murinae and hypsodont "Cricetidae" (Rodentia) from the Iberian Plio-Pleistocene. *Coloquios de Paleontología Volumen Extraordinario 1*, 237-251.
- Hernández Fernández, M., 2005. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico. *PhD. Thesis*, University Complutense of Madrid, Madrid, p. 379.
- Hugueney, M., 1999. Family Castoridae., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 281-300.
- Kálin, D., 1999. Tribe Cricetini., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 373-387.
- Lacomba, J.I., Morales, J., Robles, F., Santisteban, C., Alberdi, M.T., 1986. Sedimentología y Paleontología del yacimiento finimioceno de La Portera (Valencia). *Estudios Geológicos* 42, 167-180.
- Lacomba, J.I., 1988. Rodents and lagomorphs from a Lower Vallesian fissure filling near Molina de Aragon (Prov. de Guadalajara, Spain). *Scripta Geologica Special Issue 1*, 19-38.
- Lazzari, V., Aguilar, J.-P., 2007. Les Megacricetodon du gisement karstique miocène moyen de Blanquatière (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologique et phylogénique. *Geobios* 40, 91-111.
- López-Antoñanzas, R., Álvarez-Sierra, M.A., García Paredes, I., Morales, J., Peláez-Campomanes, P., 2008. On the presence of *Hispanomys peralensis* (Rodentia, Cricetinae) at Batallones (Madrid, Spain). *Journal of Vertebrate Paleontology* 28, 68-69.
- López Martínez, N., García Moreno, E., Álvarez-Sierra, M.A., 1986. Paleontología y bioestratigrafía (micromamíferos) del Mioceno medio y superior del sector central de la Cuenca del Duero. *Studia Geologica Salmanticensia*. Universidad de Salamanca 22, 191-212.
- López-Guerrero, P., 2007. Paleontología del yacimiento de vertebrados Aragoniense de Casa Montero (Madrid), in: Cambra-Moo, O., Martínez-Pérez, C., Chamero, B., Escaso, F., de Esteban Trivigno, S., Marugán-Lobón, J. (Eds.), *Cantera Paleontológica*. Diputación Provincial de Cuenca, Cuenca, pp. 247-254.
- 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). *Paleontologica Nova* 8, 259-271.
- López-Guerrero, P., Álvarez-Sierra, M.A., García-Paredes, I., López-Antoñanzas, R., Oliver Pérez, A., 2009. Cricetodontini (Rodentia, Mammalia) from the Upper Aragonian and Lower Vallesian of the Toril-Nombrevilla section (Middle and Upper Miocene, Calatayud-Daroca Basin, Zaragoza, Spain). *Journal of Vertebrate Paleontology* 29, 161A.
- 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, XIII Jornadas de la Sociedad Española de Paleontología, Caravaca.
- Martín-Suárez, E., 1988. Sucesiones de micromamíferos en la Depresión Guadix-Baza (Granada, España). Universidad de Granada, Granada, p. 241.

- Martín-Suárez, E., Freudenthal, M., 1993. Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). *Scripta Geologica* 103, 65-118.
- Martín-Suárez, E., Freudenthal, M., 1994. *Castromys*, a new genus of Muridae (Rodentia) from the Late Miocene of Spain. *Scripta Geologica* 106, 11-34.
- Martín-Suárez, E., Freudenthal, M., 1998. Biostratigraphy of the Continental Upper Miocene of Crevillente (Alicante, SE Spain). *Geobios* 31(6), 839-847.
- Martín-Suárez, E., Mein, P., 1998. Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). *Geobios* 31(1), 87-97.
- Martín-Suárez, E., Freudenthal, M., Krijgsman, W., Fortuin, A.R., 2000. On the age of the continental deposits of the Zorreras Member (Sorbas Basin, SE Spain). *Geobios* 33, 505-512.
- Martín-Suárez, E., Freudenthal, M., Civis, J., 2001. Rodent palaeoecology of the continental Upper Miocene of Crevillente (Alicante, SE Spain). *Palaeogeography Palaeoclimatology Palaeoecology* 165, 349-356.
- Mein, P., 1999. The Late Miocene small mammal succession from France, with emphasis on the Rhône Valley localities., in: Agustí, J., Rook, L., Andrews, P. (Eds.), *Hominoid evolution and climatic change in Europe*. Vol. 1. The evolution of Neogene terrestrial ecosystems in Europe. Cambridge University Press, Cambridge, pp. 140-164.
