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A new quantitative biochronological ordination for the Upper Neogene mammalian localities of Spain

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Abstract

The MN scale is the most widely used biochronological scale for the mammalian fossil record of Europe but at the same time it has brought a high amount of criticism with it. The fossil record of Neogene macromammals from Spain is one of the most complete of the world and provides an interesting test of the MN biochronology.

We used maximum likelihood appearance event ordination (ML AEO), a quantitative biochronological method, to provide not only an ordination but also a numerical age estimate for each of the 90 macromammalian fossil faunas that constitute our data base. Originally, only 13 of these localities were numerically dated (mainly by means of paleomagnetism). The ordination of macromammalian fossil faunas matches quite well with the MN chronology at least in the Miocene. The pattern of ordination is less coherent in the Pliocene partly due to the relative poverty of macromammalian fossil sites of this age in Spain.

The controversy on whether the age of the first appearance of hipparionine horses in the Iberian Peninsula (*Hipparion* dispersal event) was around 10.8–10.7 Ma or 11.1 Ma is discussed. Our estimated MN7/8–MN9 boundary lies between 11.008 and 10.873 Ma. We conclude that the arrival of hipparionine horses in the Iberian Peninsula happened between these two ages and that the oldest record is found in the locality of Nombrevilla 1 with an age of 10.873 Ma.

Keywords: Mammalian faunas; Maximum likelihood appearance event ordination (ML AEO); Miocene; Pliocene; Spain; *Hipparion* dispersal event

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1. Introduction

1.1. The continental fossil record of mammals

One of the main challenges we face when working with the continental fossil record is to establish the temporal relationships among fossil sites. Unlike most marine invertebrate fossils, mammal remains often occur in localized fossiliferous horizons, in fissure fillings or in isolated pockets or quarries without stratigraphic superposition, and it is difficult to infer their temporal sequence (Fahlbusch, 1976, 1991; Lindsay and Tedford, 1990; Prothero, 1995; Alberdi et al., 1997a; Azanza et al., 1997; Palombo et al., 2000–2002; Hernández Fernández et al., 2004). The frequency of intracontinental barriers to the dispersal of terrestrial mammals results in greater geographic differentiation (provincialism) of terrestrial faunas in comparison with marine faunas (Walsh, 1998). Moreover, in subaerial conditions

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organic remains have a much lower probability of preservation than in aquatic environments (Murphy, 1994,). These constraints on continental records make the establishment of a biochronological timescale sometimes more feasible than a biostratigraphical one, which requires accurate placement of localities in a stratigraphic section (Azanza et al., 1997). For these reasons and because the term "biochronology" is not considered acceptable in the International Stratigraphic Guide (ISG2, Salvador, 1994, pp. 105, 109), continental large vertebrate palaeontologists have been obliged to base their work on methodologies outside of the stratigraphic codes (Lindsay and Tedford, 1990; Walsh, 2000; Lindsay, 2003). Some authors have tried to give the "less accurate" biochronological scales a stratigraphical foundation (see, for example, Steininger, 1999 for the European Land Mammal Ages and MN units and Woodburne, 2004 for the North American Land Mammal Ages). Others defend biochronology as a useful tool for vertebrate paleontology and encourage the stratigraphic codes to take it into account (Walsh, 1998; Lindsay, 2003). Walsh (2005a,b,c) provides recent reviews of this debate.

The present work has two purposes. The primary goal is to present a temporal sequence of the numerous mammalian fossil sites from the upper Neogene of Spain in order to evaluate temporal relationships with the most widely used biochronological timescale in Europe, that is, the MN timescale. A secondary goal is to provide a quantitative estimate of the age of the *Hipparion* dispersal event, one of the most important migratory events in Eurasia. The timing of this event is a continuing controversy for the Neogene record of Spain.

This paper is organized as follows. In the next two sections we review the current biochronological framework of the Spanish Neogene mammalian record and the controversy about the timing of the *Hipparion* dispersal event in Spain. Next, we explain the materials and methods, including the procedure for the construction of the faunal database, the sources of data for numerical ages and stratigraphical sections and a brief explanation of the ordination method used to infer a temporal sequence of the fossil sites. The results are presented as a ML AEO ordination of the sites, calibrated with localities of known age. In the discussion, we evaluate the ordination in relation to current biochronologies both for the Miocene and the Pliocene. Finally, boundaries of the MN units are established and compared to those from earlier studies and the age for the *Hipparion* dispersal event is discussed in the light of our results.

1.2. The biochronological framework of the Spanish Neogene

The importance of Spain for a quantitative biochronological analysis lies in the fact that the Spanish Cenozoic basins include the highest density of mammalian fossil localities in Europe, making it possible to obtain a higher resolution for the pattern and timing of mammalian evolution and dispersals than in other areas of Europe (Agustí et al., 2001).

The Spanish Neogene biochronological framework follows the one established for the European continent, that is the European Land Mammal Ages (ELMAs, named by Sen, 1997, following the practice of Savage, 1962, in creating the North American Land Mammal Ages or NALMAs) and the MN (Mammal Neogene) units defined by Mein (1975). The MN units, which have experienced numerous revisions (Mein, 1979, 1990, 1999; de Bruijn et al., 1992), are based on: (1) faunal associations, (2) first appearances and (3) last appearances of both large and small mammals. There are 17 MN units, each represented by a reference locality. The MN framework has been criticized on several grounds. One criticism is that the reference localities do not belong to the same bioprovince, thus, geographical and stratigraphical factors may be confounded (Daams and Freudenthal, 1981; de Bruijn et al., 1992; Sen, 1997; Agustí, 1999). Second, the selected taxa are heterogeneous (Agustí and Moyà-Solà, 1991). Third, diachrony of the paleobiological events across Europe (Agustí and Moyà-Solà, 1991; Sen, 1997; Agustí, 1999; van Dam et al., 2001). Finally, incongruities arise from the use of the three criteria that define the MN units because they are supposed to define at the same time a single unit (Agustí and Moyà-Solà, 1991).

A team of Dutch and Spanish paleontologists who have worked together in the Spanish Neogene for more than 40 yr, proposed a series of regional biozones (based on small mammals) as defined in the ISG1 (Hedberg, 1976; "Local Zones" as named by Daams and Freudenthal, 1981; Daams and van der Meulen, 1983; Daams et al., 1987; Daams and Freudenthal, 1988; van der Meulen and Daams, 1992; Daams et al., 1999; van Dam et al., 2001; Álvarez Sierra et al., 2003). These biozones, which extend from A to M, with three underlying biozones, X, Y and Z, were defined in the Calatayud (Zaragoza, Spain) and Teruel basins (Teruel, Spain). The biozones have undergone several revisions and modifications as more data have been collected (Daams et al., 1999). The time covered by these biozones corresponds to MN1 to MN13 as shown in Fig. 1. Although widely used in Spain, this biozonation has a local meaning so is not appropriate for continent-wide extension. Other local biozonations have been erected in different Cenozoic basins of Spain (Agustí, 1982; Agustí, 1986; Agustí et al., 1997) but their use is even more restricted geographically.

