

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

Ana Rosa Gómez Cano*, Manuel Hernández Fernández, María Ángeles Álvarez-Sierra

Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, José Antonio Novais 2, 28040, Madrid, Spain
Departamento de Cambio Medioambiental, Instituto de Geociencias (UCM-CSIC), José Antonio Novais 2, 28040, Madrid, Spain

A B S T R A C T

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 Iberocctitanian 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 Iberocctitanian 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 Iberocctitanian 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.

Keywords:
Biochronology
Diachrony
Maximum Likelihood Appearance Event
Ordination
Rodentia
Vallesian
Turolian

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 Ilobateres (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,

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-Roussillon 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

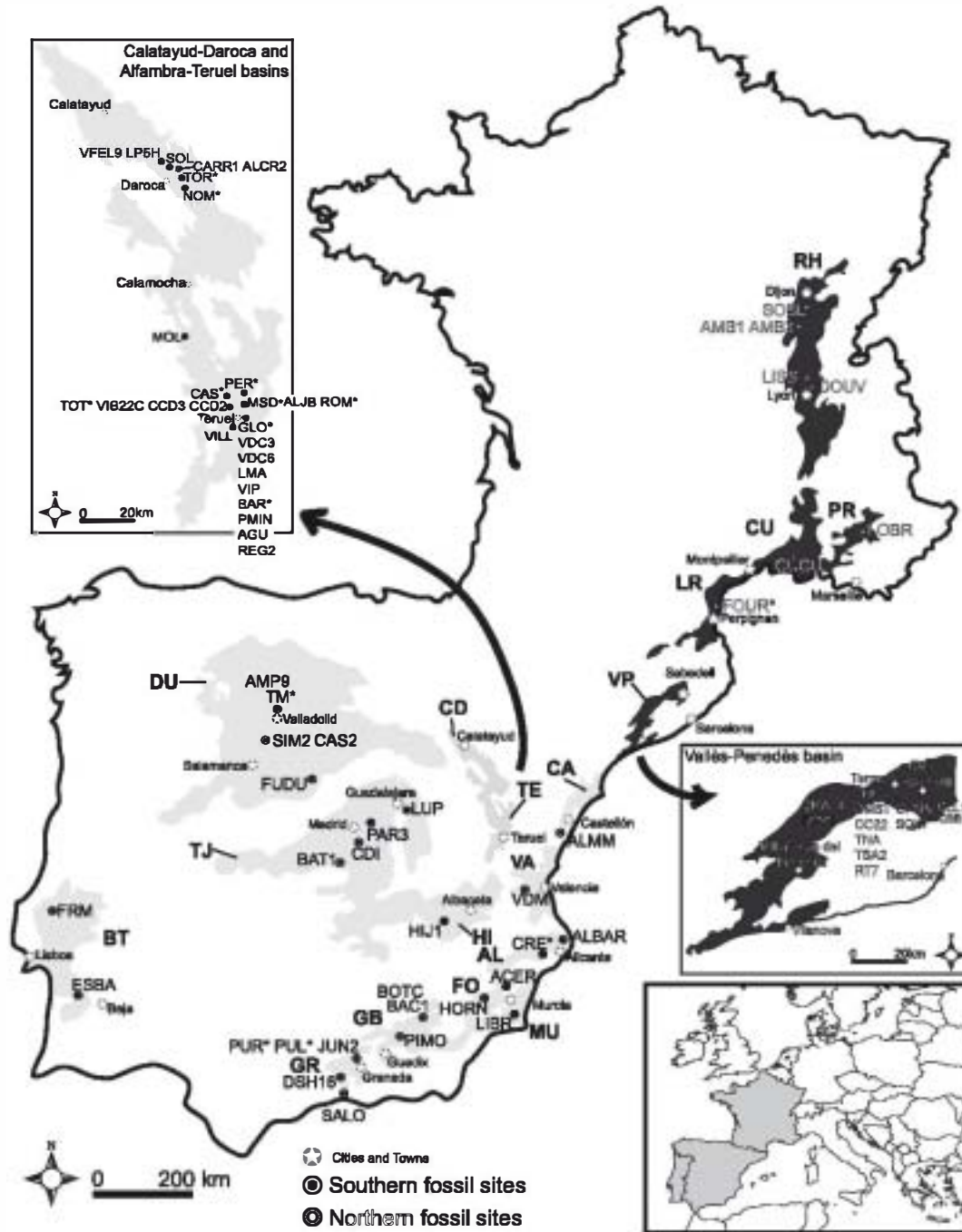


Fig. 1. Miocene fossil sites from the Iberocccitanian Region (Iberian Peninsula and central-southeastern France, Europe) considered in this study. Black basins, northern biogeographic province; Grey basins southern biogeographic province. *, stratigraphic sections with several sites; abbreviations for 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 faunalists, 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 Conill22	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
Toril3B	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.