- Mein, P., Michaux, J., 1970. Un nouveau stade dans l'évolution des rongeurs Pliocènes de l'Europe sud-occidentale. *Comptes Rendus de l'Académie des Sciences de Paris* 270, 2780-2783.
- Mein, P., Michaux, J., 1979. Une faune de petits mammifères d'âge Turolien moyen (Miocène supérieur) à Cucuron (Vaucluse) données nouvelles sur le genre *Stephanomys* (Rod.) et conséquences stratigraphiques. *Geobios, paléontologie, stratigraphie et paléoécologie* 12, 481-485.
- Mein, P., Martín-Suarez, E., Agustí, J., 1993. *Progonomys* Schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe. *Scripta Geologica* 103, 41-64.
- Michaux, J., 1966. Sur deux faunules de micromammifères trouvés dans des assises terminales du Pliocène en Languedoc. *Comptes Rendus Sommaires de la Société Géologique de France* 9, 343-344.
- Michaux, J., Aguilar, J.-P., Montuire, S., Wolff, A., Legendre, S., 1997. Les Murinae (Rodentia, Mammalia) Néogènes du Sud de la France: Évolution et Paléoenvironnements. *Geobios* 20, 379-385.
- Minwer-Barakat, R., 2005. Roedores e insectívoros del Turoliense Superior y el Plioceno del sector central de la cuenca de Guadix. *PhD. Thesis*, Universidad de Granada, Granada, p. 535.
- Minwer-Barakat, R., Garcia-Alix, A., Martín-Suárez, E., Freudenthal, M., 2008. The latest Ruscinian and early villanyian arvicolinae from southern Spain re-examined: biostratigraphical implications. *Journal of Vertebrate Paleontology* 28, 841-850.
- Montes, M., Beamud, B., Garcés, M., Calvo, J.P., 2006. Magnetoestratigrafía de las unidades inferior e intermedia del Mioceno de la cuenca de Madrid. *Revista de la Sociedad Geologica de Espana* 19, 281-298.
- Montoya, P., Alberdi, M.T., 1995. Crevillente 15 y Crevillente 16, dos nuevos yacimientos con macromamíferos en el Mioceno Superior de Alicante (España). *Estudios Geológicos* 51, 159-182.
- Montoya, P., Ginsburg, L., Alberdi, M.T., van der Made, J., Morales, J., Soria, M.D., 2006. Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy. *Geodiversitas* 281, 137-173.
- Montuire, S., Maridet, O., Legendre, S., 2006. Late Miocene-Early Pliocene temperature estimates in Europe using rodents. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 247-262.
- Morales, J., 1984. Venta del Moro: su macrofauna de mamíferos, y biostratigrafía continental del Mioceno terminal Mediterraneo, Paleontología. Universidad Complutense, Madrid, p. 340.

- Morales, J., Capitán, J., Calvo, J.P., Sesé, C., 1992. Nuevo yacimiento de vertebrados del Mioceno Superior al Sur de Madrid (Cerro Batallones, Torrejón de Velasco). *Geogaceta* 12, 77-80.
- Morales, J., Alcalá, L., Amezua, L., Antón, M., Fraile, S., Gómez, E., Montoya, P., Nieto, M., Pérez, B., Salesa, M.J., Sánchez, I.M., 2000. El yacimiento de El Cerro de los Batallones, in: Morales, J., Nieto, M., Amezua, L., Fraile, S., Gómez, E., Herráez, E., Peláez-Campomanes, P., Salesa, M.J., Sánchez, I.M., Soria, D. (Eds.), *Patrimonio Paleontológico de la Comunidad de Madrid*, 12/99 ed. Consejería de Educación de la Comunidad de Madrid, Madrid, pp. 179-190.
- Morales, J., Alcalá, L., Álvarez-Sierra, M.A., Antón, M., Azanza, B., Calvo, J.P., Carrasco, P., Fraile, S., García-Paredes, I., Gómez, E., Hernández Fernández, M., Merino, L., van der Meulen, A., Martín Escorza, C., Montoya, P., Nieto, M., Peigné, S., Pérez, B., Peláez-Campomanes, P., Pozo, M., Quiralte, V., Salesa, M.J., Sánchez, I.M., Sánchez-Marco, A., Silva, P.G., Soria, M.D., Turner, A., 2004. Paleontología del sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid. *Geogaceta* 35, 139-142.