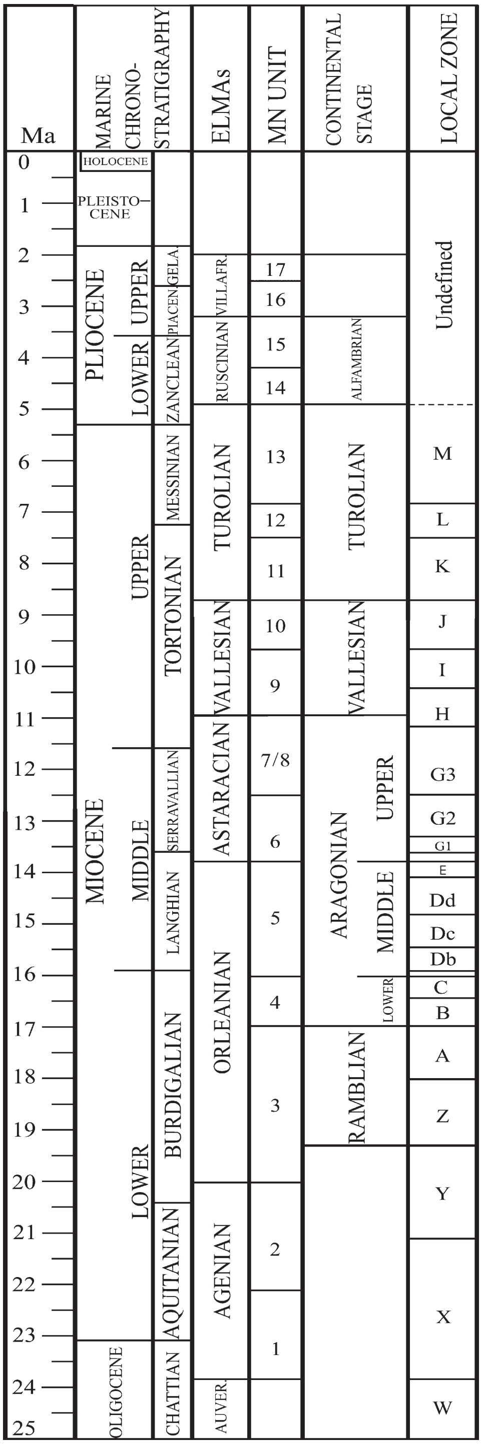

Fig. 1. Chronological scheme of the Neogene of Spain. Data were taken from Daams et al. (1999), Agustí et al. (2001), van Dam et al. (2001), Álvarez Sierra et al. (2003), Gradstein et al. (2004) and this paper. Piacen. = Piacenzian. Gela. = Gelasian. Auver. = Auvernian. Villafr. = Villafranchian. The adjustment between the local zones and the MN units is problematic in the lower part of this scale because Daams et al. (1999) used the works of Krijgsman et al. (1994, 1996), Lévêque (1992), Odin et al. (1997) and their own work for the calibration of MN units whereas we use Agustí et al. (2001) and our own work.

The European Mammal Ages or ELMAS are biochronological units of a higher order and represent the sum of several MN units (Fig. 1). The Agenian is the sum of MN1 and MN2, the Orleanian corresponds to the sum of MN3, MN4 and MN5, and so on. Only the Vallesian and Turolian were formally defined as continental stages following the rules of the ISG1 (Hedberg, 1976) (Marks, 1971a,b; Aguirre et al., 1975a,b). The Alfambrian was proposed as a continental stage by Mein et al. (1989–1990) after studying the outcrops of the Alfambra–Teruel Basin (Teruel, Spain) and covers the Ruscinian ELMA. The rest of the ELMAs lack stratigraphical meaning and are defined by the faunal content of the MN units, so the criticisms of the MN units also apply to the ELMAs (Fahlbusch, 1991).

In parallel to the local zonation, the Dutch–Spanish school defined continental stages following the formalities of the ISG1 (Hedberg, 1976). These continental stages include: (1) the Ramblian defined in the Navarrete del Río area (Teruel, Spain) and originally covering part of the Agenian (Daams et al., 1987; see modifications in Daams et al., 1999) and (2) the Aragonian defined in the Villafeliche area (Zaragoza, Spain) and originally covering the Orleanian and Astaracian (Daams et al., 1977; see modifications in Daams et al., 1999) (See Fig. 1). Similarity of the mammalian faunas at the species level cannot be achieved over broad geographical areas (van Dam et al., 2001) so the value of these stages is recognized for southwestern Europe, but the names Agenian, Orleanian, Astaracian and Ruscinian are maintained for the rest of the European continent (de Bruijn et al., 1992).

The mammalian faunas of Spain are important for the biochronology of the European continent for several reasons. First, five of the 17 MN units have their reference locality in Spain. Second, the Vallesian ELMA, in which the lower boundary is defined by the appearance of the equid *Hipparion*, was defined in Spain. Third, the Iberian Peninsula has been proven to be a highly suitable area for carrying out a quantitative biochronological work due to the completeness of its Neogene mammalian fauna (more than 75% at the specific level, and more than 90% at the generic level, *sensu* Alba et al., 2001). Moreover, the focus on a relative small geographic area (the Spanish Iberian Peninsula has an area of 493,486 km^2) diminishes the constraints that arise from provincialism and diachrony.

1.3. The Hipparion dispersal event

The time of dispersal of the hipparionine horses from North America to the Old World is known as the *Hipparion* datum (Berggren and Van Couvering, 1974). In order to avoid confusion, and due to the fact that the term *datum* is considered to be a biostratigraphic term rather than a biochronologic one (see Walsh, 1998 for a wide explanation), we will refer to *the Hipparion datum* as *the Hipparion dispersal event* throughout the present work. *Hipparion* (*sensu lato*) has been widely used for biochronologic correlation due to its wide geographic distribution, abundance of fossil remains and their ease of identification.

The *Hipparion* dispersal event defines the base of the Vallesian ELMA and the base of unit MN9 for Europe and characterized the Local Zone H in the Iberian Peninsula (but see Álvarez Sierra et al., 2003). An intensive debate about the timing of this dispersal event has arisen from the controversial dates inferred for different fossil localities of Eurasia. Here, we focus on the controversy over the age of this event in the Iberian Peninsula (for reviews of the *Hipparion* dispersal event in Eurasia see Sen, 1990; Steininger et al., 1996; Garcés et al., 1997).

The application of magnetostratigraphy to the Spanish Neogene has led to a debate about the age of the *Hipparion* dispersal event in the Iberian Peninsula. Garcés et al. (1997) summarize the debate; in the literature related to the age of the *Hipparion* dispersal event, two hypotheses are most prevalent: (1) the *Hipparion* dispersal occurred between 10.8 and 10.3 Ma in the lower third of chron C5n and (2) it occurred between 11.5 and 11.0 Ma in chron C5r.

