



## 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–Rousillon, 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

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