- Morales, J., Pozo, M., Silva, P.G., Domingo, M.S., López-Antoñanzas, R., Álvarez-Sierra, M.A., Antón, M., Martín Escorza, C., Quiralte, V., Salesa, M.J., Sánchez, I.M., Azanza, B., Calvo, J.P., Carrasco, P., García-Paredes, I., Knoll, F., Hernández Fernández, M., van den Hoek Ostende, L., Merino, L., van der Meulen, A.J., Montoya, P., Peigné, S., Peláez-Campomanes, P., Sánchez-Marco, A., Turner, A., Abella, J., Alcalde, G.M., Andrés, M., DeMiguel, D., Cantalapiedra, J.L., Fraile, S., García Yelo, B.A., Gómez Cano, A.R., López Guerrero, P., Oliver Pérez, A., Siliceo, G., 2008. El sistema de yacimientos de mamíferos miocenos del Cerro de los Batallones, Cuenca de Madrid: estado actual y perspectivas. *Seminario de Paleontología de Zaragoza* 8, 41-117.
- Renaud, S., Benammi, M., Jaeger, J.-J., 1999. Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pliocene of North Africa). *Paleobiology* 25, 369-382.
- Rummel, M., 1999. Tribe Cricetodontini, in: Rössner, G.E.H., K. (Ed.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 359-364.
- Sanz, E., Sesé, C., Calvo, J.P., 1992. Primer hallazgo de micromamíferos de edad Turolense en la Cuenca de Madrid. *Estudios Geológicos* 48, 171-178.
- Sen, S., 1999. Family Hystricidae., in: Rössner, E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 426-434.
- Sesé, C., 2006. Los roedores y lagomorfos del Nogeno de España. *Estudios Geológicos* 62, 429-480.
- Sesé, C., López Martínez, N., 1981. Los micromamíferos (Insectivora, Rodentia y Lagomorpha) del Vallesense inferior de los Valles de Fuentidueña. *Estudios Geológicos* 37, 369-481.
- Sesé, C., Alonso, A.M., Calvo, J.P., 1990. Nuevas faunas de micromamíferos del Terciario continental del NE de la cuenca de Madrid (prov. de Guadalajara, España). *Estudios Geológicos* 46, 433-451.
- van Dam, J., 1997. The small mammals from the Upper Miocene of the Teruel-Alfambra region (Spain): Paleobiology and Paleoclimatic reconstructions. *Geologica Ultraiectina* 156, p. 204.
- van Dam, J., 2004. Anourosoricini (Mammalia: Soricidae) from the Mediterranean region: a pre-Quaternary example of recurrent climate-controlled North-South range shifting. *J. Paleontology* 78, 741-764.
- van Dam, J., Weltje, G.J., 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modelling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 151, 267-305.
- van Dam, J., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The upper Miocene mammal record from the Teruel-Alfambra region (Spain). The MN system and continental stage/age concepts discussed. *Journal of Vertebrate Paleontology* 21, 367-385.
- van de Weerd, A., 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletins, Special Publications* 2, 1-218.

- van de Weerd, A., Daams, R., 1978. Quantitative composition of rodent faunas in the Spanish Neogene and paleoecological implications. I & II. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Series B 81, 448-473.
- van der Made, J., Morales, J., Montoya, P., 2006. Late Miocene turnover in the Spanish mammal record in relation to palaeoclimate and the Messinian Salinity Crisis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 228-246.
- 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). *Coloquios de Paleontología Volumen Extraordinario* 1, 385-441.
- Wessels, W., 1998. Gerbilidae from the Miocene and Pliocene of Europe. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 38, 187-207.
- Wessels, W., 1999. Family Gerbilidae, in: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Dr. Friedrich Pfeil, München, pp. 301-318.

Appendix 2

Appearance Event Ordination (AEO) mean value and concurrent range zones. defined by the youngest first appearance event (FAE) and oldest last appearance event (LAE). for the 130 fossil sites maintained in the analysis for the Iberocceanian region. Basin abbreviations: TE. Alfambra-Teruel; AL. Alicante; BT. Baixo Tejo; CA. Castellón; CD. Calatayud-Daroca; CU. Cucuron-Basse Durance; DU. Duero; FO. Fortuna; GR. Granada; GB. Guadix-Baza; HI. Hija; LR. Languedoc-Roussillon; MU. Murcia; PR. Provence; RH. Rhône; TJ. Tajo; VA. Valencia; VP. Vallès Penedès. S. number of species (without singletons).