Magnetostratigraphy conducted in the Vallesian type area, that is, the Vallès–Penedès Basin (Basin 1 in Fig. 2) gave a minimum age of 11.1 Ma (chron C5r.1n) for the *Hipparion* dispersal in the Iberian Peninsula (Garcés et al., 1996), supporting the second hypothesis. The fact that pre-*Hipparion* large mammal sites have not been found in the magnetostratigraphic sections of the Vallès–Penedès Basin together to the fact that the first occurrence of *Hipparion* in the Vallès–Penedès was not strictly placed on but laterally traced to the local magnetostratigraphy section, took Garcés et al. (2003) to admit some possible inaccuracy in the location of the datum. In the same work,

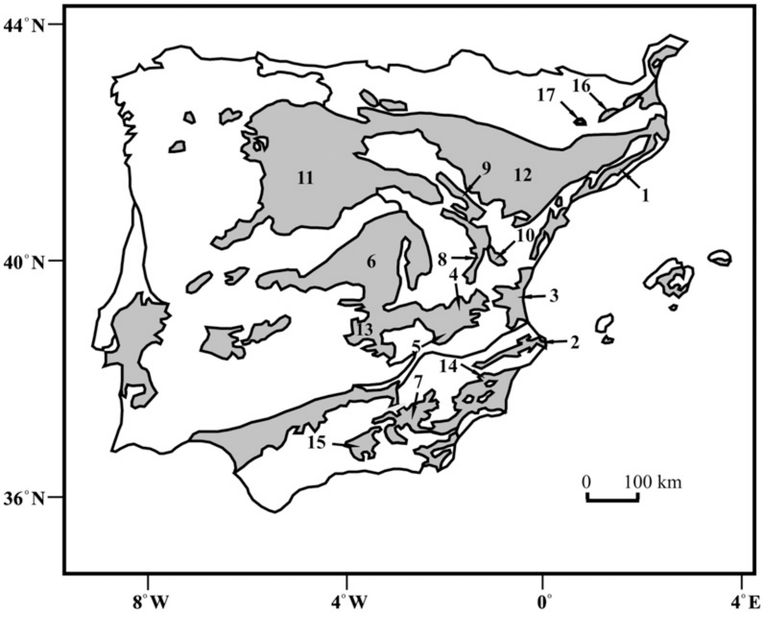

Fig. 2. Cenozoic basins from the Iberian Peninsula. In these 17 Cenozoic basins are concentrated the most important macromammal fossil sites for the time covered in this work. 1. Vallès–Penedès Basin; 2. Alicant North Prebetic Basin; 3. Valencia Basin; 4. Cabriel Basin; 5. Júcar Basin; 6. Tagus Basin; 7. Guadix–Baza Basin; 8. Teruel Basin; 9. Calatayud Basin; 10. Sarrión–Mijares Basins; 11. Duero Basin; 12. Ebro Basin; 13. Calatrava Basin; 14. Fortuna Basin; 15. Granada Basin; 16. Cerdanya Basin; and 17. Seu d'Urgell Basin.

Garcés et al. (2003) documented the magnetostratigraphy of the Nombrevilla section in the Calatayud Basin (Basin 9 in Fig. 2). This section contains one of the best late Aragonian to early Vallesian records of large and small vertebrates in Europe, including important occurrences of *Hipparion*. The First Appearance Datum of *Hipparion* in the Nombrevilla section is correlated to the lower third of chron C5n, resulting in an interpolated age of 10.8–10.7 Ma, supporting the first hypothesis.

One of the aims of this study is to use the results from a quantitative biochronological method to evaluate which of the two hypotheses in the debate concerning the age of the *Hipparion* dispersal event fits better with the ordination of the macromammal fossil sites.

2. Material and methods

2.1. Material

We compiled the faunal lists of 90 macromammalian fossil sites from the Middle Miocene to the end of the Pliocene (MN7/8, Aragonian, ca. 12.5 Ma to MN17, Villafranchian, ca. 2.0 Ma). Under the term "macromammal" we include species in the following orders: Artiodactyla, Perissodactyla, Hyracoidea, Proboscidea, Primates and Carnivora. The micromammals have been excluded because of differences in the sampling methods and the taphonomic biases compared to macromammals (Behrensmeyer and Chapman, 1993; Azanza et al., 2003).

The selection of the time interval covered in the present work is deliberate. The biochronological method used here requires numerical dates from independent sources such as radiometric or paleomagnetic methods. Although the Spanish record has an increasing number of numerical dates for macromammalian fossil sites, especially from paleomagnetism, the bulk of them occur in the middle to upper part of the Neogene. Some works give numerical ages for fossil sites older than MN7/8 (Krijgsman et al., 1996; Daams et al., 1999) but these dates are referred to micromammalian fossil sites. The exceptions to this pattern (Larrasoaña et al., 2006) are too scarce to be included in this analysis. For this study, 13 out of the 90 fossil sites are numerically dated (Table 1). Most of these dates refer to the whole chron to which the fossil site belongs.

The 90 macromammalian fossil sites that constitute the basis for the present work are located in 17 Cenozoic basins of Spain (Fig. 2). Fifteen of the fossil sites are located in stratigraphic sections (Table 2). The faunal lists were updated searching carefully for the most recent works on taxonomy and systematics in order to avoid duplications of taxa due to synonymies. We adopted a conservative attitude toward taxonomy, so that taxa identified as cf., aff. or ? were considered to belong to their nominal species (Alroy, 1994; McKee, 2001; Hernández Fernández et al., 2004). The species is our chosen unit of study as the species gives biochronological resolution bigger than the genus.

In order to prepare the data base for ordination we eliminate those taxa that only appear in one fossil site (singletons) as they do not contribute to the temporal information (Alroy, 1996). To polarize the biochronological sequence of the temporal range studied (MN7/8–

Table 1
Fossil sites numerically dated by magnetostratigraphy

Fossil site	Chron	Age (Ma)			Reference
		Max.	Min.	Mean	
Puebla de Valverde	C2r.1r	2.140	1.950	2.0450	Sinusía et al. (2004)
El Rincón 1	C2An.1n	2.700	2.600	2.6500	Alberdi et al. (1982); Alberdi et al. (1997b)
Villarroya	C2An.1n	3.040	2.581	2.8105	Agustí and Oms (2001) from Pueyo et al. (1996)
Orrios 3	C2Ar	4.180	3.580	3.8800	Opdyke et al. (1997); Oms et al. (1999)
Orrios 1	C3n.1n	4.290	4.180	4.2350	Opdyke et al. (1997); Oms et al. (1999)
Venta del Moro	C3r			5.8000	Opdyke et al. (1990); Opdyke et al. (1997); Garcés et al. (1998)
Librilla	C3An.1n	6.137	5.894	6.0155	Garcés et al. (1998)
Masia del Barbo 2B	C4Ar.1n	9.308	9.230	9.2690	Garcés et al. (1999); van Dam et al. (2001)
Masia del Barbo 2A	C4Ar.2r	9.580	9.308	9.4440	Garcés et al. (1999); van Dam et al. (2001)
Can Llobateres	C4Ar.3r	9.740	9.642	9.6910	Agustí et al. (1996); Agustí et al. (1997)
Nombrevilla 1	C5n.2n	10.800	10.700	10.7500	Garcés et al. (2003)
Nombrevilla 9	C5r.1n	11.099	11.052	11.0755	Garcés et al. (2003)
Nombrevilla 2	C5r.3r	11.935	11.531	11.7330	Garcés et al. (2003)

The age is given in Ma and follows Cande and Kent (1995). Max.: maximum age assigned to each chron. Min.: minimum age assigned to each chron. Mean: mean age of the chron (except for Venta del Moro and El Rincón 1, which are given a more precise age from the works cited).