	Iberocitanian 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 delmi*) 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*, *Trogotherium 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 IAE	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	Purcal23	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	Alcocer 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	Toril3B	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 IAE	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	CLI1	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).

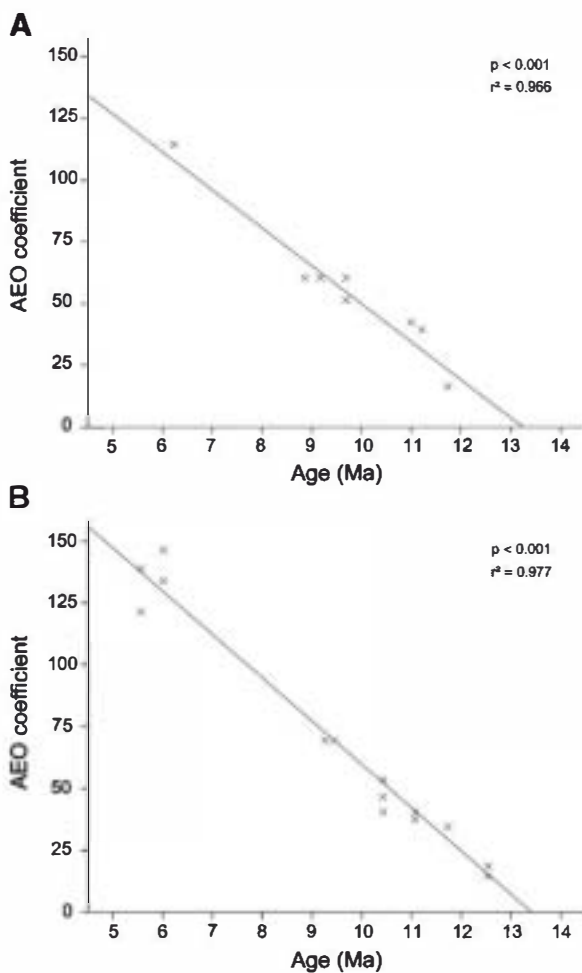


Fig. 2. Calibrations of the Iberocctanian mammal fossil site sequences for the northern (A) and southern (B) provinces, showing the linear regressions of the concurrent range zone mean value for each fossil site obtained in the appearance event ordination of mammal faunas (AEO coefficient) against the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