| Basin | Fossil site | Fossil site abbreviation | S | MN unit | AEO coefficient | Oldest LAE | Youngest FAE |
|-------|-----------------------|--------------------------|----|---------|-----------------|------------|--------------|
| GR | Purcal 25 | PUR25 | 7 | 13 | 231 | 232 | 231.5 |
| GR | Purcal 24A | PUR24A | 8 | 13 | 231 | 232 | 231.5 |
| AL | Alcoy Barranco | ALBAR | 6 | 13 | 226 | 232 | 229.0 |
| BT | Esbarrodoiro | ESBA | 10 | 13 | 226 | 232 | 229.0 |
| GB | Bacochas 1 | BAC1 | 7 | 13 | 226 | 227 | 226.5 |
| TJ | Canteras de Iberia | CDI | 3 | 13 | 220 | 232 | 226.0 |
| VA | Los Mingos 1C | MIN1C | 2 | 13 | 211 | 232 | 221.5 |
| GB | Botardo C | BOTC | 8 | 13 | 220 | 221 | 220.5 |
| AL | Crevillente 6 | CRE6 | 5 | 13 | 220 | 221 | 220.5 |
| TE | Las Casiones superior | KSSS | 7 | 13 | 203 | 232 | 217.5 |
| GR | Purcal 3 | PUR3 | 5 | 13 | 203 | 232 | 217.5 |
| GR | Dehesa 16 | DHS16 | 9 | 13 | 211 | 212 | 211.5 |
| GR | Purcal 23 | PUR23 | 7 | 13 | 211 | 212 | 211.5 |
| CA | Almenara M | ALMM | 9 | 13 | 207 | 208 | 207.5 |
| GB | Negratín 1 | NGR1 | 7 | 13 | 207 | 208 | 207.5 |
| GB | Pino Mojón | PIMO | 6 | 13 | 207 | 208 | 207.5 |
| GR | Salobreña | SALO | 12 | 13 | 207 | 208 | 207.5 |
| TE | Las Casiones | KSS | 9 | 13 | 203 | 212 | 207.5 |
| FO | Hornera | HORN | 4 | 13 | 176 | 232 | 204.0 |
| TE | Villastar | VILL | 9 | 13 | 203 | 204 | 203.5 |
| TE | Masada Del Valle 7 | MDV7 | 7 | 13 | 191 | 212 | 201.5 |
| VA | Venta del Moro | VDM | 10 | 13 | 200 | 201 | 200.5 |
| TE | La Gloria 5 | GLO5 | 9 | 13 | 196 | 197 | 196.5 |
| GR | Jun2 | JUN2 | 5 | 12 | 196 | 197 | 196.5 |
| TE | Valdecebro 3 | VDC3 | 9 | 13 | 193 | 194 | 193.5 |
| TE | Valdecebro 6 | VDC6 | 9 | 13 | 193 | 194 | 193.5 |
| AL | Crevillente 14 | CRE14 | 8 | 13 | 191 | 192 | 191.5 |
| AL | Crevillente 22 | CRE22 | 6 | 13 | 191 | 192 | 191.5 |

| | | | | | | | |
|----|---------------------------|--------|----|----|-----|-----|-------|
| AL | Crevillente 17 | CRE17 | 5 | 12 | 191 | 192 | 191.5 |
| FO | Casa del Acero | ACER | 4 | 12 | 184 | 197 | 190.5 |
| AL | Crevillente 8 | CRE8 | 6 | 12 | 184 | 192 | 188.0 |
| MU | Librilla | LIBR | 7 | 13 | 187 | 188 | 187.5 |
| AL | Crevillente 15 | CRE15 | 9 | 12 | 184 | 185 | 184.5 |
| CU | Cucuron | CUCU | 6 | 12 | 182 | 183 | 182.5 |
| TE | Concud 2 | CCD2 | 7 | 12 | 168 | 194 | 181.0 |
| TE | Tortajada | TOT | 5 | 12 | 168 | 194 | 181.0 |
| TE | Villalba baja 22C | VIB22C | 5 | 12 | 168 | 194 | 181.0 |