Table 2
Stratigraphic sections used in this work

Section	Fossil sites	Reference
Orrios	Orrios 3 (MN15) Orrios 1 (MN14)	Opdyke et al. (1997)
Masada del Valle	Masada del Valle 5 (MN12) Masada del Valle 2 (MN12)	van Dam et al. (2001)
Los Orones–Cerro de Castro	Crevillente 15–16 (MN12) Crevillente 2 (MN11)	Montoya (1994)
Masía de la Roma 604	Masía de la Roma 604B (MN10) Masía de la Roma 604A (MN10)	Alcalá et al. (2005)
Masía del Barbo	Masía del Barbo 2B (MN10) Masía del Barbo 2A (MN10)	van Dam et al. (2001)
Nombrevilla	Nombrevilla 1 (MN9) Nombrevilla 9 (MN7/8) Nombrevilla 2 (MN7/8)	Garcés et al. (2003)
Toril	Pedregueras 2A (MN9) Toril 3A(MN7/8)	Álvarez Sierra et al. (2003)

MN17), we added a faunal list of species that reach the Pleistocene in order not to artificially increase the number of last appearances in the MN17 (surviving *taxa sensu* Wing et al., 1995). Some authors (Azanza et al., 1997; Hernández Fernández et al., 2004) have also polarized the lower end of the sequence by using fossil sites which are older than those being analysed. We investigated the inclusion of some MN6 fossil sites for this purpose. However, the lack of absolute ages in MN6 together with the high similarity of the MN6 and MN7/8 faunas in the Spanish record results in a mixture of fossil sites from both MN units which is not effective. Since the ordination method relies on overlapping stratigraphic ranges (conjunctions), we included in the analysis all those lists with at least two taxa (at the species level); in addition, we included fossil sites that have only one species but are located in a stratigraphic section. In summary, our data base consists of 90 faunal lists formed by 216 species. Of these, 82 singleton species were eliminated.

2.2. Methods

In order to analyze the chronological relationships by ordination of Middle to Upper Neogene macromammalian faunas of Spain we applied the appearance event ordination (AEO) method proposed by Alroy (1994) in its more derived form of maximum likelihood appearance event ordination (ML AEO, Alroy, 2000). AEO and ML AEO come from an earlier method, disjunct distribution ordination (DDO, Alroy, 1992), but they allow the incorporation of stratigraphic information. This group of methods is based in a simple observation: when comparing a set of faunal lists, there are taxa whose occurrences overlap (conjunctions) while others do not (disjunctions). Two properties make of this methodology a solid one. The first property is convergence: conjunctional distributions improve as the number of taxonomic lists increases. Any study including enough samples will eventually demonstrate all conjunctions and, therefore, all disjunctions (Alroy, 1992). The second property is the “Rosetta Stone” property: larger lists or “Rosetta Stone” lists contribute disproportionately to conjunction data sets and illuminate the conjunction relationships of rare taxa that usually only appear in these long lists (Alroy, 1992).

AEO analysis is related to correspondence analysis (Hammer and Harper, 2006) but makes use of both faunal association and stratigraphic data instead of raw presence–absence data (as in faunal similarity indices) (Tsubamoto et al., 2004). The AEO method is based on a particular observation: which first appearance events (FAE) predate which last appearance events (LAE), that is, FAE<LAE or the F/L relationship. A conjunction corresponds to two F/L relationships, i.e. if taxa *i* and *j* are conjunct then $FAE_i<LAE_j$ and $FAE_j<LAE_i$. A parsimony criterion is used to obtain an ordination sequence that implies a minimum number of F/L relationships that have not been proven (Alroy, 1992, 1994). F/L relationships can be obtained first, through the analysis of the faunal list; second, using the known stratigraphical relationships among faunal lists; and third, by means of the algorithm called *square graph* (Alroy, 1996). This algorithm makes up for the effect of apparent disjunction among taxa that having overlapping ranges fail to appear in the same basin. The result is an appearance event sequence numbered from oldest to youngest, from which is derived the event position of each faunal list. The chronologic position of

Table 3
Results of the biochronological analysis of the Spanish Neogene macromammalian faunas

	Conjunctions	F/L relationships
Faunal lists	2221	4442
Stratigraphical relationships		40
Events sequence	2729	11640
CI=Conjunction Index	0.814	

Conjunction index: known conjunctions/implied conjunctions.

each list is defined by an assemblage of taxa (or concurrent range zone following Alroy, 1994), which is the interval between the youngest FAE and oldest LAE of any species within these lists (Alroy, 1994). We used the midpoint of this concurrent range zone [(youngest FAE + oldest LAE) / 2] to assign a numerical age to each faunal list.

The ML AEO method involves generating a maximally likely hypothesis of the relative order of first and last appearances. This method takes into account faunal occurrences, stratigraphic relationships, and the sampling probability of individual species (Alroy, 2000). We used this method since it has been demonstrated to act better than the earlier DDO and AEO (see Alroy, 2000).

The ML AEO method was performed using the program CONJUNCT (Version 3.1.0.) developed by John Alroy and obtained from www.nceas.ucsb.edu/~alroy/. Recently, the ML AEO analysis has been incorporated to the PAST package (Hammer et al., 2001).

3. Results

Of the 90 faunal lists initially included in the analysis, 30 were eliminated because they were subsets of longer lists and provided no information about conjunctions or F/L relationships (Wing et al., 1995), or because they had fewer than two taxa identified at the species level. For the latter reason, two fossil sites that are part of stratigraphical sections, Masía de la Roma 604B and Masada del Valle 5, disappear from the analysis. Consequently, the sections of Masia de la Roma 604 and Masada del Valle (Table 2), each constituted by two fossil sites, lose their stratigraphical value.

Table 3 shows the numerical results of the ML AEO analysis. We highlight the fact that in our analysis, the greater proportion of the F/L relationships [4442 / (4442 + 40) = 99.1%] comes from the conjunctions.

The ordination of the 60 fossil sites maintained in our analysis is shown in Table 4. In order to assign a numerical age to each of our localities, we used the 13 fossil sites previously dated by paleomagnetism (Table 1) as the basis for a regression analysis of age on ordination position. We explored several regression models to determine which model provided low standard errors on the age estimates and met the characteristics of a sound regression model (see Appendix A). We first fit a linear regression to our data and then added a quadratic term to the regression equation to determine whether significantly more variance was explained in the dependent variable (Sokal and Rohlf, 1981). Based on this approach, our best fit model is a quadratic regression with two outliers omitted (model (c) in Appendix A and Fig. 3). These two outliers are Librilla and El Rincón 1. In the discussion, we explain the discrepancies in the ages assigned to these localities. In this regression, the independent variable is the mean age of the chron in which the localities are recorded and the dependent variable is the midpoint of the concurrent range zone of each faunal list. The regression model is highly significant, with regression coefficients significant at $p = 0.05$, $R^2 = 0.995$ and SE for the estimate = 0.276 Ma.

4. Discussion

The ordination and estimation of numerical ages are given in Table 4 and Fig. 4. For each fossil site, we also indicate the MN to which it has traditionally been assigned. The ordination provides a sequence that is quite consistent with the MN scale except for the part corresponding to the Pliocene.