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	–	–	–

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

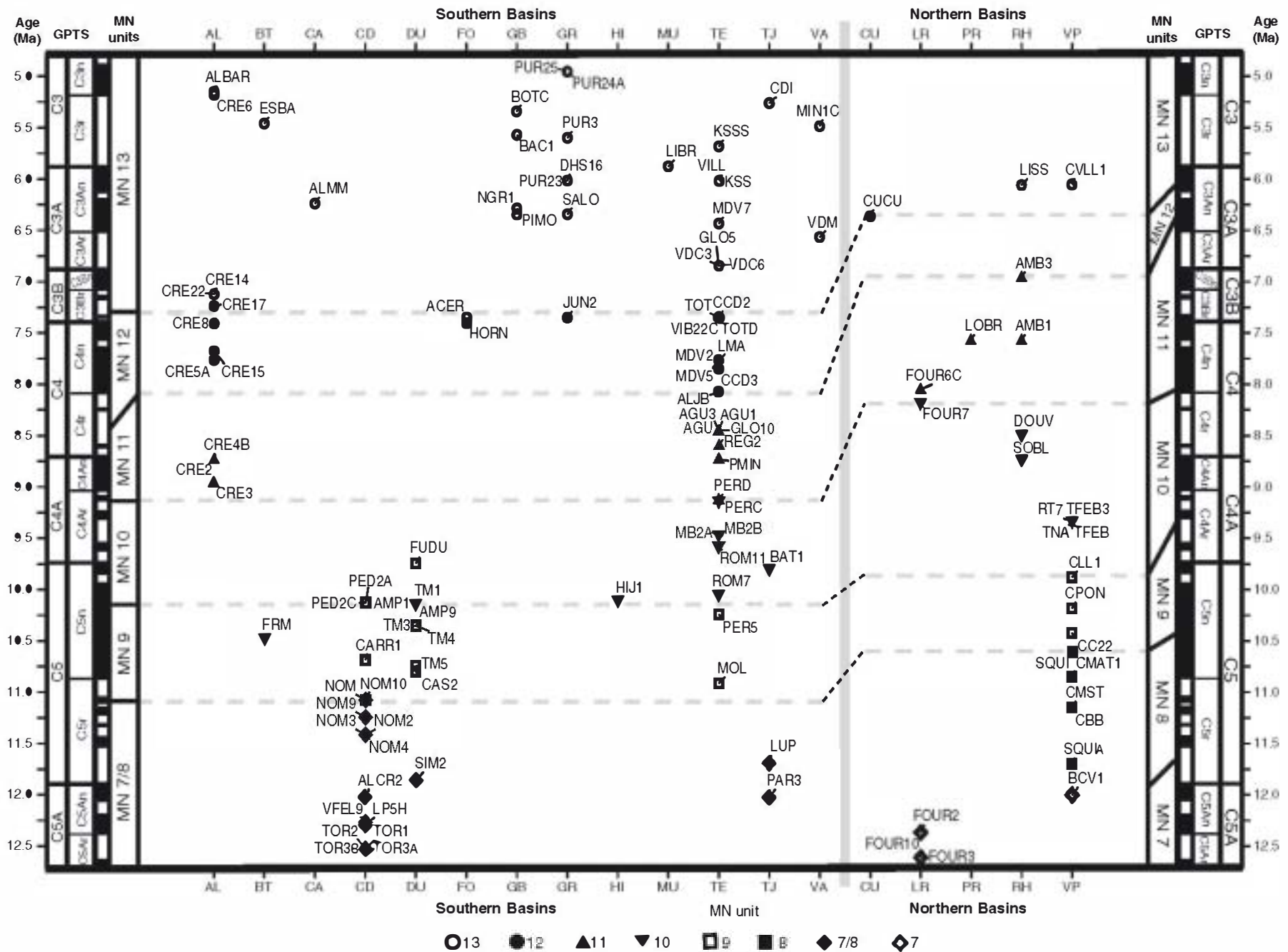


Fig. 3. Temporal distribution of the Iberocctanian rodent fossil sites obtained following calibration of the ordination with the AEO coefficient. Geomagnetic polarity time-scale after [Gee and Kent \(2007\)](#). The Mammal Neogene units (MN) are shown. Dashed lines represent the diachrony between the 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](https://doi.org/10.1016/j.palaeo.2011.05.014).

Acknowledgments

We dedicate this paper to the memory of our mentor, colleague and friend Nieves López Martínez (UCM). In addition, we are very grateful to P. López Guerrero (UCM), I. Casanovas-Vilar (ICP), P. Peláez-Campomanes (MNCN-CSIC), P. Montoya (UV) and R. López-Antoñanzas (MNCN-CSIC) for their comments during the development of the database. We would also like to thank all our colleagues and friends from the Paleontology and Paleobiology departments of the UCM and MNCN-CSIC, especially those from the PMMV team (<http://pmmv.com.es>), who contributed with productive discussions on these topics. Furthermore, we wish to show our appreciation to the many paleontologists who conducted fieldwork at the fossil sites studied herein and who published their results on the fossil record of the Iberocitanian micromammals from the Middle and Late Miocene, all of which made this research possible. We thank to the editor A.P. Kershaw (Monash University) as well as to L.J. Flynn (Harvard University), D.S. Kostopoulos (Aristotle University) and an anonymous referee for their comments, which substantially improved the original manuscript. Finally, we wish to thank our Irish translator, Conmac De Brun, who helped us with the English. This research was supported by projects CGL2006-01773/BTE, CGL-2008-05813-C02-01/BTE, CGL-2008-04200/BTE and CGL-2010-19116/BOS, as well as by a FPU predoctoral contract to A.R.G.C. During this study, M.H.F. availed of a UCM contract from the Ramón y Cajal Program, belonging to the Spanish Ministry of Education and Science. This research is a contribution by the research group BSCH-UCM910607 on Evolution of Cenozoic Mammals and Continental Palaeoenvironments.

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-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., 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., Alméjida, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l’Anoia, Cataluña), una sucesión de localidades del Aragonense 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 Villarroja (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. Bioestratigrafía 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 congrés 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 Aragonense–Vallesiense (Mioceno medio–Mioceno superior) en la sección de Torremormojón (Cuenca del Duero, Provincia de Palencia). *Studia Geologica Salmanticensia, 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 Aragonense–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, 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.

Azanza, B., Alberdi, M.T., Cerdeño, E., Prado, J.L., 1997a. Contribución de los análisis multivariantes a la biocronología 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.I., 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 *Pterolopithecus catalaunicus* (Primates, Hominoidea). *Journal of Human Evolution* 55, 589–603.

Casanovas-Vilar, I., García-Paredes, I., Alba, D.M., van der 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., Solounias, 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 Gliridae 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, Reischensburg 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 *Hippurion* 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.
- Fauquet, S., Suc, J.-P., Bertini, A., Poeschi, S.M., Wamny, S., Taoufik, 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.
- Fauquet, S., Suc, J.-P., Jiménez-Moreno, G., Favre, E., Jost, A., Micheels, A., Bachiri-Taoufik, 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., Hayward, 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. *Hippurion* 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., Velizelos, 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.
- Heilmann, 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 ELMAS 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., Civiş, 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 Aragonense. 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 Helléniques* 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., Amezua, 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 Lorca (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., Beaud, 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* 1922, 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 Paleoclimatología*. 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 Vallesiano 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 Miocenerodent 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.