| TE | Tortajada D | TOTD | 5 | 12 | 168 | 194 | 181.0 |
| VP | Can Vilella 1 | CVLL1 | 6 | 13 | 176 | 177 | 176.5 |
| RH | Lissieu | LISS | 12 | 13 | 176 | 177 | 176.5 |
| TE | Los Mansuetos | LMA | 9 | 12 | 168 | 185 | 176.5 |
| AL | Crevillente 5A | CRE5A | 5 | 12 | 168 | 185 | 176.5 |
| TE | Masada del Valle 5 | MDV5 | 8 | 12 | 168 | 185 | 176.5 |
| TE | Concud 3 | CCD3 | 7 | 12 | 168 | 169 | 168.5 |
| TE | Masada del Valle 2 | MDV2 | 9 | 12 | 168 | 169 | 168.5 |
| TE | Aljezar B | ALJB | 7 | 12 | 165 | 166 | 165.5 |
| TE | Aguanaces | AGU | 7 | 11 | 159 | 160 | 159.5 |
| TE | Vivero de Pinos | VIP | 8 | 11 | 159 | 160 | 159.5 |
| TE | Aguanaces 3 | AGU3 | 7 | 11 | 159 | 160 | 159.5 |
| TE | Aguanaces 1 | AGU1 | 3 | 11 | 159 | 160 | 159.5 |
| TE | La Gloria 10 | GLO10 | 7 | 11 | 159 | 160 | 159.5 |
| TE | Tortajada A | TOTA | 8 | 11 | 159 | 160 | 159.5 |
| TE | Puente Minero | PMIN | 9 | 11 | 155 | 156 | 155.5 |
| TE | Regajo 2 | REG2 | 4 | 11 | 151 | 160 | 155.5 |
| AL | Crevillente 4B | CRE4B | 7 | 11 | 155 | 156 | 155.5 |
| AL | Crevillente 2 | CRE2 | 7 | 11 | 155 | 156 | 155.5 |
| TE | Peralejos D | PERD | 5 | 11 | 151 | 152 | 151.5 |
| RH | Amberieu 3 | AMB3 | 15 | 11 | 143 | 144 | 143.5 |
| RH | Amberieu 1 | AMB1 | 20 | 11 | 133 | 134 | 133.5 |
| LR | Lo Fournas 6C | FOUR6C | 6 | 11 | 127 | 128 | 127.5 |
| LR | Lo Fournas 7 | FOUR7 | 7 | 10 | 127 | 128 | 127.5 |
| TJ | Batallones 1 | BAT1 | 3 | 10 | 94 | 152 | 123.0 |
| RH | Douvre | DOUV | 15 | 10 | 122 | 123 | 122.5 |
| RH | Soblay | SOBL | 19 | 10 | 120 | 121 | 120.5 |
| BT | Freiria do Rio Maior | FRM | 5 | 10 | 94 | 134 | 114.0 |
| AL | Crevillente 3 | CRE3 | 4 | 11 | 112 | 113 | 112.5 |
| PR | Lobieu | LOBR | 11 | 11 | 112 | 113 | 112.5 |
| VP | Torrent de Febulines 3 | TFEB3 | 2 | 10 | 103 | 104 | 103.5 |
| VP | Trinxera Sud Autopista II | TSA2 | 6 | 10 | 103 | 104 | 103.5 |
| VP | Torrent de Febulines | TFEB | 6 | 10 | 103 | 104 | 103.5 |
| VP | Trinxera Nord Autopista | TNA | 4 | 10 | 103 | 104 | 103.5 |
| TE | Peralejos C | PERC | 4 | 10 | 103 | 104 | 103.5 |
| DU | Los Valles de Fuentidueña | FUDU | 4 | 9 | 99 | 100 | 99.5 |
| TE | Masia del Barbo 2B | MB2B | 8 | 10 | 97 | 98 | 97.5 |
| TE | Masia del Barbo 2A | MB2A | 5 | 10 | 97 | 98 | 97.5 |
| HI | Hijar 1 | HIJ1 | 4 | 10 | 94 | 100 | 97.0 |
| TE | Masia la Roma 11 | ROM11 | 7 | 10 | 94 | 95 | 94.5 |
| TE | Masia la Roma 7 | ROM7 | 6 | 10 | 94 | 95 | 94.5 |

| | | | | | | | |