4.1. Miocene

For the Miocene, we find the ordination of the MN7/8 sites in the lowest part of the sequence as expected. The age estimated for Toril 3A is younger than the 12.5 Ma proposed in other works (Daams et al., 1999; Garcés et al., 2003). In these works, Toril 3A is correlated to the numerically dated micromammalian fossil site of Las Planas 5H. We did not utilize this date, as it is not a direct one but a correlation with another locality.

Nombrevilla 9 is given the same age as Nombrevilla 1 even though Nombrevilla 9 occurs lower in the stratigraphic section of Nombrevilla. Recently, Álvarez Sierra et al. (2003) assigned Nombrevilla 9 to the Aragonian due to the absence of the equid *Hipparion*. This assignment implies that the first appearances of *Hipparion* and of the giraffid *Decennatherium* (included in the faunal list of Nombrevilla 9), which defined the beginning of the Vallesian, are not simultaneous but, in fact, staggered in time, with *Decennatherium* appearing first in the upper part of the Aragonian and *Hipparion* later at the beginning of the Vallesian. In our ordination, *Decennatherium pachecoi* and *Hipparion primigenium* receive the same inferior score (first appearance score = 50, which corresponds to an age of 10.887 Ma); as a result, Nombrevilla 9 and Nombrevilla 1 receive the same age. As Nombrevilla 9 lies below Nombrevilla 1 in a stratigraphic section, we would expect *Decennatherium* to receive a lower inferior score than that of *Hipparion*. The discrepancy can be understood from the fact that the faunal list of Nombrevilla 9 is a subset

Table 4
Ordination of the 60 fossil sites maintained in the analysis

Youngest FAE	Oldest LAE	Mean	Time (Ma)	±(Ma)	Number of taxa	Fossil sites	MN unit	Basin
250	251	250.5	2.127	0.030	18	Puebla de Valverde	MN17	10
240	241	240.5	2.720	0.029	20	Villarroya	MN16	12
230	231	230.5	3.297	0.028	10	Huélago	MN16	7
230	231	230.5	3.297	0.028	6	El Rincón 1	MN16	5
219	220	219.5	3.912	0.028	7	Layna	MN15	6
214	220	217	4.049	0.163	1	Orrios 3	MN15	8
214	215	214.5	4.186	0.027	4	Orrios 1	MN14	8
214	215	214.5	4.186	0.027	7	La Calera	MN14	8
214	215	214.5	4.186	0.027	5	La Gloria 4	MN14	8
208	209	208.5	4.508	0.027	4	Pozo de Piedrabuena	MN16	13
204	205	204.5	4.720	0.026	3	Alcalá del Júcar	MN15	5
202	203	202.5	4.825	0.026	3	Alcoy Mina	MN14	2
194	195	194.5	5.238	0.025	4	Librilla	MN13	14
185	186	185.5	5.689	0.025	10	Venta del Moro	MN13	4
185	186	185.5	5.689	0.025	8	Milagros	MN13	8
185	186	185.5	5.689	0.025	4	Arenas del Rey	MN13	15
185	186	185.5	5.689	0.025	3	Tariego de Cerrato	MN13	11
177	178	177.5	6.080	0.024	18	Las Casiones	MN13	8
172	173	172.5	6.319	0.024	16	El Arquillo 1	MN13	8
157	158	157.5	7.011	0.022	24	Cerro de la Garita	MN12	8
157	158	157.5	7.011	0.022	18	Los Mansuetos	MN12	8
157	158	157.5	7.011	0.022	7	Concud Barranco	MN12	8
157	158	157.5	7.011	0.022	6	Valdecebro 5	MN12	8
146	158	152	7.255	0.261	6	Crevillente 15–16	MN12	2
146	158	152	7.255	0.261	3	Masada del Valle 2	MN12	8
148	149	148.5	7.408	0.022	6	Aljezar B	MN12	8
146	147	146.5	7.494	0.022	10	Ademuz	MN12	8
138	139	138.5	7.834	0.021	12	Puente Minero	MN11	8
136	137	136.5	7.917	0.021	12	Piera	MN11	1
114	158	136	7.938	0.870	3	La Cantera	MN10	8
133	134	133.5	8.040	0.020	5	Vivero de Pinos	MN11	8
130	131	130.5	8.163	0.020	14	Crevillente 2	MN11	2
121	122	121.5	8.520	0.019	19	Terrassa	MN10	1
117	118	117.5	8.675	0.019	2	Masía de la Roma 604A	MN10	8
114	115	114.5	8.789	0.019	7	Masía del Barbo 2B	MN10	8
114	115	114.5	8.789	0.019	6	La Roma 2	MN10	8
109	110	109.5	8.976	0.018	10	Batallones 1	MN10	6
109	110	109.5	8.976	0.018	7	Sant Miguel de Taudell	MN10	1
103	104	103.5	9.195	0.018	16	Viladecavalls	MN10	1
93	94	93.5	9.547	0.017	20	Los Valles de Fuentidueña	MN9	11
54	115	84.5	9.850	0.927	2	Masía del Barbo 2A	MN10	8
80	81	80.5	9.980	0.016	35	Can Llobateres	MN9	1
80	81	80.5	9.980	0.016	14	Santiga	MN9	1
80	81	80.5	9.980	0.016	2	Pedregueras 2A	MN9	9
69	70	69.5	10.325	0.015	9	El Firal	MN9	17
64	65	64.5	10.475	0.015	18	Hostalets de Pierola Superior	MN9	1
64	65	64.5	10.475	0.015	9	Ballestar	MN9	17
60	61	60.5	10.592	0.014	26	Can Ponsic	MN9	1
54	55	54.5	10.763	0.014	8	Polinya	MN9	1
54	55	54.5	10.763	0.014	6	Estavar	MN9	16
50	51	50.5	10.873	0.014	8	Nombrevilla 1	MN9	9
50	51	50.5	10.873	0.014	4	Nombrevilla 9	MN7/8	9
45	46	45.5	11.008	0.013	20	Castell de Barbera	MN7/8	1
45	46	45.5	11.008	0.013	14	Sant Quirze	MN7/8	1
37	38	37.5	11.215	0.013	23	Host. de Pierola Inferior–Can Mata	MN7/8	1
37	38	37.5	11.215	0.013	4	Montejo de la Vega	MN7/8	11
21	22	21.5	11.597	0.011	8	Nombrevilla 2	MN7/8	9
15	16	15.5	11.729	0.011	10	Toril 3A	MN7/8	9
15	16	15.5	11.729	0.011	6	Escobosa	MN7/8	11
5	6	5.5	11.937	0.010	5	La Ciesma	MN7/8	12

Each list is defined by the mean between its oldest LAE and its youngest FAE but the deviation (±Ma) of this mean age is also provided. Basin numbers as in Fig. 2.

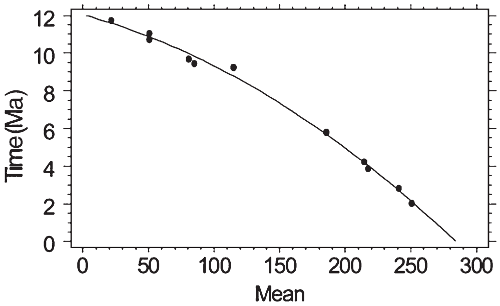

Fig. 3. Polynomial regression of 11 numerically dated localities against their respective mean values (two ouliers omitted). The mean value is the midpoint of the concurrent range zone of each list, i.e., (youngest FAE+oldest LAE)/2.

of the faunal lists of Terrassa and Los Valles de Fuentidueña. We eliminated all the faunal lists that were subset of longer ones except for those that were part of a stratigraphical section in an attempt to include as much information as possible. Consequently, Nombrevilla 9 has been considered as an incomplete list and the ordination assigned the same score to *Hipparion* and *Decennatherium* since they appear together in the supposed complete lists. We conclude that the age assigned here to Nombrevilla 9 is not the proper one.

Some fossil sites, such as Masía de la Roma 2A or La Cantera, have poorly located scores because: (1) they have a very small number of taxa, and (2) these taxa have long temporal ranges so that their biochronological signal does not provide high temporal resolution.

Some known temporal relationships are reflected in the ordination results. Examples include the position of Toril 3A as older than the fossil sites of the Nombrevilla section (Garcés et al., 2003) and the position of Viladecavalls as older than Terrassa (Agustí et al., 1997).

The Upper Miocene fossil site of Librilla was omitted from the regression analysis as an outlier, since its inclusion decreased the quality of the fit (Appendix A). Although omitted from the regression, Librilla is still given an age in our analysis (Table 4). This locality appears above Venta del Moro, even though numerical ages for both sites indicate that Venta del Moro is younger than Librilla (Table 1). The anomalous position of Librilla in this analysis results from the presence of the bovid *Parabos cordieri*. Gromolard and Guerin (1980) and Alberdi et al. (1981b) indicate that this species is typically found in the Ruscinian. In fact, this species appears in the Ruscinian locality of Alcalá del Júcar and in other Ruscinian fossil sites outside of Spain, such as Montpellier (France). In any case, the *Parabos* material from Librilla is rare and needs a further revision (J. Morales, pers. comm.).

For the Miocene sites, we can check how the ML AEO, by means of the *square graph* algorithm, is able to compensate for the effects of faunal provincialism. A typical example of paleobiogeographic separation within Spain is observed between the faunas of the Vallés–Penedés Basin (Basin 1 of Fig. 2) and the interior basins during the Late Aragonian and Vallesian (Alberdi et al., 1981a; Morales et al., 1999). The small mammal faunas follow the same paleobiogeographic pattern (Agustí, 1978, 1981; Sesé, 1988). In faunal-similarity analysis (Morales et al., 1999), the fossil sites of the Vallés–Penedés tend to be grouped together, whether they are MN7/8, MN9 or MN10, rather than with other localities of the same age, due to the peculiarities of the faunas (for example, Castell de Barbera, Can Ponsic, Can Llobateres, Viladecavalls and Terrassa, are clustered together). Typical components of the Vallés–Penedés faunas are primates, tapirs, ursids and suids, which indicate more humid conditions in this basin compared to the interior basins for the same period of time. Our ordination groups localities from Vallés–Penedés by their age and not by the faunal resemblance among them (Fig. 2 and Table 4).

4.2. Pliocene

The ordination of the Pliocene localities shows a less coherent pattern. This may be due to the poorer knowledge of these faunas in Spain compared to the Miocene ones (Torres and Mazo, 1991; Azanza et al., 2003). For example, only one MN15 fossil site has more than three taxa (Layna). Of the four MN17 localities initially included in the analysis (Casablanca 1, Fuentesnuevas 1, Valdeganga II and Puebla de Valverde) only Puebla de Valverde is maintained in the ordination as the rest of them are subsets of longer lists so that they do not contribute to the analysis.

The age of the Alcoy Mina locality has been discussed previously. In a recent work, the age considered most suitable for this locality is Early Ruscinian (=MN14) (Montoya et al., 2006). Our results are in agreement with these authors; the age estimate here is 4.825 Ma (Table 4), i.e., Early Ruscinian, since the boundary between the Turolian and Ruscinian is considered to be 4.9 Ma (Opdyke et al., 1997) or even older than 4.9 Ma (Agustí et al., 2001).

Alcalá del Júcar, a fossil site that has been traditionally located in the MN15, appears in the ordination among MN14 localities. Its fauna consists of *Anancus arvernensis*, *Stephanorhinus miguelcrusafonti* and *Parabos*