|----|---------------------------------|--------|----|-----|----|-----|------|
| TE | Peralejos 5 | PER5 | 7 | 9 | 94 | 95 | 94.5 |
| VP | Autopista Rubí-Terrasa 7 | RT7 | 5 | 10 | 79 | 104 | 91.5 |
| DU | Ampudia 1 | AMP1 | 2 | 10 | 90 | 91 | 90.5 |
| DU | Torremormojón 1 | TM1 | 6 | 10 | 90 | 91 | 90.5 |
| CD | Peralejos 2A | PE2A | 6 | 9 | 90 | 91 | 90.5 |
| CD | Peralejos 2C | PE2C | 6 | 9 | 90 | 91 | 90.5 |
| VP | Can Llobateres 1 | CLL1 | 18 | 9 | 83 | 84 | 83.5 |
| DU | Ampudia 9 | AMP9 | 7 | 9 | 79 | 80 | 79.5 |
| DU | Torremormojón 3 | TM3 | 5 | 9 | 76 | 80 | 78.0 |
| DU | Torremormojón 4 | TM4 | 4 | 9 | 76 | 80 | 78.0 |
| CD | Carrilanga 1 | CARR1 | 7 | 9 | 76 | 77 | 76.5 |
| VP | Can Ponsic | CPON | 10 | 9 | 73 | 74 | 73.5 |
| DU | Torremormojón 5 | TM5 | 4 | 9 | 65 | 77 | 71.0 |
| VP | Creu Conill 22 | CC22 | 5 | 9 | 69 | 70 | 69.5 |
| VP | Can Mata I (Bretxa de Can Mata) | CMAT1 | 8 | 7/8 | 69 | 70 | 69.5 |
| DU | Casasola 2 | CAS2 | 4 | 9 | 65 | 66 | 65.5 |
| TE | Molina de Aragón | MOL | 9 | 7/8 | 63 | 64 | 63.5 |
| CD | Solera | SOL | 10 | 7/8 | 61 | 62 | 61.5 |
| VP | Sant Quirze | SQUI | 17 | 7/8 | 59 | 60 | 59.5 |
| VP | Castell de Barberà | CBB | 15 | 7/8 | 54 | 55 | 54.5 |
| VP | Can Misert | CMST | 9 | 7/8 | 54 | 55 | 54.5 |
| VP | Sant Quirze A | SQUIA | 6 | 7/8 | 50 | 51 | 50.5 |
| CD | Nombrevilla (classical) | NOM | 8 | 9 | 47 | 48 | 47.5 |
| CD | Nombrevilla 10 | NOM10 | 4 | 9 | 47 | 48 | 47.5 |
| CD | Las Planas 5H | LP5H | 6 | 7/8 | 38 | 51 | 44.5 |
| CD | Toril 3B | TOR3B | 13 | 7/8 | 43 | 44 | 43.5 |
| CD | Toril 3A | TOR3A | 12 | 7/8 | 43 | 44 | 43.5 |
| CD | Toril 2 | TOR2 | 7 | 7/8 | 43 | 44 | 43.5 |
| CD | Toril 1 | TOR1 | 10 | 7/8 | 43 | 44 | 43.5 |
| CD | Nombrevilla 9 | NOM9 | 4 | 9 | 33 | 48 | 40.5 |
| VP | Barranc de Can Vila 1 | BCV1 | 8 | 7/8 | 38 | 39 | 38.5 |
| CD | Villafeliche 9 | VFEL9 | 5 | 7/8 | 33 | 44 | 38.5 |
| CD | Nombrevilla 4 | NOM4 | 3 | 7/8 | 33 | 34 | 33.5 |
| CD | Nombrevilla 3 | NOM3 | 8 | 7/8 | 33 | 34 | 33.5 |
| CD | Nombrevilla 2 | NOM2 | 8 | 7/8 | 33 | 34 | 33.5 |
| TJ | Lupiana | LUP | 7 | 7/8 | 26 | 27 | 26.5 |
| CD | Alcocer 2 | ALCR2 | 6 | 7/8 | 23 | 24 | 23.5 |
| TJ | Paracuellos 3 | PAR3 | 6 | 7/8 | 20 | 21 | 20.5 |
| DU | Simancas 2 | SIM2 | 8 | 7/8 | 20 | 21 | 20.5 |
| LR | Lo Fournas 2 | FOUR2 | 8 | 7/8 | 11 | 12 | 11.5 |
| LR | Lo Fournas 10 | FOUR10 | 8 | 7/8 | 7 | 8 | 7.5 |
| LR | Lo Fournas 3 | FOUR3 | 8 | 7/8 | 7 | 8 | 7.5 |