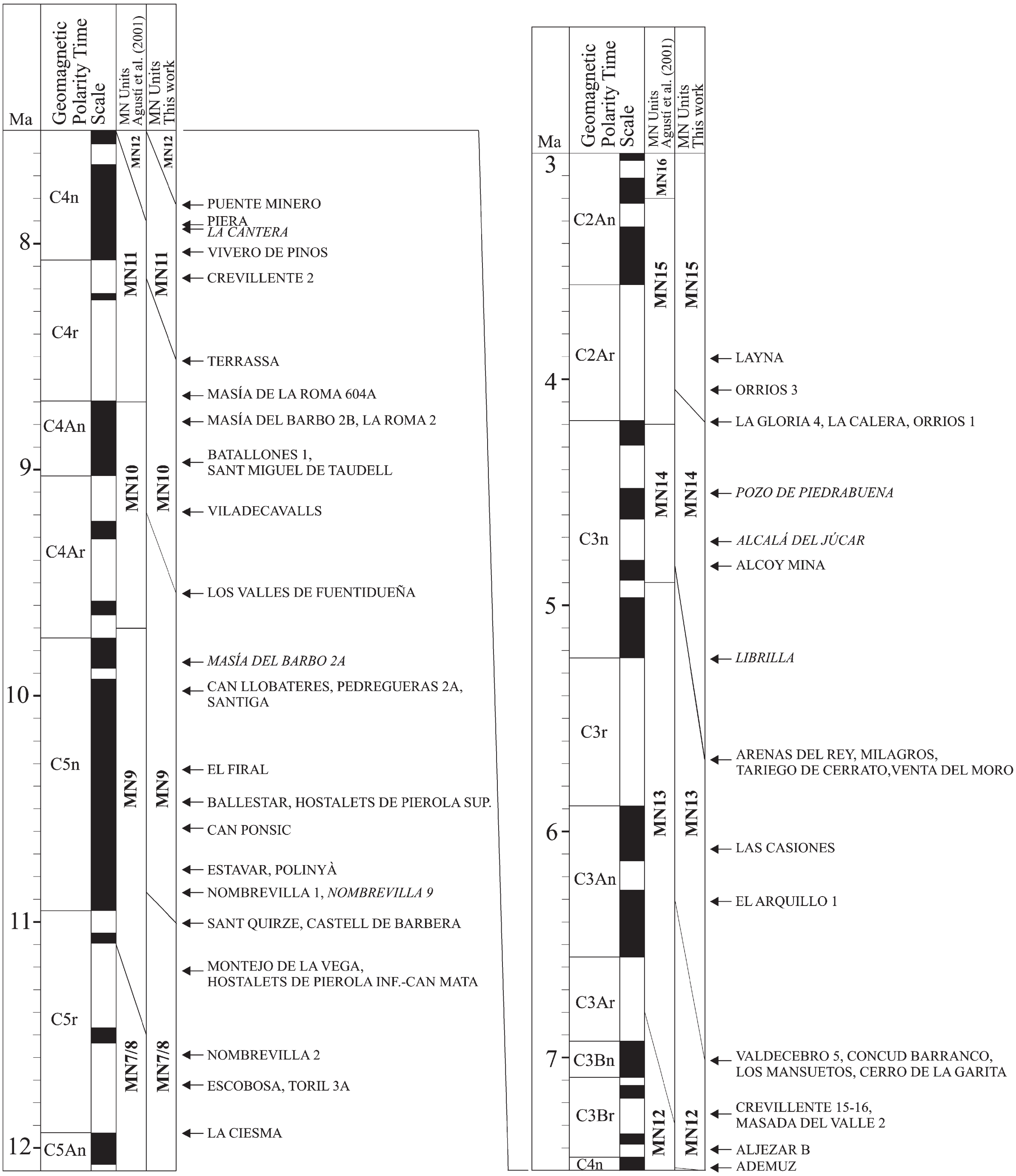

Fig. 4. Summary diagram showing the ordination of the fossil sites and the MN boundaries obtained in the present work as well as their comparison with the MN boundaries established by Agustí et al. (2001). The boundaries between MN15–MN16 and MN16–MN17 cannot be determined in this work (see text) so they are not given here. Fossil sites in italics show some discrepancies in their ordination (see text). Geomagnetic Polarity Time Scale following Cande and Kent (1995).

cordieri (this is the complete faunal lists; it has not got other taxa identified at higher level than the species level; Mazo, 1999). The proboscidean *A. arvernensis* is found in Spain from the Turolian until the Lower Villafranchian so it is not a good biochronological indicator. The rhinoceros *S. miguelcrusafonti* appears in the Iberian

Peninsula over the entire Ruscinian (MN14+MN15; Cerdeño, 1992). As for *P. cordieri*, Gromolard and Guerin (1980) pointed out that this taxon is typically Early Ruscinian (=MN14). Taking into account all of the evidence we can conclude that the assignment of Alcalá del Júcar to the MN14 is perfectly reasonable from the viewpoint of its macromammalian fauna.

The MN16 fossil site of Pozo de Piedrabuena contains *Caracal* cf. *issiodorensis*, *Stephanorhinus* cf. *etruscus*, *Sus arvernensis* and *Protoryx* sp. nov. 2. In Table 4, this locality is situated with MN14 fossil sites. In this case, this ordination cannot be correct since *Stephanorhinus etruscus* is a Villafranchian species (Cerdeño, 1992). The fact that the other three taxa also appear in older fossil sites results in the placement of Pozo de Piedrabuena among them. Torres and Mazo (1991) also found it difficult to assign an age to this locality. They admitted that *S. etruscus* indicates a Villafranchian age, whereas the Hippotraginae *Protoryx* suggests a Ruscinian one. This incongruence was attributed to the poor record of macromammals in the Late Ruscinian and Lower Villafranchian and the difficulty to assess the biochronological significance of some taxa (Torres and Mazo, 1991). Consequently, they assigned this locality to the Ruscinian/Villafranchian transition (MN15/MN16), which still does not justify our ordination of Pozo de Piedrabuena.

The paleomagnetic age of El Rincón 1 was removed from our statistical analysis since it acted as an outlier. Even after removing it, we find some incongruity in the age assigned to it. The numerical ages of Huélago and El Rincón 1 are overestimated in our results and Villarroya lies above them (Table 4) when, in fact, it is an older locality (Table 1 indicates a numerical age of 2.81 Ma for Villarroya compared to 2.65 Ma for El Rincón 1). Two reasons seem to explain this discrepancy. First, a large number of taxa from Villarroya appear also in MN17, especially carnivoran taxa. *Vulpes alopecoides*, *Ursus etruscus*, *Chasmaporthetes lunensis*, *Pliocrocuta perrieri*, *Caracal issiodorensis*, *Acinonyx pardinensis*, *Viretailurus schaubi*, *Homotherium latidens* and *Megantereon cultridens* appear both in the MN16 fossil site of Villarroya and in the MN17 fossil site of Puebla de Valverde. Second, the inclusion of the list of species surviving until the Pleistocene exerts an influence on this ordination. Villarroya possesses six taxa reaching the Pleistocene, while Huélago and El Rincón 1 each have two of them. These anomalous ordination results agree with the biochronological estimates of other works (Alberdi et al., 1997a; Azanza et al., 2003) and also with the magnetostratigraphic datation proposed by Pueyo et al. (1996). However, the ordination of Villarroya as a younger locality than El Rincón 1 and Huélago can be ruled out in the light of two facts: (1) the Villarroya magnetostratigraphic datation of Pueyo et al. (1996) is not consistent with the magnetostratigraphic data available for El Rincón 1 (Alberdi et al., 1997b) and Puebla de Valverde (Sinusía et al., 2004), thus an alternative datation of Villarroya was adopted (Table 1; Agustí and Oms, 2001), showing that Villarroya is older than El Rincón 1, and (2) the Elephant–*Equus* event (Lindsay et al., 1980; Azzaroli, 1995), i.e., the entrance of *Mammuthus* and *Equus* (that brings with it the disappearance of *Hipparion*) in Eurasia, which is an important dispersal event, occurs between Villarroya and El Rincón 1/Huélago. The fauna of Villarroya testifies to the presence of *Hipparion* (*Hipparion rocinantis*), while *Mammuthus* appears in Huélago and *Equus,* occurs both in Huélago and El Rincón 1.

4.3. MN boundaries

Taking all these results into account, we estimated the age boundaries between the MN units in light of our ordination to see how they compare to those of Agustí et al. (2001) (Table 5 and Fig. 4). The comprehensive work of Agustí et al. (2001) consists of a synopsis and revision of the MN boundaries for the Neogene of Western Europe by using magnetostratigraphy. We estimate here the boundaries of MN7/8–MN9, MN9–MN10, MN11–MN12, MN13–MN14 and MN14–MN15 by means of those fossil sites that are in the uppermost part of a given MN unit and the lowermost part of the next MN unit (Fig. 4). We prefer to give the MN boundaries as intervals rather than as a specific age (the mean age of the interval) to be more consistent with the reality. The discovery of more fossil localities will lead us ultimately to a more accurate dating of these boundaries. As the boundaries between MN15–MN16 and MN16–MN17 depend on the ordination of El Rincón 1, Huélago and Villarroya and, as explained earlier, there are some discrepancies

Table 5
MN boundaries inferred in the present work and comparison with the boundaries of Agustí et al. (2001)

MN unit	This work	Agustí et al. (2001)
MN14–MN15	4.186–4.049	4.2
MN13–MN14	5.689–4.825	>4.9
MN12–MN13	7.011–6.319	6.8 (7.3 Max.)
MN11–MN12	7.834–7.494	7.5–7.9
MN10–MN11	8.520–8.163	8.7
MN9–MN10	9.547–9.195	9.7
MN7/8–MN9	11.008–10.873	11.1 (11.5 Max.)

in their calibration, we omitted them from Table 5 and Fig. 4. In general, the boundaries established in our work are younger than those given by Agustí et al. (2001). This is due to the differences in the nature of the data and the analytical approaches followed in each work. The use of fossil sites from larger areas than those used by Agustí et al. (2001), the data base consisting in macromammalian taxa and a quantitative biochronological approach were the basis of our work. It is notable that the MN13–MN14 boundary remains quite broad. The explanation is that we do not include the fossil site of Librilla for the establishment of this boundary but instead the transition between Tariego de Cerrato/Arenas del Rey/Milagros/Venta del Moro (5.689 Ma)–Alcoy Mina (4.825 Ma).

4.4. The timing of the Hipparion dispersal event

Taking into account Tables 4 and 5, we can extract our conclusions about the age of the *Hipparion* dispersal event. In spite of having a specific age for the FAE of *Hipparion* (=10.887 Ma), we prefer to take this datation cautiously because it seems feasible the discovery of new *Hipparion* remains in the section of Nombrevilla below the fossil site of Nombrevilla 1. In consequence, the age of the *Hipparion* dispersal event is situated between 11.008–10.873 Ma (coincident with the MN7/8–MN9 boundary), that is, our ages extend from the upper part of chron C5r to the lower third of chron C5n. Thus, our data do not support clearly either of the two hypotheses explained earlier but lead to an intermediate result. Sant Quirze and Castell de Barbera are the youngest pre-*Hipparion* localities in our ordination and Nombrevilla 1 is the oldest locality with *Hipparion* in this work (see above for an explanation on the Nombrevilla 9 controversy).

The most recent assessment of the Spanish *Hipparion* dispersal event favours the younger age. The MN7–8/MN9 boundary given by Agustí et al. (2001) is based on a previous study of paleomagnetic dating in the Vallès–Penedès Basin (Garcés et al., 1996). However, recently, Garcés et al. (2003; p. 177) admitted that the section studied in the Vallès–Penedès area lacks pre-*Hipparion* fossil sites and that a section covering the Aragonian–Vallesian transition would be necessary. This coverage occurs in the Calatayud Basin, so that, after carrying out magnetostratigraphy studies in this area, an age of 10.8–10.7 Ma is the preferred one.

After evaluating the data more thoroughly, our datation of the younger pre-*Hipparion* fossil sites, that is 11.008 Ma for Sant Quirze and Castell de Barbera, lead us to positively think that the age of 11.1 Ma proposed by Agustí et al. (2001) as the minimum age for the dispersal of *Hipparion* in the Iberian Peninsula is a too old one. We agree with Garcés et al. (2003) that further research in the Vallès–Penedès basin is necessary to confirm such an old age. Besides this, we can exclude the age of 11.008 Ma for the first appearance of *Hipparion* in Spain since, as explained before, Sant Quirze and Castell de Barbera are still pre-*Hipparion* localities. This fact brings us nearer the base of chron C5n as being the time when *Hipparion* arrived in the Iberian Peninsula. Moreover, if we strictly follow the premise that the lower boundary of the Vallesian stage is defined by the oldest record of *Hipparion*, then we could accept that the entrance of *Hipparion* occurred close the age of Nombrevilla 1 (10.873 Ma±0.014; 10.887 Ma for the FAE of *Hipparion* according to our results), and the first hypothesis would be supported. The first *Hipparion*-producing locality in a sedimentary sequence or in a sequence of localities has been traditionally used to infer the appearance of this equid but as Pilbeam et al. (1996) state, this is an estimate for the age of the oldest record of hipparionines not necessarily the age of their first appearance. So in the light of our analysis and as for the hipparionine horses in Spain we can state: 1) the first *Hipparion*-producing locality (oldest record) is Nombrevilla 1 with an age of 10.873 Ma; 2) the arrival of *Hipparion* to the Iberian Peninsula happened in some moment between 11.008 and 10.873 Ma; 3) the age of 11.1 Ma proposed by Agustí et al. (2001) for the entrance of *Hipparion* in the Iberian Peninsula is a too old one.

5. Conclusions

The present work assigns for the first time numerical age estimates to a number of macromammalian faunas from Spain and compares them with the most widely used biochronological scale of Europe, the MN scale. The rich Neogene faunas of the Iberian Peninsula make it worthwhile to carry out this kind of analysis. The ML AEO method (Alroy, 2000) in combination with a regression model uses only some numerically dated localities to calibrate the ordination of fossil localities and estimate an age for each of them. This method, in its earlier versions, DDO and AEO, has been used for the Spanish record of both macromammals (Azanza et al., 1997) and micromammals (Hernández Fernández et al., 2004) but the present analysis encompasses a broader time span.

We conclude that our ordination results compare quite well to the MN unit traditionally assigned to these fossil localities, at least for the Miocene. The sequence for the Pliocene localities is less coherent because the faunas have fewer species of biochronological significance. When comparing the age boundaries of the MN units for the Neogene of Western Europe given by us with those established by Agustí et al. (2001), we note the ages estimated here are younger, due to the differences in the approaches. In our ordination, the first *Hipparion*-bearing locality is Nombrevilla 1 (10.873 Ma) but this equid arrived in the Iberian Peninsula in some moment between 11.008 and 10.873 Ma.

The importance of carrying out a quantitative biochronological analysis lies not only in the results presented here but also in the fact that it is a necessary prerequisite to further paleobiological analyses. The ordering of the appearance events of taxa of the Spanish Neogene macromammalian faunas provides the basis for analyses of turnover rates, paleobiogeography or community paleoecology. These analyses will be of great interest since the Iberian Peninsula acted as a *cul de sac* where the dispersal events happening in Eurasia ended.

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Appendix A

Regression models explored in the present work. The best fit was elected by taking into account the standard error of the estimate, the significance of the coefficients and a high coefficient of determination. (c) is the model used here.

(a) Linear regression; $n=13$

Regression model
Time (Ma) = 13.1592 − 0.0422074 * Mean + error

Regression diagnostics
$R^2=0.9764$
Standard Error for the estimation = 0.571519
F-ratio = 454.52 (*P*-value = 0.0000)

Appendix A (*continued*)

Independent variable	Coefficient	Standard Error of coefficient	*P*-value
Mean	0.0422074	0.00197976	0.0000

(b) Quadratic regression; $n=13$ (1 coefficient non-significant at $P=0.05$)

Regression model
Time (Ma) = 11.8307 − 0.0138077 * Mean − 0.000101474 * Mean^2 + error

Regression diagnostics
$R^2=0.9898$
Standard error for the estimation = 0.394422
F-ratio = 483.71 (*P*-value = 0.0000)

Independent variable	Coefficient	Standard Error of coefficient	*P*-value
Mean	−0.01381	0.00797	0.1137
Mean^2	−0.00010	0.00003	0.0047

(c) Quadratic regression; $n=11$ (two outliers omitted) (all coefficients significant at $P=0.05$)

Regression model
Time (Ma) = 12.0438 − 0.0190319 * Mean − 0.0000820657 * Mean^2 + error

Regression diagnostics
$R^2=0.9953$
Standard Error for the estimation = 0.276489
F-ratio = 853.42 (*P*-value = 0.0000)

Independent variable	Coefficient	Standard Error of coefficient	*P*-value
Mean	−0.01903	0.00583	0.0115
Mean^2	−0.00008	0.00002	0.0039

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